

Rosamonde R. Cook · Paul L. Angermeier ·
Debra S. Finn · N. LeRoy Poff · Kirk L. Krueger

Geographic variation in patterns of nestedness among local stream fish assemblages in Virginia

Received: 31 December 2002 / Accepted: 17 May 2004 / Published online: 23 July 2004
© Springer-Verlag 2004

Abstract Nestedness of faunal assemblages is a multi-scale phenomenon, potentially influenced by a variety of factors. Prior small-scale studies have found freshwater fish species assemblages to be nested along stream courses as a result of either selective colonization or extinction. However, within-stream gradients in temperature and other factors are correlated with the distributions of many fish species and may also contribute to nestedness. At a regional level, strongly nested patterns would require a consistent set of structuring mechanisms across streams, and correlation among species' tolerances of the environmental factors that influence distribution. Thus, nestedness

should be negatively associated with the spatial extent of the region analyzed and positively associated with elevational gradients (a correlate of temperature and other environmental factors). We examined these relationships for the freshwater fishes of Virginia. Regions were defined within a spatial hierarchy and included whole river drainages, portions of drainages within physiographic provinces, and smaller subdrainages. In most cases, nestedness was significantly stronger in regions of smaller spatial extent and in regions characterized by greater topographic relief. Analysis of hydrologic variability and patterns of faunal turnover provided no evidence that inter-annual colonization/extinction dynamics contributed to elevational differences in nestedness. These results suggest that, at regional scales, nestedness is influenced by interactions between biotic and abiotic factors, and that the strongest nestedness is likely to occur where a small number of organizational processes predominate, i.e., over small spatial extents and regions exhibiting strong environmental gradients.

The Virginia Cooperative Fish and Wildlife Research Unit is jointly sponsored by United States Geological Survey, Virginia Polytechnic Institute and State University, and Virginia Department of Game and Inland Fisheries.

R. R. Cook
Department of Fisheries and Wildlife Biology, Colorado State University,
Fort Collins, CO, 80523, USA

Present address:
R. R. Cook (✉)
US National Park Service, Sequoia and Kings Canyon National Parks,
47050 Generals Highway,
Three Rivers, CA, 93271, USA
e-mail: Rose_Cook@nps.gov
Tel.: +1-559-565-3788
Fax: +1-559-5654283

P. L. Angermeier
US Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit, Virginia Polytechnic Institute and State University,
Blacksburg, VA, 24061, USA

D. S. Finn · N. L. Poff
Department of Biology, Colorado State University,
Fort Collins, CO, 80523, USA

K. L. Krueger
Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University,
Blacksburg, VA, 24061, USA

Keywords Stream fish · Nested subsets · Nestedness · Species assemblages · Spatial scale

Introduction

Explaining patterns of local and regional variation in species composition is a central goal in community ecology. A growing interest in how and why community composition varies across large areas (e.g., Wiens et al. 1986; Menge and Olson 1990; Gaston 2000), has led to the recognition that community patterns reflect not only local interactions but also regional processes such as dispersal and speciation (e.g., Ricklefs and Schluter 1993; Hubbell 2001). Analysis of nested subset patterns is one approach for exploring the potential effects of various environmental factors and ecological processes on patterns of local and regional diversity (e.g., Patterson and Atmar 1986; Cook and Quinn 1995; Wright et al. 1998). Nestedness represents the degree to which small assem-

blages of species are subsets of successively larger assemblages, and results from ordered patterns of distribution in which species with the lowest frequencies of occurrence occur only in the richest assemblages, while the most common species occur in all. Strong nestedness implies consistency through space in the factors regulating species occurrences.

Nestedness can be viewed as the region-wide outcome of a species pool being “filtered” by site-specific environmental constraints (Patterson and Brown 1991; Poff 1997; Angermeier and Winston 1998; Wright et al. 1998), with each species’ distribution among sites determined by its ability to overcome the constraints. Nested patterns of species occurrence are common in patch-structured regions such as island archipelagoes. The most important condition for meaningful interpretation of nestedness is that all localities in the region share a common species pool. Nestedness will then develop if there is a hierarchical relationship (1) among species in their sensitivity to key limiting factors, and (2) among localities in the restrictiveness of their limiting factors (Fig. 1). The “aperture size” of environmental filters determines the species composition at a given locality via control of environmental suitability. Nestedness is especially likely if a single limiting factor predominates the ranking of local suitability among species. If multiple factors are limiting across localities, nestedness will be exhibited only if species’ tolerance ranks are highly correlated among factors.

Three principal filtering mechanisms are generally recognized: area, which influences extinction probability through its effect on population size; distance of localities from a colonizing source; and environmental conditions (Patterson and Brown 1991). Specifically, nestedness can arise if there exists a hierarchical relationship among species in susceptibility to extinction (e.g., Patterson and Atmar 1986; Patterson 1987; Bolger et al. 1991), in colonizing ability (Cook and Quinn 1995; Kadmon 1995; Butaye et al. 2001), or in sensitivity to the suite of biotic and abiotic factors that define the realized niche. One way that the latter condition can generate nested patterns is if species’ habitats exhibit a nested subset structure (Patterson and Brown 1991; Cook and Quinn 1995; Calmé and Desrochers 1999). Less widely recognized in the literature is the potential for environmental gradients to generate nested subset patterns. Such may be the case where species with the broadest tolerance persist throughout the gradient while others with more limited tolerances are restricted to one end of it. A case in point is a study by Worthen et al. (1996), who found insect assemblages to exhibit nestedness along temperature and moisture gradients due to interspecific variation in tolerance of these factors.

The distribution of stream fish species is often ordered along environmental gradients. Progressive addition of species to local assemblages as stream size increases is especially common (Burton and Odum 1945; Sheldon 1968; Angermeier and Schlosser 1989). Several environmental factors that influence the distribution of fishes, such as temperature, temporal variability in flow, avail-

