



Rashleigh
2008

Nestedness in riverine mussel communities: patterns across sites and fish hosts

Brenda Rashleigh

B. Rashleigh (rashleigh.brenda@epa.gov) U.S. Environmental Protection Agency, 960 College Station Road, Athens, GA 30605, USA.

The pattern of nestedness, where species present in depauperate locations are subsets of species present in locations with higher species diversity, is often found in ecological communities. Mussel communities examined in four rivers in the upper Tennessee River basin appeared significantly nested. Mussel species distributions were mostly unrelated to differences in immigration and only weakly related to downstream direction, giving some indication of structuring by differences in extinction. Mussel species distributions were not related to the number of fish species used as hosts for mussel larvae. Mussel species were more likely to overlap on common fish hosts; however, the host-use matrix was not nested – groups of mussel species used different sets of host fish species in a pattern that appeared phylogenetically related. Sites with high fish host abundance may support high mussel diversity by promoting the survival of mussel species that are less able to attract and infect hosts. Thus, nestedness in freshwater mussel communities may be driven by the array of host fish resources, combined with differences in species' abilities to use fish hosts. An understanding of the nested pattern in this region can aid conservation of this imperiled fauna.

The pattern of nestedness, where species present in depauperate assemblages are successive subsets of assemblages with higher species diversity, has been demonstrated for many ecological communities. The nested pattern was originally described in island biogeography to characterize the distribution of species across a set of islands (Atmar and Patterson 1993). This pattern has been observed in other ecological systems, such as mountain canyons (Fleishman et al. 2002), fragmented forest patches (Fischer and Lindenmayer 2005a), ponds (Baber et al. 2004), and streams (Cook et al. 2004). Nestedness has been found for such diverse taxa as plants (Wright and Reeves 1992), mycophagous fly communities (Worthen et al. 1998), invertebrates (McAbendroth et al. 2005), and amphibians (Ficetola and DeBernardi 2004). Nestedness has also been found for communities where a set of species interacts with another set of species, such as plant-animal mutualistic networks (Bascompte et al. 2003) and scavenger communities (Selva and Fortuna 2007).

Nestedness has received considerable interest in ecology because it may indicate the processes that are structuring communities (Wright et al. 1998). Nestedness across sites may be driven by differences in either immigration probabilities or extinction probabilities (Wright and Reeves 1992, Worthen 1996). Differences in immigration among species may promote nestedness due to the interaction of patch size and geographic isolation with differential dispersal properties of species; species with lower immigration probabilities are expected to be nested within the

distributions of species with higher immigration probabilities (Kadmon 1995).

Ficetola and DeBernardi (2004) found that nestedness for amphibians in northern Italy was driven by isolation effects, combined with difference in species mobility. Nestedness may result from species' differences in extinction probabilities, resulting from differences in species' environmental tolerances coupled with differences in patch size or quality (Wright et al. 1998). For example, McAbendroth et al. (2005) found that nestedness in pond macroinvertebrate assemblages was best explained by pond area, with habitat and isolation of secondary importance. An alternative explanation for nestedness is that species either have nested habitat requirements (Wright and Reeves 1992, Worthen 1996) or are responding to a nestedness of critical resources (Fleishman et al. 2002). Hylander et al. (2005) hypothesized that nestedness may occur due either to nested discrete habitats, or to nested habitat quality across sites, where species differ in specialization or tolerance.

Communities of freshwater mussels of the family Unionidae in rivers tend to be found across a series of patches that differ in the number of mussel species they support, and generally appear to be nested. Many North American rivers support high diversities of similar freshwater mussel species over long periods of time (Bates and Dennis 1978). Patches are connected in ecological time by dispersal of larvae, so it is possible that diversity reflects differences in immigration, where more isolated patches

support lower diversity. It is also possible that reduced extinction occurs on patches of higher quality, in terms of habitat and food; however, neither of these resources appears to be limiting to mussels (Fuller 1980, Strayer 1993). Reduced extinctions may also occur at sites that provide more stability (Schlosser 1987, Haag and Warren 1998).

