

A geostatistical approach for describing spatial pattern in stream networks

Lisa M Ganio¹, Christian E Torgersen², and Robert E Gresswell³

The shape and configuration of branched networks influence ecological patterns and processes. Recent investigations of network influences in riverine ecology stress the need to quantify spatial structure not only in a two-dimensional plane, but also in networks. An initial step in understanding data from stream networks is discerning non-random patterns along the network. On the other hand, data collected in the network may be spatially autocorrelated and thus not suitable for traditional statistical analyses. Here we provide a method that uses commercially available software to construct an empirical variogram to describe spatial pattern in the relative abundance of coastal cutthroat trout in headwater stream networks. We describe the mathematical and practical considerations involved in calculating a variogram using a non-Euclidean distance metric to incorporate the network pathway structure in the analysis of spatial variability, and use a non-parametric technique to ascertain if the pattern in the empirical variogram is non-random.

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Branched networks form pathways that interconnect organisms and their habitats; for example, the movement of organisms may be restricted to corridors of suitable habitat (Rosenberg *et al.* 1997). Physiographic features such as mountain ranges, ridge tops, water bodies, and climate patterns create spatial barriers that restrict migration and dispersal (Figure 1). Similarly, species interactions, such as competition, predation, and disease, can limit the direction and distance over which individuals or resources may relocate. The branched structure of streams is perhaps the most visible example of a network on the landscape (Figure 2). However, beyond a casual acceptance that physical and biological systems are often organized in branched networks, the influence of network structure on ecological processes is not well understood, and there are few studies of spatial structure that explic-

itly consider the branching patterns of the network.

In ecological studies of streams, where the drainage network is immediately apparent, studies can be conducted at a scale that effectively reduces the network to an unbranched linear system. In this case, conceptual models are based on a linear, as opposed to a network, perspective (Fisher 1997). The lack of information on relationships between network structure and ecological patterns in streams indicates that a more spatially explicit examination of stream networks is needed (Power and Dietrich 2002; Benda *et al.* 2004). In the analysis of networks, the objective is to quantify connectivity and identify the mechanisms through which network structure influences the physical and ecological processes within the network system.

In three-dimensional space, streams have width, depth, and length. However, for the purpose of network analysis, a stream may be thought of as a series of line segments joined together at nodes to form a branched network that eventually ends in a single outlet (Haggett and Chorley 1969). Nodes occur where attributes of the system change (eg channel morphology and tributary junctions). The configuration of the connections in the network, but not the shape or orientation of the branches, is called the network topology (Figure 3). For example, the network commonly depicted in studies of food webs is a mesh topology, whereas hydrologic drainage patterns typically have branched (rivers) or star (lakes and estuaries) topologies.

Network configuration can influence physical and ecological processes in networks. Connectivity among sites in a branched network differs from connectivity over a plane or in an unbranched linear system. Fagan (2002) used mathematical modeling to show that population persistence and the effects of fragmentation events dif-

In a nutshell:

- Branched networks are ubiquitous in aquatic and terrestrial environments, and their role in physical and ecological processes is an expanding field of research in ecology
- Commercially available software for quantifying pattern in auto-correlated data from networks is lacking, making it difficult for ecologists to explore data collected along stream networks
- We provide an overview of statistical considerations and a way to adapt a standard geostatistical tool, the empirical variogram, to describe spatial pattern in stream networks

¹Department of Forest Science, 321 Richardson Hall, Oregon State University, Corvallis, OR 97331 (lisa.ganio@oregonstate.edu); ²US Geological Survey, Forest and Rangeland and Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97331; ³US Geological Survey, Northern Rocky Mountain Science Center, 229 AJM Johnson Hall, Bozeman, MT 59717-3492.

ferred between a branched network and a linear system. Downstream flow in a stream network has also been reported to provide a means for plant communities to compensate for local extinction processes (Honnay *et al.* 2001). Benda *et al.* (2004) proposed the Network Dynamics Hypothesis that relates geomorphic heterogeneity in streams to network structure and disturbance regimes. Because thermal and productivity regimes are discontinuous at tributary junctions, these points can influence the distribution of aquatic organisms. For example, the abundance and composition of macroinvertebrate species that are commonly associated with sediment size were found to change at tributary junctions (Rice *et al.* 2001).