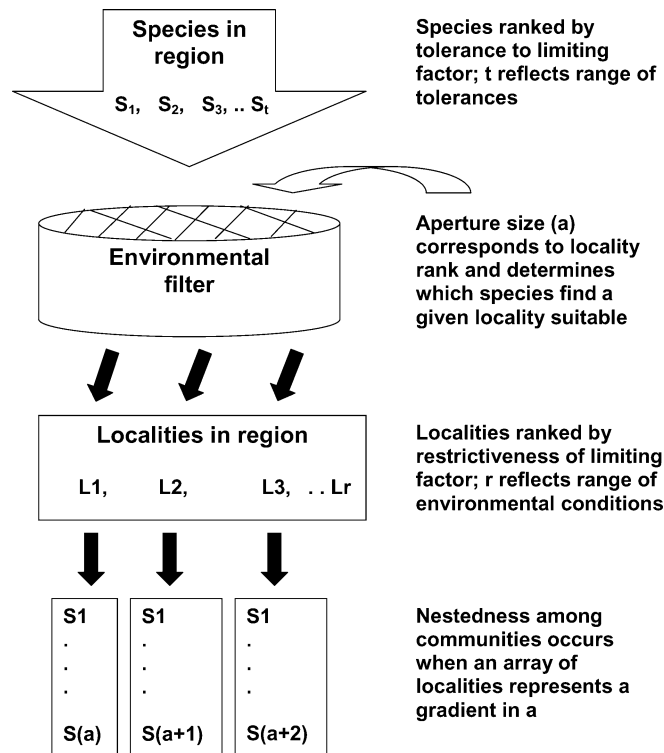


Fig. 1 Conceptual model of how nestedness develops among communities. All species in the regional pool have similar access to localities but differ in their tolerances to limiting factors associated with vulnerability to extinction, colonization ability, and environmental conditions. The range of tolerances (t) is a function of species richness and interspecific variation. Occurrence in a community is contingent on passage through all locality-specific environmental filters. Filters with smaller apertures (a) are more restrictive and allow fewer species to occur. The range of conditions (r) represented in the region reflects its spatial heterogeneity. No a priori relationship between t and r is implied, but if $r > t$ some communities will include all species in the region. Nestedness results when a gradient in species traits is juxtaposed on a spatial gradient in an environmental factor that limits the distribution of multiple species

ability of food and habitat, and predation intensity, also tend to vary with stream size (Horwitz 1978; Vannote et al. 1980; Schlosser 1987). Any of these could produce nested subset patterns if species are ordered in their tolerances to them. Recent studies have used nested subsets analysis to examine effects of flow regime on fish community composition (Kodric-Brown and Brown 1993; Taylor 1997; Taylor and Warren 2001). Like their terrestrial counterparts, these have emphasized the roles of colonization and extinction in producing nested subset patterns. For example, Taylor and Warren (2001) reported strongly nested patterns associated with high extinction rates in localities with highly variable streamflow.

In large regions, many environmental factors influence species distributions, although the most-limiting factors vary among localities. In theory, nestedness is most likely to occur within regions that share a similar biogeographic history and are ecologically similar enough that each locality is populated by the same species pool (Patterson and Atmar 1986; Patterson and Brown 1991). Heteroge-

neity in either of these factors, which tend to be correlated with spatial scale, will tend to disrupt nestedness. Further, the number of environmental factors that influence local occupancy will also tend to increase with region size. In small regions, species distributions are likely to be controlled by a smaller array of limiting factors than in large regions, making nestedness more likely. We therefore expect nestedness to be negatively correlated with regional area.

We also expect some regions to exhibit greater nestedness than others (holding effects of region size constant). In particular, regions with a strong, pervasive environmental gradient among localities (a restrictive filter) should exhibit stronger patterns of nestedness than regions where spatial gradients are weaker or nonexistent. In streams, the same factors that produce nestedness along stream-size gradients within watersheds (i.e., water catchment basins) might also produce nestedness across a region comprising many watersheds. Environmental factors such as temperature, variability of flow, and predation intensity, which vary with stream size, are often associated with elevation. Elevation is therefore a good candidate for a landscape descriptor capable of representing multiple environmental factors important to fish distributions (Rahel and Hubert 1991). Most lotic species exhibit restricted ranges of elevation in their distribution (Hynes 1970), thereby reflecting species' sensitivities to environmental correlates of elevation. Segregation of species along elevational gradients in montane regions is one of the most pervasive zoogeographic patterns of fish distribution worldwide (Matthews 1998, p. 354). Thus, we predict that regions exhibiting greater topographic relief (steeper elevation gradients) will exhibit stronger patterns of nestedness.

We tested these predictions with an extensive data set for fish assemblages of Virginia streams. Stream systems are inherently hierarchical over a wide range of spatial scales (Frissell et al. 1986; Schlosser 1991; Imhoff et al. 1996), which make them good subjects for studying relationships between spatial scale and nestedness. Virginia is a good choice for this investigation because intensive sampling of stream fish assemblages has occurred across the state for more than 30 years and the distributions of its many (>195) fish species have been well documented (Jenkins and Burkhead 1994). Virginia also encompasses a wide variety of stream habitats, including portions of 11 major drainages and five physiographic provinces, each of which supports distinctive fish assemblages (Angermeier and Winston 1999). Our specific objectives were to: (1) estimate nestedness in a hierarchical series of regions; (2) assess the relationship between nestedness and region size; (3) assess the relationship between nestedness and elevation among regions; and (4) draw inferences regarding the mechanisms that contribute to inter-regional variation in nestedness of fish assemblages.

Materials and methods

The data

Data were obtained from a statewide database maintained by the Virginia Department of Game and Inland Fisheries, of more than 3,000 collections of stream fishes made since 1965 from the Chowan, Roanoke, Potomac, James, Rappahannock, New, and Clinch River drainages. The collections are the result of surveys conducted by a variety of agencies using a variety of sampling methods and gear. To minimize any potential variation in the quality of data used in this analysis, we omitted records that represented a single taxon or contained game species only, as well as those representing collections with questionable species identifications and collections lacking precise location information. We selected only collections from intermediate-sized streams of orders 3, 4, 5, and 6 (Strahler 1952), as smaller and larger streams were relatively under-represented. Stream order is an index of stream size based on branching pattern, where the smallest streams are first-order. A second-order stream is formed by the confluence of two first-order streams, a third-order stream is formed by the confluence of two second-order streams, and so on. Collections from fifth and sixth-order streams were combined because there was little difference in size between them and there were relatively few collections from sixth-order streams. We also omitted collections made during the winter and early spring (November–April) in order to reduce potential influences of natural seasonal turnover, but also because comparatively little sampling occurred in these months (approximately 10% of all collections), and because sampling effectiveness for most species is lower during this period than the rest of the year.

Localities were operationally defined by river reaches under the classification system developed by the United States Environmental Protection Agency (1998). Thus, the suite of species inhabiting a single reach constituted a local assemblage. The length of reaches varies, with most being between 2 and 10 km long. Approximately 29% of reaches were represented by more than one collection in the database and these sometimes differed in numbers and identities of species. Such differences could be due to variation in effectiveness of different sampling gear, changes in local species assemblages between samples, or to variation in habitats within a reach. Such variation represents random error in our analysis. Its effect would be to reduce measures of nestedness and produce underestimates in the strength of organized community-level pattern. To minimize this effect, we chose a single collection, drawn at random from reaches with multiple samples. An alternative would have been to combine multiple collections into single samples. However, this could have created a condition in which some reaches were effectively sampled more intensively than others. Our final dataset consisted of 773 collections. Although random error is likely to remain, its presence would only obscure the types of relationships that we are examining as

there is no evidence that sampling variation is spatially correlated.