Nestedness of freshwater mussel species may instead be influenced by their use of fish host resources. Virtually all North American freshwater mussel larvae (glochidia) are obligate parasites on fish for a period of weeks to months during recruitment. Larvae of a particular mussel species can only develop successfully on a subset of the fish species in a river. There are differences in mussel species' ability to attract and infect the hosts (Watters 1994). Mussel species diversity is often positively and significantly related to fish species diversity (Watters 1992), and fish communities are often nested (Taylor and Warren 2001, Cook et al. 2004). The patterns in the fish communities, coupled with differences in host use among mussel species, could generate nestedness in mussel communities.

Here, I examined riverine mussel communities previously sampled from four rivers in the Upper Tennessee River watershed for significant nestedness. The roles of immigration, extinction, and fish host resources in driving the pattern of nestedness in mussels were then considered. The pattern of nestedness can support the selection of sites and species for conservation and protection (Kerr et al. 2000, Baber et al. 2004). This is particularly important for the Tennessee River Basin, which is among the most diverse regions for freshwater mussels in the world. Environmental constraints such as human land use, pollution, and toxic spills may further impact all of the mussel species, as well as the host fish, in the upper Tennessee River watershed (Neves and Angermeier 1990). A better understanding of how these communities are structured can inform conservation activities for mussel species in this region.

Methods

Detection of nested pattern across sites

Nestedness was examined for rivers in the Tennessee River basin using mussel survey data taken from the Cumberlandian Mollusk Conservation Program, one of the most comprehensive surveys for freshwater mussels ever conducted (Ahlstedt 1986). The Tennessee Valley Authority conducted a longitudinal survey of the mainstems of nine rivers in 1979–1980; the four Upper Tennessee rivers with ≥ 20 sites containing mussels were included in this analysis (Fig. 1). The Tennessee Valley Authority identified mussel beds with best professional judgment and sampled each mussel bed encountered with a sampling effort standardized by time at each mussel bed. They used a combination of techniques, including snorkeling, scuba diving, raking, and examination of muskrat middens. Free-flowing river reaches were selected for this analysis, in order to assume that all species had access to all sites. Clinch, Powell, and Copper were free-flowing through the survey reach, but the Nolichucky River has a dam located 12.2 km above the river mouth, so two sites located below this dam were dropped from this analysis. The numbers of sites containing mussels and the number of mussel species for each river are given in Table 1.

Nestedness was tested with the BINMAT program of Rodríguez-Gironés and Santamaría (2006), using recommended parameters. The BINMAT program arranges the matrix to maximal nestedness by reordering the rows and columns to minimize unexpected presences and absences, then uses the formula of Atmar and Patterson (1993) to calculate a matrix "temperature" (T_{obs} , observed temperature) normalized to a scale of 0–100, with 100 being maximally disordered (non-nested). The observed temperature (T_{obs}) was compared to the temperature predicted by 1000 simulations of null model 3 (T_{null}) to assess the