Response values collected from contiguous channel units throughout a stream network may not meet the assumptions of traditional statistical methods. When values are related by virtue of nearness in space they are likely to be spatially correlated; thus, the statistical assumption of independence is violated, and standard analysis procedures are inappropriate (Carroll and Pearson 1998). In contrast, spatial statistical methods incorporate the distance between data points into the analysis to account for correlation among nearby values (spatial autocorrelation), increase precision, and correct for bias (Cressie 1993).

Concepts of distance and connectedness in a stream network are more complicated than in planar space. Distances between points along a network may not be adequately represented by the shortest, “as the crow flies” distance, because of limitations to movement imposed by the network structure (Fagan 2002; Figure 4). Alternative measures of distance may be necessary, depending on the nature and ecological setting of the questions posed (Wenbug and Bentzen 2001). However, new measures must conform to specific mathematical criteria. The distance through water between sampling stations has been used in estuaries to predict patterns of water quality (Little *et al.* 1997; Rathbun 1998), and a distance measure based on stream order has been used for temperature data (Gardner *et al.* 2003). For some response values, such as water chemistry, the direction of stream flow may provide a basis for distance measures. Other types of models for connectivity based on stream flow are also being investigated (J Ver Hoef pers comm), and further research is needed. For the purposes of this paper, we define network distance as the shortest distance along the stream channel between nodes.

A spatial statistic, the empirical variogram, is used to graphically describe spatial relatedness in a set of data collected over a surface (Matheron 1963). Here, we demonstrate how empirical variograms can be used as an exploratory tool to detect spatial dependence in a network and to characterize different patterns of spatial variability in



Courtesy of the US Forest Service

Figure 1. The complex topography of the Oregon Coast Range mountains restricts the movement and dispersal of aquatic and terrestrial organisms to corridors and network pathways.

relative fish abundance in a headwater stream network. The objective of this paper is to make the analysis of spatial networks more accessible to ecologists by: (1) explaining the statistical model that is used to estimate empirical variograms in a stream network; (2) describing the integration



Courtesy of NASA

Figure 2. Dendritic drainage pattern in the Republic of South Yemen.

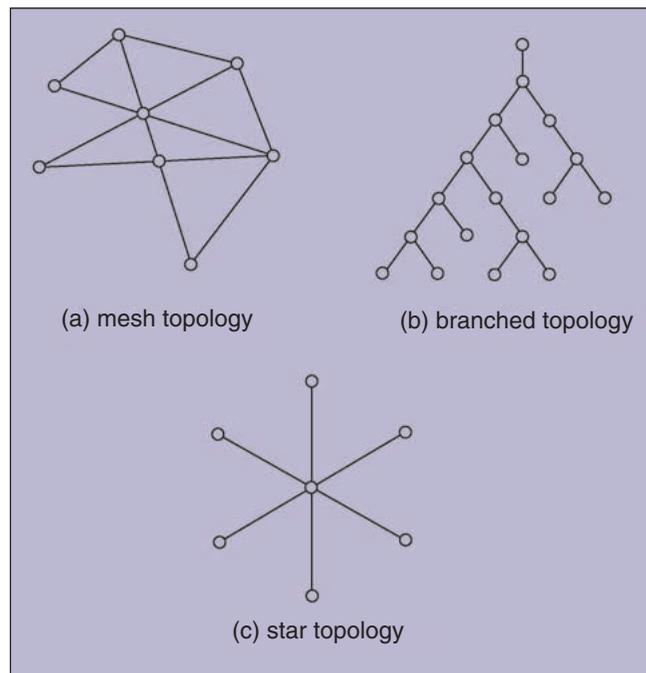


Figure 3. Network topology is defined by connections between nodes. Three common networks found in nature are (a) the mesh, (b) branched, and (c) star topologies.

of a geographical information system (GIS) and statistical programming in commercially available software to calculate a network variogram; and (3) demonstrating the utility of these methods for describing spatial patterns of fish distribution in different stream networks.