Regional definitions

The four region types over which nestedness was examined were defined within a nested spatial hierarchy. The largest region (statewide) comprised seven major drainage basins (Fig. 2a). The second largest regions consisted of the individual drainages. All seven drainages have lacked freshwater connections since the last glacial recession and can therefore be considered independent regions. Within drainages were drainage/physiographic regions, defined by dividing drainages into component physiographic provinces (following Angermeier and Winston 1999) (Fig. 2b). The data set included collections from three of the five provinces represented in Virginia: coastal plain, piedmont, and valley and ridge. Data for more than a single province were available for only two major drainages, the James and Rappahannock Rivers. The James data set included collections from all three provinces, the Rappahannock from the coastal plain and piedmont. All other drainages represented a single physiographic province and were treated as drainage/physiographic regions in analyses conducted at that scale. Of these, all Chowan collections were located in the coastal plain, Roanoke collections in the piedmont, and Clinch, New, and Potomac collections in the valley and ridge. The smallest regions, subdrainages, were defined as the eighth digit hydrologic units of the National Hydrography Dataset (NHD) for Virginia (United States Geological Survey 1980, Fig. 2c). Subdrainages approximate watershed level, although they are often delineated by locations of confluence with mainstems and may actually include portions of individual neighboring watersheds.

We followed Jenkins and Burkhead (1994) in distinguishing native versus non-native fish species for each major drainage. Thus, species native to some drainages were non-native to others if their appearance in the latter succeeded record keeping. Species were considered native to an entire region if they were native to one or more of the smaller regions nested within it. Numbers of native species represented in our data set ranged from 30 to 76 among drainages, with 153 species represented statewide.

Measures of nestedness

The original species abundance data were converted to presence/absence matrices for analysis. Nestedness was measured using the C index developed by Wright and Reeves (1992). C is a standardized form of the metric N_c , calculated directly from the presence/absence matrix.

$$N_c = \sum_{i=1}^{K-1} \sum_{m=i+1}^K \sum_{j=1}^S X_{ij} X_{mj} \quad (1)$$

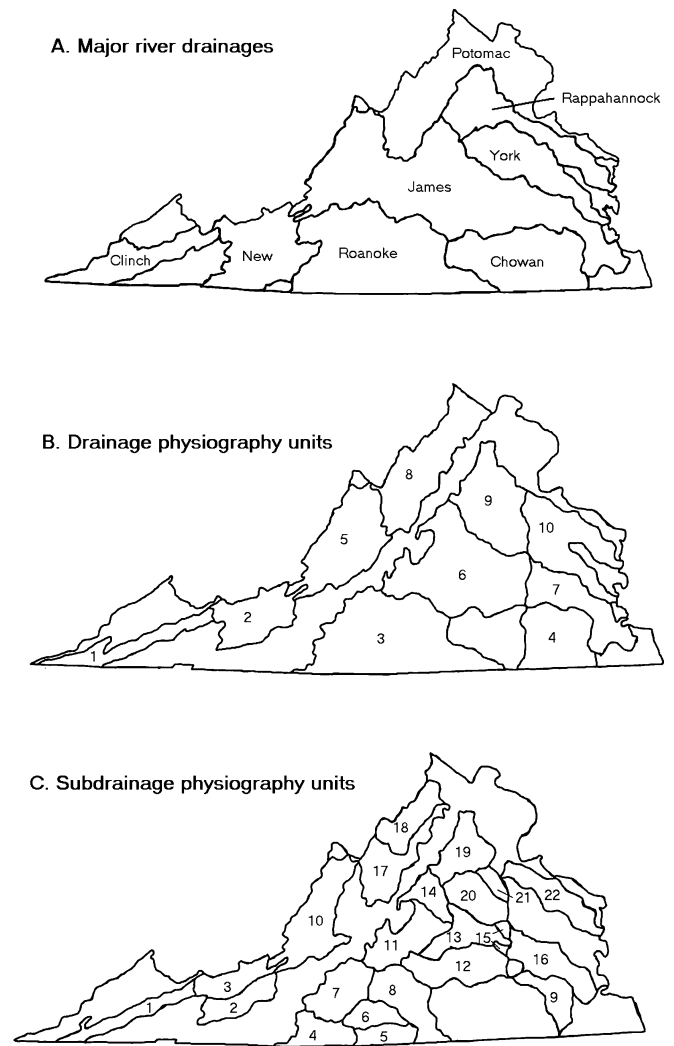


Fig. 2a–c Maps of Virginia showing the three regional definitions used to analyze nestedness of stream fish assemblages: **a** major river drainages; labeled drainages were used (the Rappahannock and York were treated as a single drainage); **b** drainage-physiography units (1 Clinch, valley and ridge; 2 New, valley and ridge; 3 Roanoke, piedmont; 4 Chowan, coastal plain; 5 James, valley and ridge; 6 James, piedmont; 7 James, coastal plain; 8 Potomac, valley and ridge; 9 Rappahannock, piedmont; 10 Rappahannock, coastal plain); **c** subdrainage-physiography units (1 06010205, valley and ridge; 2 05050001, valley and ridge; 3 05050002, valley and ridge; 4 03010103, piedmont; 5 03010104, piedmont; 6 03010105, piedmont; 7 03010101, piedmont; 8 03010102, piedmont; 9 03010202, coastal plain; 10 02080201, valley and ridge; 11 02080203, piedmont; 12 02080207, piedmont; 13 02080205, piedmont; 14 02080204, piedmont; 15 02080206, piedmont; 16 02080206, coastal plain; 17 02070005, valley and ridge; 18 02070006, valley and ridge; 19 02080103, piedmont; 20 02080106, piedmont; 21 02080105, piedmont; 22 02080104, coastal plain)

where K is the number of sites being compared and S is the total number of species over all sites. X 's are equal to 1 for presence or 0 for absence of species j at sites i and m , such that N_c is equal to the sum of the number of species shared across all pairs of sites. Like many other published indices of nestedness (see Cook 1995), N_c is sensitive to the size of the presence/absence matrix and tends to

increase with greater numbers of species and/or sites. We therefore standardize N_c into another index, C in order to compare among matrices of different size. C is derived by the formula:

$$C = \left(\frac{N_c - E(N_c)}{\text{Max}(N_c) - E(N_c)} \right) \quad (2)$$

where $E(N_c)$ is the expected value of N_c , or the value that N_c would take if the distributions of species among sites were unordered with respect to site richness. It is the smallest value that N_c could have given the number of species and sites in a dataset. $\text{Max}(N_c)$ is the value that N_c would take if a matrix were perfectly nested, or the largest value that N_c could attain. Standardization enables the comparison of nestedness values without the confounding influence of matrix size. This is important in our analysis because of potential relationships between stream size, species richness, and elevation (Angermeier and Winston 1998). C varies between 0, when species are completely unordered in distribution, and 1 when assemblages are perfectly nested.