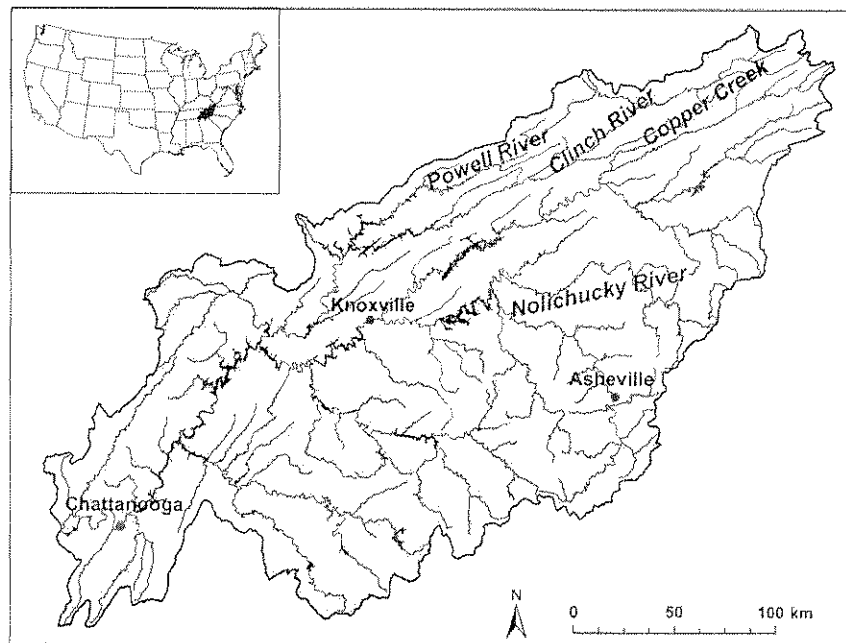


Figure 1. Location and map of the upper Tennessee River basin-labeled rivers were sampled longitudinally for freshwater mussels.

Table 1. Freshwater mussel data summary for four rivers in the Tennessee River Valley (Ahlstedt 1986); results from nestedness analysis using BIMNAT (Rodríguez-Gironés and Santamaría 2006); and the spatial correlation approach of Hausdorf and Hennig (2007).

	Copper Creek	Nolichucky River	Powell River	Clinch River
River kilometers sampled	85.3	57.9	164.2	278.4
Number of sites with mussels present (total number of sites)	36 (36)	38 (39)	73 (78)	135 (141)
Total number of mussel species	19	21	35	43
Number of fish species reported for river	43	38	51	61
T _{obs} , observed nestedness temperature (% matrix fill)	7.2 (26%)	11.1 (24%)	10.8 (24%)	14.6 (29%)
T _{null} , average temperature from BINMAT null model 3 (variance over 1000 runs)	30.1 (16.2)	30.0 (12.4)	38.6 (4.5)	48.7 (2.7)
Probability of generating T _{obs} from BINMAT null model 3	p < 0.0001	p < 0.0001	p < 0.0001	p < 0.0001
p-value considering spatial autocorrelation (1000 runs)	p = 0.01098	p = 0.06993	p = 0.04995	p = 0.01298

significance of the nestedness pattern. This null model, which fixes both row and column totals, has been shown by Ulrich and Gotelli (2007) to have excellent properties for avoiding type 1 errors.

Leibold and Mikkelsen (2002) found that nestedness metrics could not distinguish nestedness from patterns of species turnover in communities, and may therefore be misleading. Thus, in addition to examining nestedness, the mussel presence-absence matrix for each river in this study was examined with ordination by reciprocal averaging (RA) in PC-Ord software, ver. 4.0 (McCune and Medford 1999). Reciprocal averaging orders the matrix so that sites with the most similar species compositions and species with the most similar distributions are close to each other. Leibold and Mikkelsen (2002) have found that the ordered matrix can be examined visually for patterns that indicate nestedness (upper right triangular matrix) as opposed to species turnover (occurrences along the diagonal with absences in both corners of the matrix). Matrices were also investigated visually for clumped boundaries, which would indicate that discrete assemblages are replacing each other with little overlap among them (Leibold and Mikkelsen 2002). Strong indications of turnover or clumped boundaries would suggest non-nestedness even if nestedness tests were significant.

Hausdorf and Hennig (2007) found that spatial autocorrelation can drive nestedness, and that nestedness may be a rare pattern when the spatial autocorrelation of sites is taken into account. They developed a test statistic that was used here to test for nestedness of the presence/absence matrix with the constraint of spatial structure. For this test, the user specifies a neighborhood table indicating which sites are geographical neighbors, and the null model is generated based on the probability of a species occurring at a site and the probability of a species occurring on a non-neighboring site. The prabclus package (prabtest routine) in the statistical software R was run with default parameters to perform a parametric bootstrap test for nestedness. A significant result for this test indicates that significant nestedness was detected in the matrix in comparison to the null model constrained by spatial autocorrelation.