■ A statistical model for spatial data

Models for spatially referenced data differ, depending on the structure of the data and the region in which the data exist. Models to describe spatial relatedness are often based on the

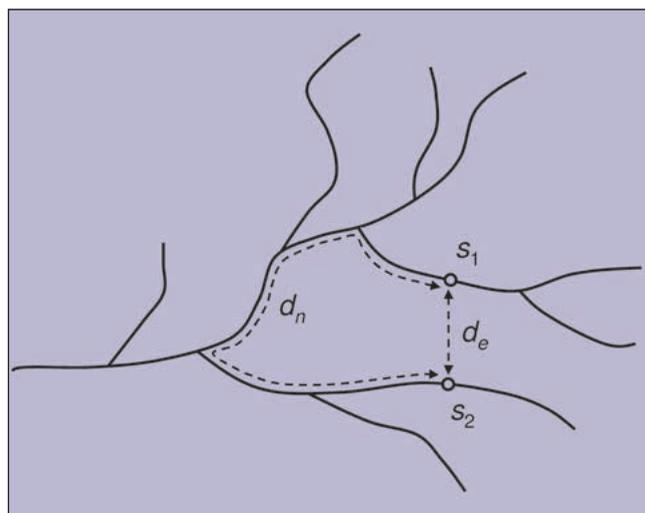


Figure 4. Separation distance between points s_1 and s_2 can be measured either as the shortest distance between two points, i.e. Euclidean distance (d_e), or as the distance along the network pathway (d_n).

statistical covariance and variance among paired values. The covariance describes the extent to which the values covary. The variance is a measure of the variability in the values. Correlations are covariances that have been scaled by variances to have values between positive and negative one. Geostatistical methods were developed for data that varies continuously over a predefined, fixed spatial region (Matheron 1963). In contrast, lattice data models are defined for values associated with a finite number of locations in a grid, and point pattern analysis evaluates the clustering of point occurrences over a region of interest (Cressie 1993). We have chosen to use a geostatistical model in a stream network. Important features of this model for network data are: (1) correlations between values at neighboring points are estimated and describe the relationship between near-neighbor values; (2) the correlation structure between neighboring response values depends only on the distance between locations, not on their particular locations; (3) distance can be defined in a number of ways, depending on the question of interest; (4) the variogram is a function of the correlation structure between values (or alternatively the covariance) and depends only on the distance between the locations of the values; and (5) statistical models for variograms must be evaluated to ensure that, in combination with the definition of distance, they allow statistical variances to be non-negative.

Geostatistical analysis requires response values that are labeled with the spatial coordinates at which measurements were collected. Euclidean distance is defined as the shortest straight line between any two points, but any metric can be used to quantify the distance between two points as long as it is non-negative, symmetrical, and satisfies the triangle inequality (Rathbun 1998). The triangle inequality states that for three points separated in space, the distance between two of these points cannot be longer than the sum of the other two distances. Other valid distance metrics include Manhattan (city-block) and Mahalanobis distances (McCune and Grace 2002). The Manhattan distance between points is analogous to the distance between points along streets in a city made up of blocks. The route between the points must fall along one dimension at a time. Mahalanobis distance is often used to measure distance between two groups in multivariate space. The distance between the centroids of two groups is inversely weighted by the correlation among the dimensions of the multivariate space. In practical applications, the distance between points may need to reflect more than physical distance (Legendre and Legendre 1983). Gardner *et al.* (2003) describe a distance metric for temperature data in a network that defines the distance between pairs of points based on stream order rather than physical distance. Newly proposed distance metrics should be evaluated against the above conditions, to ensure that they are a valid measure of distance. For example, a metric that implies different distances between two points, depending on the direction of travel, is not an appropriate measure of distance.

We used the empirical variogram as an exploratory

graphical tool to detect the presence of spatial pattern and identify differences in spatial structure in data collected along stream networks; however, it can also be used in predictive applications. The variogram function is the variance of the difference between response values that are a given distance apart. Because it describes the covariance structure among the values along the network, the variogram is useful for both applications (Cressie 1993; Matheron 1963; Palmer 2002). In the predictive geospatial application called “kriging”, an empirical, nonparametric variogram is estimated from the data and a parametric model is used to approximate this estimated variogram. The modeled variogram is subsequently incorporated into the prediction of the response values over space (Journel *et al.* 1978). Parametric models for the variogram must allow the variance of the differences between values at two locations to be positive and, thus, should be checked to insure they are valid when used with non-typical measures of distance (Armstrong and Jabin 1981). For example, not all parametric forms of the covariance function are valid for the water distance metric (Rathbun 1998). The exponential model is a valid form, but Matérn, Whittle, and Gaussian models are not.