We used z -scores to determine whether C values differed significantly from 0. Because N_c tends to be skewed toward higher values and have wide tails, especially for smaller data sets (Wright and Reeves 1992), we used Cochran's Q test for related observations (Conover 1980), a type of χ^2 test modified to account for differences in row totals. We used a z test to compare nestedness between pairs of matrices, following Wright and Reeves' (1992) formula:

$$z = C_a - C_b \sqrt{\left[\text{Var}(N_c)_a d_a^2 + \text{Var}(N_c)_b d_b^2 \right]} \quad (3)$$

where d is equal to the denominator in Eq. 2, $\text{Var}(N_c)$ is the variance in N_c , and a and b represent two matrices. However, $E(N_c)$ and $\text{Var}(N_c)$ may not be exact when assemblages are highly nested. Thus, we use z only for delineating major differences between C values, assuming conservative confidence intervals, with a critical value of 2.34 ($P=0.01$).

Random sampling error will tend to have a larger effect on measures of nestedness for data sets containing small numbers of assemblages. To control for any potential bias among comparisons (which differ in numbers of assemblages) that could occur as a result, we identified the range over which C varied with sample size using a resampling procedure in which sets of collections, ranging from five to 25, were drawn at random from the set of all collections in the Chowan dataset, also chosen at random. C increased with the number of collections up to 12, at which point increasing the number of collections did not change C . We therefore limited all comparisons to those represented by at least 12 collections. We further verified that C was not correlated with sample size for all comparisons made.

Analyses

We examined relationships between nestedness and spatial extent by comparing C values within regions of successively larger size, from subdrainages to drainage/province regions of the James and Rappahannock, to whole drainages, and to all drainages combined. We examined the association between C and spatial scale for all regions using a Spearman's rank correlation test, and compared C values by performing a z test between regions of successively larger size within spatially nested regions. Since smaller regions are parts of larger ones, their data sets are not independent. However, the lack of independence only makes detecting significant differences more difficult in this case by increasing the chance of a Type II statistical error.

We examined relationships between nestedness and mean elevation for drainage/physiographic regions and subdrainages. In these analyses, regional data sets comprised unique sets of collections and were therefore independent. We used mean elevation, derived from collection locations, as a proxy for elevation gradients within regions because higher elevations are associated with greater topographic relief. We used correlation analysis to examine the relationship between C and mean elevation for all regions, although such tests may be uninformative, particularly if sample sizes are small, because nestedness can be influenced by differences among drainages in species pools and environmental conditions. The best comparisons are among regions within drainages. We therefore also used z tests to compare C values among physiographic regions within individual drainages and among subdrainages within drainage/physiographic regions. Since stream size has the potential to affect community composition through its influence on biotic (e.g., large predators) and abiotic (e.g., temperature) conditions, we also conducted these analyses for individual stream orders, but only for drainage/physiographic regions; data sets were generally too small ($n < 12$) for individual stream order comparisons across subdrainages.

Results

Regional scale

Nestedness was apparent at all four regional levels (Table 1). Stream fish assemblages were significantly nested ($P < 0.01$) in every region examined except fifth- + sixth-order streams of the Rappahannock coastal plain. Results of Spearman's rank correlation failed to reveal a relationship between C and regional extent across all regional levels ($r = 0.168$, $P > 0.05$). However, in pairwise comparisons among spatially nested regions, C was strongly associated negatively with regional extent except at the subdrainage level. Specifically, C was significantly greater in eight of the ten drainage/physiographic regions compared with the statewide region (binomial probability = 0.055), the exceptions being the coastal plain of the

James and Rappahannock drainages (Table 2). *C* was also significantly greater in physiographic provinces within the James and Rappahannock compared with entire drainages, except for the coastal plain in both cases (Table 2). *C* was greater in 14 of 24 subdrainages compared with their drainage/physiographic regions (binomial probability=0.095), but significantly greater only in ten (Table 2).

Elevation

C was significantly correlated with mean elevation of all drainage/physiographic regions ($r=0.645$, $P=0.047$) (Fig. 3). Within-drainage comparisons were possible only for the James and Rappahannock drainages. Among these, *C* was significantly greater in the valley and ridge of the James ($z=17.8$, $P<0.001$) and the piedmont of the Rappahannock ($z=15.09$, $P<0.001$) compared with the coastal plain. Patterns were the same for individual stream orders in these drainages. *C* increased with mean elevation (Spearman rank correlation) among third-, fourth-, and fifth- + sixth-order streams of the James ($r=0.954$, $P<0.001$) (Fig. 4a) and the Rappahannock ($r=0.886$, $P=0.033$) (Fig. 4b).

Trends in *C* with mean elevation (all stream orders combined) were also apparent at the level of subdrainages within drainage/physiographic regions (Fig. 5). Although *C* was weakly associated with mean elevation for all subdrainages combined ($r=0.406$, $P=0.134$), *C* was significantly greater among subdrainages with the highest mean elevation versus subdrainages with the lowest mean elevation in each drainage/physiographic region examined (Roanoke: $z=20.94$, $P<0.001$; Potomac: $z=4.62$, $P<0.001$; James piedmont: $z=11.62$, $P<0.001$; and Rappahannock piedmont: $z=6.05$, $P<0.001$).