Two additional considerations are needed if the nestedness pattern is to be used to inform conservation and support the protection of species-rich sites and rare species: whether rare species deviate from the overall nested pattern (Fischer and Lindenmayer 2005b), and if the most species-rich sites have small populations of all species and might therefore not be the best conservation choice (Hylander et al. 2005). To test whether rare species deviate from the

nested pattern, I used the approach of Fischer and Lindenmayer (2005b), who determined the percentage of largest patches required to capture 80% of the sensitive bird species at least once in their Australian study area. Here, I determined the percentage of the most diverse sites needed to capture 80% of the mussel species considered threatened/endangered (Williams et al. 1992) at least once. In order to test whether most species-rich sites have small populations of all species, mussel species richness was correlated with average abundance of mussels per site for each river.

Mechanisms behind nestedness

The roles of differences in mussel species' immigration and extinction probabilities in generating nestedness were examined with Pearson correlation. The role of differences in immigration was examined through a regression of the isolation of patches to the mussel diversity of patches. Isolation was calculated as the average distance to the two neighboring patches, or the distance to the nearest patch for patches at either end of the sampled river reach. This correlation would be negative if isolated patches were less diverse due to reduced immigration. The role of differences in extinction for generating nestedness was examined through a regression of mussel diversity to downstream river kilometer. This assumes that extinction is reduced on the larger downstream patches, leading to higher diversity (Schlosser 1987). Spatial locations for the sites were taken from Ahlstedt (1986).

Next, the role of fish host resources in generating nestedness was considered. A fish host-use matrix was compiled for the set of mussel species across the set of four rivers together, since all of the mussel species found in the Upper Tennessee river basin occurred in the most diverse river – Clinch River – except for *Quadrula intermedia*, found only in the Powell River, and *Alamidonta viridis*, found only in Copper Creek. Host-use information was taken mainly from the Ohio State Univ. Mussel/Host Database <<http://128.146.250.235/MusselHost>> Watters (1994), but also from O'Brien and Lytle (2004) and Culp et al. (2006). Five mussel species had no known fish hosts, so they were left out of this analysis: *Fusconaia barnesiana*, *F. subrotunda*, *Cumberlandia mondonata*, *Quadrula sparsa*, *Pleurobema plenum*. The list of fish hosts was limited to fish species found in the four rivers during sampling for the Cumberlandian Mollusk Conservation Program (Barr et al. 1993–1994, pp. 172–174). Four additional mussel species

(*Elliptio crassidens*, *Leptodea fragilis*, *Potamilus alatus*, *Truncilla truncata*) had no known hosts within the set of fishes collected in the rivers and were dropped, which resulted in a total of 36 species of mussels considered.

Once the host-use matrix was compiled, the number of fish hosts per mussel species was related to the number of sites where each mussel species was found (summed across all four rivers), to test whether rare mussel species were more specialized in their use of fish hosts. Also, the distributions of hosts and non-hosts were compared, in order to assess whether mussel species were preferentially using common or rare hosts. The host-use matrix was then tested for nestedness as described above for the mussel species-sites matrices, using the BINMAT null model 3, and examined for turnover and clumping using reciprocal averaging. Initial analysis of the matrix indicated phylogenetic relationships among mussels and fish, so in order to examine these patterns, mussel species were identified by tribe (Graf and Cummings 2006) and fish species were identified by family. The ECOSIM software (Gotelli and Entsminger 2001) was used with default options to assess niche overlap among species, to better characterize the use of fish host resources.

Results

Detection of nested pattern

Mussel communities in four rivers of the upper Tennessee River basin appeared to be significantly nested (Table 1, Fig. 2). Nestedness was indicated by the finding that the observed temperatures (T_{obs}) were significantly lower ($p < 0.0001$) than the temperatures from the BINMAT null model 3 (T_{null}). When spatial autocorrelation was considered with the approach of Hausdorf and Hennig (2007), all of the sites except Nolichucky River showed significant nestedness (Table 1). A significant result from this test indicated that the nested pattern was not the result of spatial autocorrelation.