■ In-stream data collection

Coastal cutthroat trout (*Oncorhynchus clarki clarki*) were sampled in five small (5–11 km²) watersheds (Racks Creek, Glenn Creek, Tucca Creek, and the North and South Forks of Hinkle Creek) in the Coast Range and Cascade Range mountains of western Oregon. These headwater basins are located above barriers to anadromous fish migration and are part of a larger broad-scale study examining the effects of landscape pattern on isolated coastal cutthroat trout populations (Gresswell *et al.* 2004). The five watersheds have mean elevations of 400–800 m and were selected randomly from a population of 268 second- and third-order catchments in mixed conifer forests of the Pacific Northwest. Stream channel units were surveyed throughout the entire fish-bearing extent of each stream network and were classified as pools, riffle-rapids, or cascades (Bisson *et al.* 1982). The abundance of adult (age ≥ 1 year) coastal cutthroat trout was assessed with single-pass electrofishing without blocknets (Jones and Stockwell 1995; Bateman *et al.* 2005) in all pools and cascades in each stream network. After fish were counted, they were released into the channel unit in which they were captured. The starting and ending points of each surveyed tributary were mapped in the field with aerial photographs and 1:24000-scale topographic maps.

■ Linking network distance and fish counts

To automate the process of calculating the network distances between all pairs of pools and cascade units in each network, a map of the stream survey was created in a GIS. Dynamic segmentation methodology in ArcInfo GIS software was used to assign a linear referencing system to the

surveyed portion of the stream network (ESRI 2002; Torgersen *et al.* 2004). The spatial network in the GIS was based on field-measured lengths of channel units and was composed of line segments connected by nodes delineating the upstream and downstream boundaries of channel units. Landmarks such as road crossings and tributary junctions were used to calibrate stream length in the GIS (derived from 1:24000-scale topographic maps) to the stream length measured in the field. Attributes associated with the channel units, including channel width, substrate composition, and fish counts were merged with the calibrated stream network information and displayed graphically. The point location of a sampled pool or cascade was defined as the midpoint of a sampled channel unit. The network distance between any two sampled units was calculated by summing the lengths of all channel units between two sample points.

Because the number of sampled channel units in each watershed was large (413–1002), a Visual Basic program in ArcGIS was used to calculate a list of distances between all pairs of sampled units along the network (Dussault and Brochu 2003). Furthermore, distance calculations required considerable computing power and the ability to work with large text files. After computing the list of network distances, the list of fish counts associated with each sampled unit and the list of pair-wise distances were merged into a single file that contained five data fields: (1) the identification number of a sampled unit, (2) the number of fish at that unit, (3) the identification number of another sampled unit, (4) the number of fish at the second unit, and (5) the network distance between the two units. This file was imported into the statistical package S-PLUS (Insightful Corporation 2002) and its associated SpatialStats module (Mathsoft 2000).

■ Estimating and interpreting empirical variograms

S-PLUS and the associated spatial statistics module are object-oriented programs with functions for computing spatial statistics, plotting empirical variograms, and fitting parametric variogram models. The program automatically creates a list of pair-wise Euclidean distances between point locations for input to other spatial analysis functions. As described earlier, we intended to use the network distance, and this prevented us from using the preprogrammed S-PLUS routine for computing variogram objects. A custom S-PLUS function was therefore created to compute a variogram object based on the network water distance that would be compatible with other spatial analysis routines in S-PLUS. To reduce the influence of unusually large or small values that were uncharacteristic of neighboring values, we calculated the robust variogram estimator (Cressie 1993).