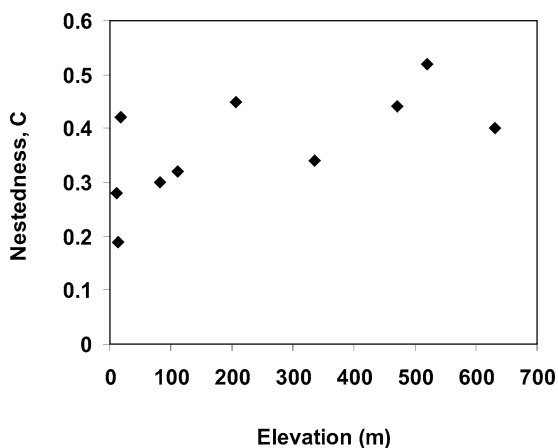


Fig. 3 Nestedness (*C*) of native stream fish assemblages versus mean elevation of collection sites in ten drainage/physiographic regions in Virginia

Table 1 Numbers of native species, collections, measures of nestedness (*C*), and Cochran's *Q* for data sets included in this analysis

Region	Species	Collections	<i>C</i>	<i>Q</i>
All drainages	183	806	0.23	23,172.74
Chowan coastal plain	55	70	0.42	1,163.06
Subdrainage 03010202	41	41	0.40	501.44
Clinch valley and ridge	65	70	0.52	1,369.74
Roanoke piedmont	65	162	0.45	3,357.64
Subdrainage 03010101	41	31	0.45	428.62
Subdrainage 03010102	50	26	0.39	441.89
Subdrainage 03010103	40	56	0.55	914.20
Subdrainage 03010104	43	24	0.24	204.40
Subdrainage 03010105	36	18	0.36	192.55
Potomac valley and ridge	36	63	0.34	521.15
Subdrainage 02070005	28	28	0.34	182.59
Subdrainage 02070006	29	21	0.22	104.06
New valley and ridge	30	43	0.40	344.13
Subdrainage 05050001	23	20	0.44	147.92
Subdrainage 05050002	28	23	0.29	132.68
James	49	249	0.29	2,345.95
James coastal plain	49	36	0.28	362.15
Subdrainage 02080206	48	33	0.27	322.13
Order 3	30	13	0.26	95.42
Order 4	10	10	0.22	34.48
Orders 5+6	37	13	0.08	58.90
James piedmont	64	140	0.32	2,007.92
Subdrainage 02080203	42	34	0.46	484.92
Subdrainage 02080204	40	21	0.52	326.71
Subdrainage 02080205	45	23	0.21	171.50
Subdrainage 02080206	29	17	0.19	86.56
Subdrainage 02080207	57	45	0.28	550.87
Order 3	50	38	0.29	384.50
Order 4	50	57	0.28	580.92
Orders 5+6	58	45	0.38	713.73
James valley and ridge	44	73	0.44	997.40
Subdrainage 02080201	44	64	0.44	848.48
Order 3	31	18	0.42	172.32
Order 4	36	29	0.42	332.17
Orders 5+6	40	26	0.39	280.64
Rappahannock	56	147	0.23	1,219.15
Rappahannock coastal plain	44	57	0.19	307.70
Subdrainage 02080104	36	24	0.24	147.35
Order 3	25	21	0.18	80.58
Order 4	40	23	0.24	156.31
Order 5+6	31	12	0.09	49.07 ^a
Rappahannock piedmont	50	93	0.30	919.97
Subdrainage 02080103	35	43	0.31	352.27
Subdrainage 02080105	38	16	0.25	120.48
Subdrainage 02080106	43	28	0.23	242.93
Order 3	34	24	0.32	180.13
Order 4	45	30	0.33	335.83
Order 5+6	45	39	0.31	404.79

Cochran's *Q* is a nonparametric test of related observations (Conover 1980), distributed as χ^2 with Species-1 df. All *Q* statistics are significant at $P \leq 0.01$ except those marked with an "a"

Table 2 Results of *z* tests for pair-wise regional comparisons of nestedness in native stream fish assemblages

Larger region	Subregion	<i>z</i> score	<i>P</i>
Individual river drainages vs. all drainages combined			
All drainages	Potomac	18.75	<0.001
All drainages	Chowan	49.09	<0.001
All drainages	New	17.45	<0.001
All drainages	Clinch	6.10	<0.001
All drainages	Roanoke	142.03	<0.001
All drainages	James	49.83	<0.001
All drainages	Rappahannock	-2.02	0.022
Physiographic provinces within drainages vs. whole drainages			
James	Coastal plain	-2.14	0.016
James	Piedmont	13.07	<0.001
James	Valley and ridge	33.71	<0.001
Rappahannock	Coastal plain	-6.08	<0.001
Rappahannock	Piedmont	17.51	<0.001
Subdrainages with drainage/province regions vs. drainage/province regions			
Potomac valley and ridge	02070005	-0.29	0.390
Potomac valley and ridge	02070006	5.35	<0.001
Chowan coastal plain	03010202	2.35	0.009
New valley and ridge	05050001	-1.77	0.038
New valley and ridge	05050002	5.05	<0.001
Roanoke piedmont	03010101	0.27	0.394
Roanoke piedmont	03010102	6.58	<0.001
Roanoke piedmont	03010103	-16.91	<0.001
Roanoke piedmont	03010104	15.35	<0.001
Roanoke piedmont	03010105	4.77	<0.001
James coastal plain	02080206	0.33	0.371
James piedmont	02080203	-14.58	<0.001
James piedmont	02080204	-12.74	<0.001
James piedmont	02080205	7.18	<0.001
James piedmont	02080206	5.45	<0.001
James piedmont	02080207	6.12	<0.001
James valley and ridge	02080201	0.42	0.337
Rappahannock coastal plain	02080104	-3.12	0.001
Rappahannock piedmont	02080103	-5.74	<0.001
Rappahannock piedmont	02080105	2.35	0.010
Rappahannock piedmont	02080106	1.97	0.024

P is the one-tailed probability that *C* of the subregion is larger than *C* of the larger region. Non-negative *z* scores indicate that the subregion was more nested. The values in *bold* indicate that the subregion was significantly more nested

Discussion

Spatial relationships

Our results suggest that nestedness is a prevalent and significant feature of Virginia stream fish assemblages and exhibits a great deal of variation with spatial scale and among regions. Few studies have specifically examined the effects of spatial scale on patterns of nestedness. An exception is Patterson and Brown (1991), who analyzed assemblages of granivorous rodents in four major deserts of the American southwest. Their results were mixed (i.e.,

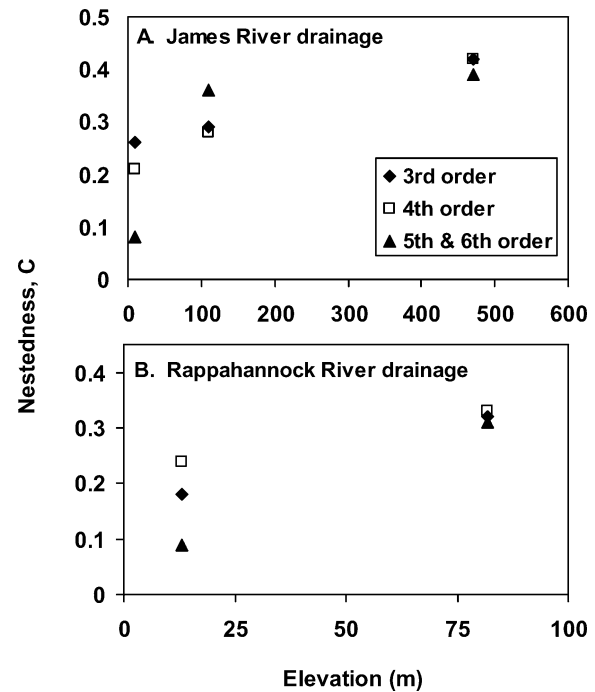


Fig. 4a, b Nestedness (*C*) of native stream fish assemblages versus mean elevation of collection sites in the coastal plain, piedmont, and valley and ridge provinces of **a** the James River and **b** the Rappahannock River drainages in Virginia. *Filled diamond* third-order streams, *open square* fourth-order streams, *filled triangle* fifth- + sixth-order streams. Symbols for third- and fourth-order streams overlap at the highest elevation in the James drainage

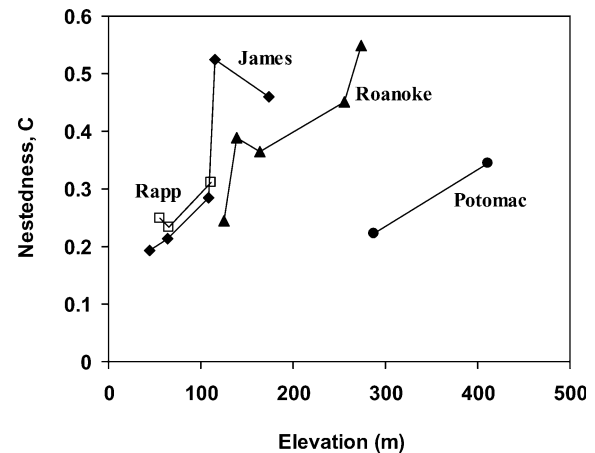


Fig. 5 Nestedness (*C*) of native stream fish assemblages versus mean elevation of subdrainages in four drainage/physiographic regions of Virginia. *Filled diamond* James piedmont; *open square* Rappahannock piedmont; *filled triangle* Roanoke piedmont; *filled circle* Potomac valley and ridge. *Lines* are drawn for visual clarity and do not represent a continuous relationship between symbols

some regions exhibited nestedness, others did not), possibly because, as the authors suggested, it was difficult to identify historically and ecologically-relevant boundaries for the regions studied. By contrast, we found nestedness to be clearly related to the spatial extent of the regions sampled, except at the subdrainage (smallest) level. Possibly, these patterns were apparent in the stream

fish assemblages we examined because regions representing relatively homogeneous areas (e.g., similar climate, topography, flow regime, physicochemical properties) with ecologically relevant boundaries are fairly easy to identify in stream systems (Angermeier and Winston 1998). Drainage basins represented the highest level of organization in our spatial hierarchy and faunas within them share a similar zoogeographic history. In areas with substantial topographic relief, drainage boundaries prevent dispersal by most fish species. Consequently, drainage basin faunas are often evolutionarily distinctive (Hocutt and Wiley 1986). Within drainages, physiographic regions differ substantially in topography, channel morphology, flow regime, and disturbance patterns (Swanson et al. 1988). Assemblages within these regions are distinctive in their composition (Angermeier and Winston 1999) and the greater nestedness observed at this level probably reflects the greater ecological homogeneity compared with whole drainages.

Contrary to expectation, subdrainage assemblages were not generally more nested than those of drainage/physiographic regions. This is possibly due to the fact that many subdrainages, as defined by the NHD, are not distinct watersheds. The rules for delineating subdrainages do not emphasize differences in geomorphology, land cover, or biotic composition. Rather, subdrainage boundaries largely reflect confluences of large tributaries to previously defined mainstem rivers. Thus, subdrainages may combine portions of watersheds that differ substantially in the processes controlling the abundance and distribution of species, which in turn could undermine nestedness. Consequently, NHD subdrainages are less likely to represent biologically meaningful regions than those defined by drainages and/or physiography. Another possibility is that the lack of independence between data sets makes differences in nestedness between regions more difficult to detect, especially where subdrainages make up a large portion of drainage/physiographic regions. Eight of 12 subdrainages that were not significantly more nested than their drainage/physiographic regions made up 30% or more of the larger regions, in terms of the number of collections. The mean for all subdrainages was 36%. By contrast, none of the drainage/physiographic regions represented more than 20% of the statewide (largest) region and the mean was only 10%.

Mechanisms

Nestedness arises when a gradient in species traits is juxtaposed on an important environmental gradient. Thus, nestedness requires both a broad range of species tolerances and a broad range of ambient states for limiting factors (Fig. 1). The former is a function of species richness and interspecific variation, while the latter is a function of spatial heterogeneity in the region of interest. The species available to inhabit a locality must differ considerably in colonization ability, vulnerability to extinction, or sensitivity to environmental factors regulat-

ing occurrence. The array of localities comprising the environmental gradient can differ in a broad range of factors, including size of habitat patch, distance between suitable patches, frequency or severity of disturbance (e.g., floods or droughts), predation intensity, food availability, and physicochemical conditions (e.g., temperature). In real landscapes, these factors are often spatially correlated, and simple descriptors such as elevation may be useful surrogates for representing important (but perhaps unknown) factors that regulate community structure. For example, elevation is strongly and widely correlated with stream temperature, which is a major determinant of fish distribution (Hynes 1970; Rahel and Hubert 1991; Matthews 1998). In Virginia, physiographic provinces also differ in water chemistry, stream-channel morphology, and hydrology (Jenkins and Burkhead 1994). Steeper elevation gradients in the higher provinces may be associated with greater variation in these features as well. For example, Herlihy et al. (1998) reported differences in nutrient concentrations between “ridge” and “valley” streams in the mid-Atlantic highlands, which include our valley and ridge streams.

Although we lack the data to differentiate directly between the various mechanisms that potentially organize Virginia’s fish communities, we can draw some inferences. Theory predicts that extinctions are more frequent in temporally variable environments (e.g., Quinn and Hastings 1987). Taylor and Warren (2001) observed a correlation between strength of nestedness among fish species assemblages and both stream size and flow variation in two Arkansas mountain river drainages. Specifically, smaller stream size and greater variability in flow (both characteristics of upstream localities) were associated with higher extinction rates and greater nestedness compared with downstream areas. In Virginia, nestedness is higher in regions with higher mean elevations and steeper elevational gradients. If these areas are also characterized by greater variation in flow and less stable communities, then extinction dynamics might also explain the patterns we observed.

We explored the potential for an extinction-based explanation of our results using two post hoc analyses. First, we assessed whether variation in stream flow rates increased with elevation in Virginia streams, and secondly, whether inter-annual variation in fish community composition increased with elevation, using data from sites that had been sampled similarly in multiple years. Greater rates of species turnover in the higher-elevation valley and ridge province, for example, would indicate that local extinctions were more frequent there.