Empirical variograms are a graph of half of the estimated variogram value, termed semivariance, plotted against the separation distance between points. For each separation distance there are varying numbers of pairs of data points, and at least 30 pairs of points should be used (Cressie

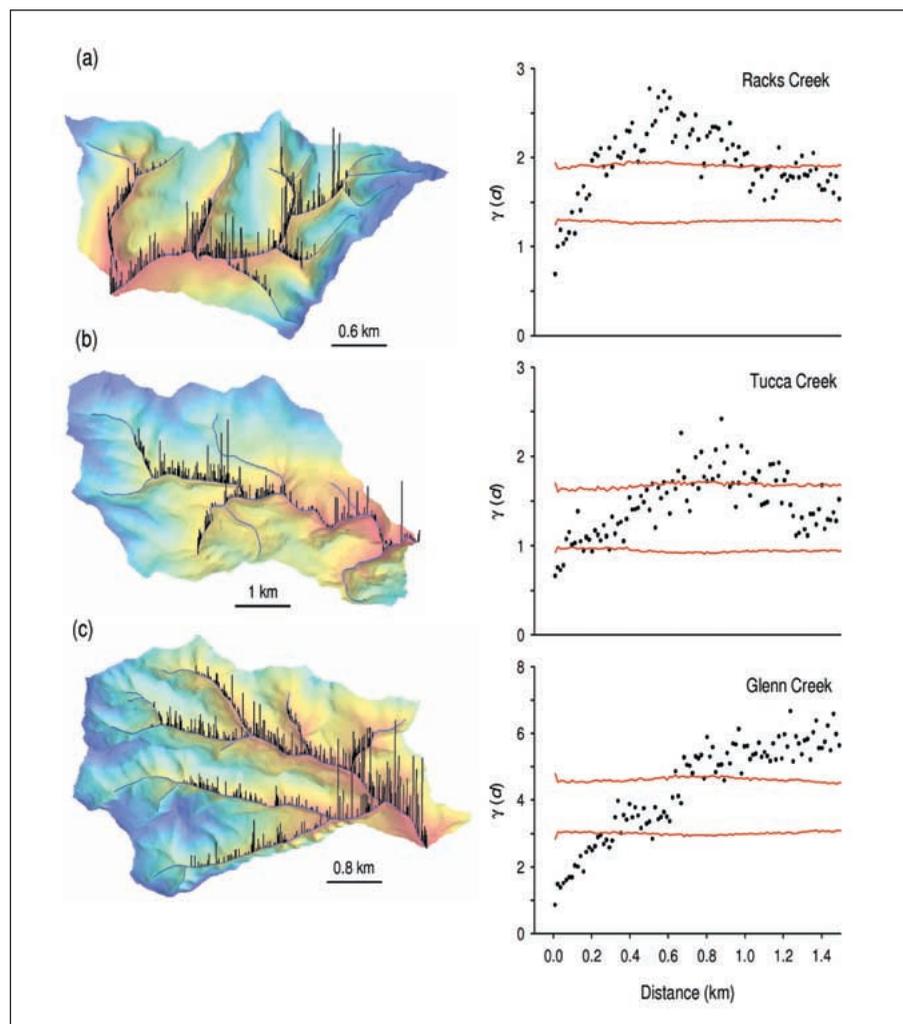


Figure 5. Spatial distribution and empirical variograms of coastal cutthroat trout counts in (a) Racks Creek, (b) Tucca Creek, and (c) Glenn Creek, in western Oregon headwater streams. Variograms depict the semivariance (\bullet) as a function of separation distance (d) with 2.5th and 97.5th percentiles from 5000 permutations displayed in red.

1993). This effectively defines the maximum separation distance for generating an empirical variogram and typically limits it to no more than half of the maximum separation distance between any two points (Rossi *et al.* 1992). In our study, half of the maximum separation distance between any two points in the smallest watershed was 1500 m, so we used this as the maximum separation distance for all watersheds. The number of pairs of points 1500 m apart ranged between 367 and 1919. Although there were sufficient pairs of points to calculate the variogram at distances of less than 5 m, we were interested primarily in describing spatial patterns in fish distribution at scales greater than 15 m. Therefore, 15 m was used as both the minimum separation distance and the incremental change in the separation distance.

A random permutation test for determining spatial pattern

Identifying and interpreting spatial pattern from a variogram is difficult without comparison to a variogram that

shows no pattern. A random ordering of spatial data produces unstructured scatter in the empirical variogram, but if spatial autocorrelation is present there is an increasing trend in the variogram. To determine whether spatial pattern was present, we wrote an S-PLUS function to randomly permute the fish counts over the stream network. This function was used to generate 5000 random permutations, and for each random ordering an empirical variogram was generated. For each separation distance, the 2.5th and 97.5th percentiles of the 5000 values at that distance were identified and compared to the variogram of the actual data (Figure 5). Variogram estimates above or below the percentile boundaries indicated the presence of spatial pattern at the spatial scale determined by the separation distance on the x-axis that was significantly different from a random spatial pattern.

Describing spatial pattern with empirical variograms

Empirical variograms for Racks, Glenn, and Tucca Creeks exhibited three important characteristics: (1) a low non-zero semivariance at short separation distances, (2) increasing semivariance with separation distance, and (3) a tendency for the semivariance to approach an asymptote at longer distances (Figure 5). In all three streams, variogram values initially occurred below the percentile bounds and then exceeded the 97.5th percentile at 0.2–0.6 km, indicating the presence of spatial structure in fish counts among pools and cascades at small and large spatial scales. In contrast, variograms of Hinkle Creek showed little evidence of spatial structuring beyond initial autocorrelation at small scales (Figure 6). The empirical variogram for the entire Hinkle Creek drainage revealed the presence of spatial structure, but separate variograms for the two forks indicated that spatial structure was much stronger in the South Fork than in the North Fork (Figure 6).

The variation in variogram patterns observed among watersheds suggested that the underlying spatial structure in fish counts differed between headwater streams and was influenced by a complex interaction of physical and biological processes (Figures 5, 6). Bedrock lithology is one factor that can affect the topography of channel net-

works (Kobor and Roering 2004) and the spatial scale of variation in trout distribution (Gresswell *et al.* in press). The distance at which the semivariance reached a peak or asymptote (known as the “range” in geostatistics; see Rossi *et al.* 1992) provided an indication of the dominant spatial scale at which fish counts were correlated. In a survey of coastal cutthroat trout distribution in 40 headwater streams in western Oregon, shorter distances to the asymptote (eg Racks Creek) were associated with more resistant rock types (basalt and resistant sedimentary) subject to small-scale, shallow debris flows; longer distances to the asymptote (eg Glenn Creek) were associated with weaker rock types (weak sedimentary) subject to large-scale, deep earthflows (Gresswell *et al.* in press). An index of stream channel complexity (ratio of summed tributary lengths to the longest length of stream per watershed) was also greater where rock types were less resistant to erosion (Guy 2004).

Other aspects of the variogram, such as the slope of the ascending limb, the γ -intercept, and the overall shape, can be used to provide useful information for characterizing spatial pattern (Legendre and Legendre 1983; Dent and Grimm 1999; Ettema and Wardle 2002). However, parametric modeling of the variogram and inference about specific features assumes that the mean of the fish counts and the covariance structure are stable over the entire drainage (ie stationary; Cressie 1993). Some of the spatial patterns and the variations among the drainages that we observed may be due to interactions between ecological processes that cause non-stationarity. Before interpreting particular features of the variogram, investigations of local effects that may alter the estimated variogram are needed. Explaining this variation in fish abundance is the current focus of a larger study that is currently underway; this aims to elucidate the nature and complexity of these spatial patterns and the processes that generate them (Gresswell *et al.* in press; Torgersen *et al.* 2004). The variograms are provided here to illustrate the utility of empirical variograms as a first step in detecting spatial pattern and to encourage ecologists to explore patterns of ecological heterogeneity in stream networks.

■ Conclusions

Stream ecologists are attempting to understand how the structure of stream networks contributes to the physical and biological functioning of rivers and