In the first analysis, we examined the coefficient of variation in daily mean flows at 30 United States Geological Survey (1980) gauging stations at elevations ranging from 6 to 1,704 m (mean=620 m), with stream flow records exceeding 15 years. We found no correlation between variation in daily flow rate and elevation ($r=0.161$, $P=0.404$).

In the second, we examined five data sets comprising 87 collection sites from North Carolina, Virginia, and Mary-

land. Each site was sampled twice by electrofishing between 1991 and 2000. Most collections were a year apart, although some (from Maryland) were three to five years apart. We measured species turnover (between years at a site) with Jaccard's index (J) of species similarity, based on presence/absence. Analysis of variance on fish collections separated by 1–3 years ($n=66$), and 3–5 years ($n=26$; Maryland data only) revealed similar rates of species turnover in the valley and ridge and coastal plain (J was higher in the valley and ridge but not significantly so; $P=0.11$ – 0.84). However, variances in turnover were consistently greater in the valley and ridge than in the coastal plain, especially for collections separated by 3–5 years.

In summary, our findings do not support the hypothesis that extinction/colonization dynamics drive patterns of nestedness in fish assemblages at regional levels. Virginia streams do not appear to exhibit greater variability in flow rates at higher elevations, and there was no evidence that montane assemblages are more annually variable or experience greater rates of extinction than those in the coastal plain. If anything, montane assemblages appeared more stable. The high variance we observed in species turnover of montane assemblages, however, suggests that extinction/colonization dynamics are important at some localities (those with high turnover). Although extinction rates may be great enough in some localities and systems to control nested subset patterns, we suggest that such high rates are not pervasive enough across entire regions of Virginia to account for large-scale patterns of nestedness.

Rather, it seems more likely that the strong correlations we observed between nestedness and elevation reflect correlations between elevation and environmental factors that regulate fish species occurrence, including temperature, productivity, habitat structure, predation pressure, variability in stream flow, and others. Thus, nestedness in Virginia stream fish assemblages is associated with elevation indirectly, through the influences of various environmental factors on fish species distribution. In streams, we generally expect extinction and colonization dynamics to drive nested subset patterns in regions where (1) harsh environmental conditions are pervasive, (2) severe disturbances are common, or (3) dispersal is severely constrained. These conditions are generally associated with patterns of extreme variation in stream flow. Our results suggest that environmental gradients can drive nestedness in any region exhibiting substantial environmental heterogeneity. Since variability in flow is only one of the factors influencing the distribution of streamfishes, extinction/colonization dynamics may be viewed as only one of a number of processes that influence patterns of nestedness in these assemblages.

Our results fit well into the conceptual model for nested subset patterns developed by Patterson and Brown (1991) and later elaborated on by Wright et al. (1998). These authors describe homogeneity as important in the broad sense in that it reduces variation in environmental and historical factors that influence regional species pools. In addition, they observed that nestedness requires a

hierarchical relationship among species, or heterogeneity of species characteristics that determine patterns of local occurrence. Factors that generate nestedness were viewed as filters which restrict species occurrence via characteristics of the species and their habitats. Although not explicitly stated by these authors, we believe it is helpful to view the spatial distribution of filters as a form of environmental heterogeneity (Fig. 1), particularly because environmental gradients are pervasive in continental regions and capable of generating nested subset patterns over habitats that are generally viewed as continuous. This type of environmental heterogeneity does not affect the composition of regional species pools, only how species assemblages are built from them.

This point of view helps us interpret the seeming paradox observed in our results, that nestedness *decreased* as regional extent (and environmental heterogeneity) increased, but *increased* as elevation (and environmental heterogeneity) increased. We suggest that these contrasting patterns reflect different degrees of spatial correlation in limiting factors (or filters) between horizontal and vertical dimensions. As regions expand horizontally, they typically encompass new areas with different limiting factors. An idealized region might be viewed as a mosaic of locally limiting factors with little spatial order. Such unordered heterogeneity undermines nestedness, although these effects may not be measurable unless the region is large enough to incorporate multiple species pools. In contrast, vertical (elevational) expansion of regions is associated with increasing environmental heterogeneity that is ordered in space. Several important limiting factors (e.g., temperature, productivity, hydrology, predation pressure) are strongly correlated with elevation, and overwhelm the effect of unordered mosaics on nestedness. In a sense, nestedness of stream fish assemblages may be stronger in regions exhibiting greater topographic relief for the same reason that it is stronger in smaller, ecologically well-defined regions: elevational gradients and smaller regions effectively reduce the number of environmental factors that limit species distribution. We would expect horizontal expansion of regions also to enhance nestedness if expansion occurred along an important environmental gradient. This notion might be testable in areas with strong latitudinal or longitudinal gradients in natural (e.g., aridity) or anthropogenic (e.g., toxicity) factors.

Conclusions

Nested occurrence of species is a pervasive feature of fish assemblages in Virginia streams, but the ecological insight provided by documenting these patterns remains obscure. Nestedness arises not only in systems with prominent extinction/colonization dynamics (e.g., streams prone to drying) but also along gradients in environmental factors that regulate species occurrence. We suspect that the latter situation makes nestedness a common feature of many systems and taxa, as gradients in temperature, rainfall, soil chemistry, and numerous other factors are common.

Human activity, involving the construction of dams or water diversion projects, can alter in-stream gradients, either weakening or strengthening inherent patterns of nestedness. Additional gradients are incidentally created by things such as chemical and thermal pollution as well. To the degree that nested patterns are strong and our understanding of their causes is solid, it may be possible to predict the effects of anthropogenic stressors such as habitat fragmentation, streamflow alteration, and pollution on local community assemblages. Conversely, this information could aid in predicting the outcome of conservation efforts such as habitat restoration or species reintroductions.

Although the levels of nestedness measured from our data set were not high compared with those of some other studies (e.g., Patterson and Atmar 1986; Wright and Reeves 1992; Cook and Quinn 1995), possibly for the reasons described in the Materials and methods section, we were able to demonstrate that the composition of local assemblages was more regular, and therefore perhaps more predictable, in streams within regions of higher elevation and greater topographic relief. This kind of information may be of value in deciding, for example, where areas designed to protect certain species or assemblages might best be located. By contrast, assemblage structure became less predictable over broader spatial scales. Thus, for large regions, greater efficiency in monitoring and conservation efforts may be possible by considering alternative mechanisms that structure assemblages. For example, where extinction/colonization dynamics are predominant, we might anticipate more species absences from locations with suitable habitats, adjust the monitoring scheme accordingly, and include unoccupied suitable locations in conservation plans. Alternatively, where assemblages are highly structured by particular environmental gradients, it might be more appropriate to locate conservation and monitoring efforts along those gradients.

Acknowledgments We thank Lenwood Hall (University of Maryland), Paul Kazyak (Maryland Department of Natural Resources), Peter Ruhl (United States Geological Survey), and Vann Stancil (Virginia Polytechnic and State University) for providing data to examine inter-annual variation in fish community composition. Two anonymous reviewers provided comments that significantly improved an earlier version of this manuscript. K.L. Krueger was supported partly by a Federal Aid grant from the Virginia Department of Game and Inland Fisheries.

References

- Angermeier PL, Schlosser IJ (1989) Species-area relationships for stream fishes. *Ecology* 70:1450–1462
- Angermeier PL, Winston MR (1998) Local vs. regional influences of local diversity in stream fish communities of Virginia. *Ecology* 79:911–927
- Angermeier PL, Winston MR (1999) Characterizing fish community diversity across Virginia landscapes: prerequisite for conservation. *Ecol Appl* 9:335–349
- Bolger DT, Alberts AC, Soulé ME (1991) Occurrence patterns of bird species in habitat fragments: sampling, extinctions, and nested species subsets. *Am Nat* 137:155–166
- Burton GW, Odum EP (1945) The distribution of stream fish in the vicinity of Mountain Lake, Virginia. *Ecology* 26:182–194
- Butaye J, Jacquemyn H, Hermy M (2001) Differential colonization causing non-random forest plant community structure in a fragmented agricultural landscape. *Ecography* 24:369–380
- Calmé S, Desrochers A (1999) Nested bird and micro-habitat assemblages in a peatland archipelago. *Oecologia* 118:361–370
- Conover WJ (1980) Practical nonparametric statistics, 2nd edn. Wiley, New York
- Cook RR (1995) The relationship between nested subsets, habitat subdivision, and species diversity. *Oecologia* 101:204–210
- Cook RR, Quinn JF (1995) The influence of colonization in nested species subsets. *Oecologia* 102:413–424
- Frissell CA, Liss WA, Warren CE, Hurlley MD (1986) A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environ Manage* 10:199–214
- Gaston K (2000) Global patterns in biodiversity. *Nature* 405:220–227
- Herlihy AT, Stoddard JL, Johnson CB (1998) The relationship between stream chemistry and watershed land cover data in the mid-Atlantic region, US. *Water Air Soil Pollut* 105:377–386
- Hocutt CH, Wiley EO (1986) The zoogeography of North American freshwater fishes. Wiley, New York
- Horwitz RJ (1978) Temporal variability patterns and the distributional patterns of stream fishes. *Ecol Monogr* 48:307–321
- Hubbell SP (2001) The unified theory of biodiversity and biogeography. Princeton University Press, Princeton
- Hynes HBN (1970) The ecology of running waters. University of Toronto Press, Toronto
- Imhoff JG, Fitzgibbon J, Annable WK (1996) A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. *Can J Fish Aquat Sci* 53:312–326
- Jenkins RE, Burkhead NM (1994) Freshwater fishes of Virginia. American Fisheries Society, Bethesda
- Kadmon R (1995) Nested species subsets and geographic isolation: a case study. *Ecology* 76:458–465
- Kodric-Brown A, Brown JH (1993) Highly structured fish communities in Australian desert springs. *Ecology* 74:1847–1855
- Matthews WJ (1998) Patterns in freshwater fish ecology. Chapman and Hall, New York
- Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of community structure. *Trends Ecol Evol* 5:46–47
- Patterson BD (1987) The principle of nested subsets and its implications for biological conservation. *Conserv Biol* 1:247–293
- Patterson BD, Atmar W (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol J Linn Soc* 28:65–82
- Patterson BD, Brown JH (1991) Regionally nested patterns of species composition in grainivorous rodent assemblages. *Biogeography* 18:395–402
- Poff NL (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J North Am Benthol Soc* 16:391–409
- Quinn JF, Hastings A (1987) Extinction in subdivided habitats. *Conserv Biol* 1:198–208
- Rahel FJ, Hubert WA (1991) Fish assemblages and habitat gradients in a Rocky Mountain—Great Plains stream: biotic zonation and additive patterns of community change. *Trans Am Fish Soc* 120:319–332
- Ricklefs RE, Schluter D (1993) Species diversity: regional and historic influences. In: Ricklefs RE, Schluter D (eds) Species diversity in ecological communities: historical and geographic perspectives. University of Chicago Press, Chicago, pp 350–363
- Schlosser IJ (1987) A conceptual framework for fish communities in small warmwater streams. In: Matthews WJ, Heins DC (eds) Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, Oklahoma, pp 17–28

- Schlösser IJ (1991) Stream fish ecology: a landscape perspective. *BioScience* 41:704–712
- Sheldon AL (1968) Species diversity and longitudinal succession in stream fishes. *Ecology* 49:193–198
- Strahler AN (1952) Hypsometric (area-altitude) analysis of erosional topography. *Bull Geol Soc Am* 63:1117–1142
- Swanson FJ, Krantz TK, Caine N, Woodmansee RG (1988) Landform effects on ecosystem processes and regional patterns. *Freshw Biol* 36:92–98
- Taylor CM (1997) Fish species richness and incidence patterns in isolated and connected stream pools: effects of pool volume and spatial position. *Oecologia* 110:560–566
- Taylor CM, Warren ML Jr (2001) Dynamics in species composition of stream fish assemblages: environmental variability and nested subsets. *Ecology* 82:2320–2330
- United States Environmental Protection Agency (1998) USEPA Office of Water, River Reach File 3 (RF3) Alpha for CONUS, Hawaii, Puerto Rico, and the US Virgin Islands. Edition 3 alpha
- United States Geological Survey (1980) Hydrologic Unit Map—1974; State of Virginia. US Geological Survey, Reston
- Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) The river continuum concept. *Can J Fish Aquat Sci* 37:130–137
- Wiens JA, Addicott JF, Case TJ, Diamond J (1986) Overview: the importance of spatial and temporal scale in ecological investigations. In: Diamond J, Case TJ (eds) *Community ecology*. Harper and Row, New York, pp 145–153
- Worthen WB, Carswell ML, Kelly KA (1996) Nested subset structure of larval mycophagous fly assemblages: nestedness in a non-island system. *Oecologia* 107:257–264
- Wright DH, Reeves J (1992) On the meaning and measurement of nestedness of species assemblages. *Oecologia* 92:416–428
- Wright DH, Patterson BD, Mikkelsen GM, Cutler A, Atmar W (1998) A comparative analysis of nested subset patterns of species composition. *Oecologia* 113:1–20