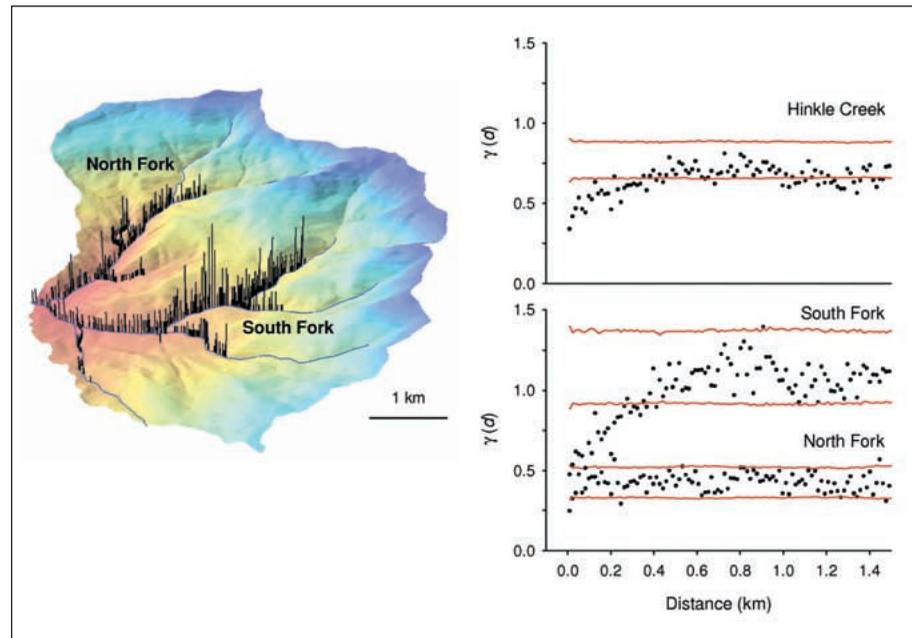


Figure 6. Spatial distribution and empirical variograms of coastal cutthroat trout counts in Hinkle Creek. Variograms were calculated for the entire Hinkle Creek watershed and individually for the North and South forks. Variograms depict semivariance (\bullet) as a function of separation distance (d) with 2.5th and 97.5th percentiles from 5000 permutations displayed in red.

streams. Connectivity among stream units may imply that effects extend upstream as well as downstream. How far does the influence of a point extend up- or downstream? Are there patterns in successive measurements along a stream? What is the minimum distance between statistically independent data? Does the covariance structure change in a predictable way along a stream network? These are all questions about spatial structure in a network. It can be difficult to identify spatial structure without analytical tools, but the empirical variogram provides explicit visual evidence that such structure exists. We believe that exploratory variogram analysis can be used as an initial step in answering questions concerning differences in response patterns among drainages (eg the range over which spatial patterns exist, and their magnitude).

In the past, one impediment to this type of analysis was the lack of commercially available software using a distance metric appropriate to a network. By linking a GIS, a user-written function, and the commercially available spatial statistics software in S-PLUS, we were able to quickly generate an empirical variogram and take advantage of other existing routines in the Spatial Statistics module of S-PLUS for fitting variogram models. The S-PLUS functions can easily be adapted to the use of other distance metrics for networks, and the method is easily transferred to other applications. Software designers may soon be adding network functionality to existing statistical analysis packages; however, in the meantime, all S-PLUS functions and scripts described in this paper are available from the authors on request.

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■ References

- Armstrong M and Jabin R. 1981. Variogram models must be positive-definite. *Math Geol* **13**: 455–59.
- Bateman DS, Gresswell RE, and Torgersen CE. 2005. Evaluating single-pass catch as a tool for identifying spatial pattern in fish distribution. *J Freshwater Ecol* **20**: 335–45.
- Bisson PA, Nielsen JL, Palmason RA, and Grove LE. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. In: Armantrout NB (Ed). *Acquisition and utilization of aquatic habitat inventory information*. Bethesda, MD: American Fisheries Society, Western Division.
- Benda L, Poff NL, Miller D, *et al.* 2004. The Network Dynamics Hypothesis: how channel networks structure riverine habitats. *BioScience* **54**: 413–27.
- Carroll SS and Pearson DL. 1998. Spatial modelling of butterfly species richness using Tiger beetles (Cicindelidae) as a bioindicator taxon. *Ecol Appl* **8**: 531–43.
- Cressie NAC. 1993. *Statistics for spatial data*. New York, NY: John Wiley & Sons, Inc.
- Dent CL and Grimm NB. 1999. Spatial heterogeneity of stream water nutrient concentrations over successional time. *Ecology* **80**: 2283–98.
- Dussault G and Brochu M. 2003. Distance matrix calculation. <http://arcscripsts.esri.com>. Quebec, Canada: Institut National de la Recherche Scientifique, Urbanisation, Culture et Société (INRS-UCS), Université du Québec. Viewed 13 May 2004.
- ESRI (Environmental Systems Research Institute). 2002. ArcInfo Desktop, Version 8.3. Redlands, CA.
- Ettema CH and Wardle DA. 2002. Spatial soil ecology. *Trends Ecol Evol* **17**: 177–83.
- Fagan WF. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology* **83**: 3243–49.
- Fisher SG. 1997. Creativity, idea generation, and the functional morphology of streams. *J N Am Benthol Soc* **16**: 305–18.
- Gardner B, Sullivan PJ, and Lembo AJ. 2003. Predicting stream temperatures: geostatistical model comparison using alternative distance metrics. *Can J Fish Aquat Sci* **60**: 344–51.
- Gresswell RE, Bateman DS, Lienkaemper GW, and Guy TJ. 2004. Geospatial techniques for developing a sampling frame of watersheds across a region. In: Nishida T, Kailola PJ, and Hollingworth CE (Eds). *GIS/spatial analyses in fishery and aquatic sciences* (vol 2). Saitama, Japan: Fishery–Aquatic GIS Research Group.
- Gresswell RE, Torgersen CE, and Bateman DS. A spatially explicit approach for evaluating relationships among coastal cutthroat trout, habitat, and disturbance in small streams. In: Hughes R, Wang L, and Seelbach P (Eds). *Influences of landscapes on stream habitats and biological communities*. In press.
- Guy TJ. 2004. Landscape-scale evaluation of genetic structure among barrier-isolated populations of coastal cutthroat trout, *Oncorhynchus clarki clarki* (MS thesis). Corvallis, OR: Oregon State University.
- Haggett P and Chorley RJ. 1969. *Network analysis in geography*. London, UK: Edward Arnold.
- Honnay O, Verhaeghe W, and Hermy M. 2001. Plant community assembly along dendritic networks of small forest streams. *Ecology* **82**: 1691–1702.
- Jones ML and Stockwell JD. 1995. A rapid assessment procedure for the enumeration of Salmonine populations in streams. *North Am J Fish Mana* **15**: 551–62.
- Journel AG and Huijbregts CJ. 1978. *Mining geostatistics*. New York, NY: Academic Press.
- Kobor JS and Roering JJ. 2004. Systematic variation of bedrock channel gradients in the central Oregon Coast Range: implications for rock uplift and shallow landsliding. *Geomorphology* **62**: 239–56.
- Legendre L and Legendre P. 1983. *Numerical ecology*. Amsterdam, Netherlands: Elsevier Scientific Publishing Company.
- Little LS, Edwards D, and Porter DE. 1997. Kriging in estuaries: as the crow flies, or as the fish swims? *J Exp Mar Biol Ecol* **213**: 1–11.
- Matheron G. 1963. Principles of geostatistics. *Econ Geol* **58**: 1246–66.
- Mathsoft. 2000. S+SpatialStats, Version 1.5 Supplement. Seattle, WA: Data Analysis Products Division, MathSoft, Inc.
- McCune B and Grace JB. 2002. *Analysis of ecological communities*. Gleneden Beach, OR: MjM Software Design.
- Palmer MW. 2002. Scale detection using semivariograms and autocorrelograms. In: Gergel SE and Turner MG (Eds). *Learning landscape ecology: a practical guide to concepts and techniques*. New York, NY: Springer.
- Power ME and Dietrich WE. 2002. Food webs in river networks. *Ecol Res* **17**: 451–71.
- Rathbun SL. 1998. Spatial modelling in irregularly shaped regions: kriging estuaries. *Environmetrics* **9**: 109–29.
- Rice SP, Greenwood MT, and Joyce CB. 2001. Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. *Can J Fish Aquat Sci* **58**: 824–40.
- Rosenberg DK, Noon BR, and Meslow EC. 1997. Biological corridors: form, function, and efficacy. *BioScience* **47**: 677–88.
- Rossi RE, Mulla DJ, Journel AG, and Franz EH. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecol Monogr* **62**: 277–314.
- Insightful Corporation. 2002. S-PLUS for Windows, Version 6.1. Seattle, WA: Insightful Corporation.
- Torgersen CE, Gresswell RE, and Bateman DS. 2004. Pattern detection in stream networks: quantifying spatial variability in fish distribution. In: Nishida T, Kailola PJ, and Hollingworth CE (Eds). *GIS/spatial analyses in fishery and aquatic sciences* (vol 2). Saitama, Japan: Fishery–Aquatic GIS Research Group. p 405–20.
- Wenbug JK and Bentzen P. 2001. Genetic and behavioral evidence for restricted gene flow among coastal cutthroat trout populations. *T Am Fish Soc* **130**: 1049–69.