Matrices ordered by reciprocal averaging appeared more consistent with a pattern of true nestedness, where matrices are upper triangular, rather than turnover, where species occurrences are found along the diagonal (Fig. 3). Only the Nolichucky River gave some indication of turnover, where four species along right side of matrix occurred at separate sites from some of the other species. In each river, ordination by reciprocal averaging indicated a dominant gradient—first and second eigenvalues are as follows: Copper (0.41, 0.35), Nolichucky (0.47, 0.31), Powell (0.35, 0.25), and Clinch (0.21, 0.14). The correlation of RA sites scores with mussel species richness was significant for three of the four rivers (Table 2), indicating that for these rivers, richness was the dominant gradient in the fauna.

Rare species followed the nested pattern for Copper Creek and the Powell and Clinch Rivers, where 80% of the threatened/endangered species could be captured at least once in <3% of the most diverse sites. For the Nolichucky River, however, 29% of the most diverse sites were needed to capture 80% of the threatened/endangered species. In a similar study on birds, Fischer and Lindenmayer (2005b) found that 25% of their sites were required to capture 80%

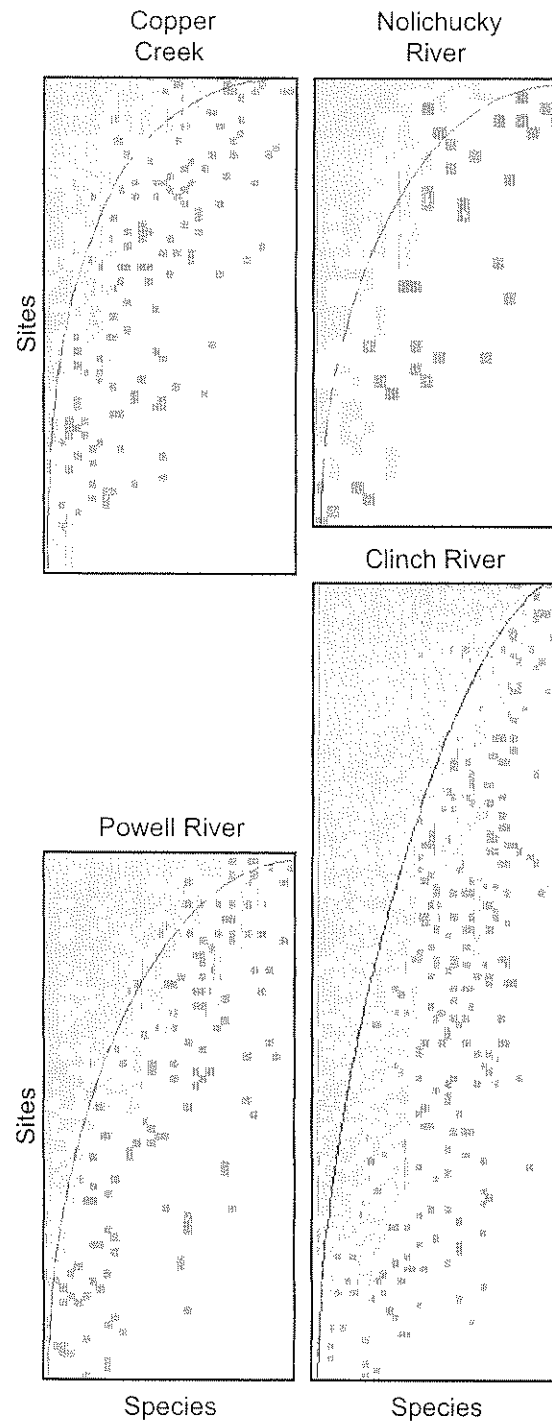


Figure 2. Matrices of sites by mussel species for each river, where a filled-square indicates that a particular mussel species was recorded at that site. The matrices are sorted to minimize unexpected presences and absences. The curved lines represent isoclines of perfect nestedness.

of the rare species, and they considered this a weak result, so the Nolichucky result can be considered weak as well. In the Nolichucky River, the three rarest species — *Epioblasma capsaeformis*, *Lasmigona costata*, and *Truncilla truncata* — each occurred at a single site that did not conform to the nestedness pattern.

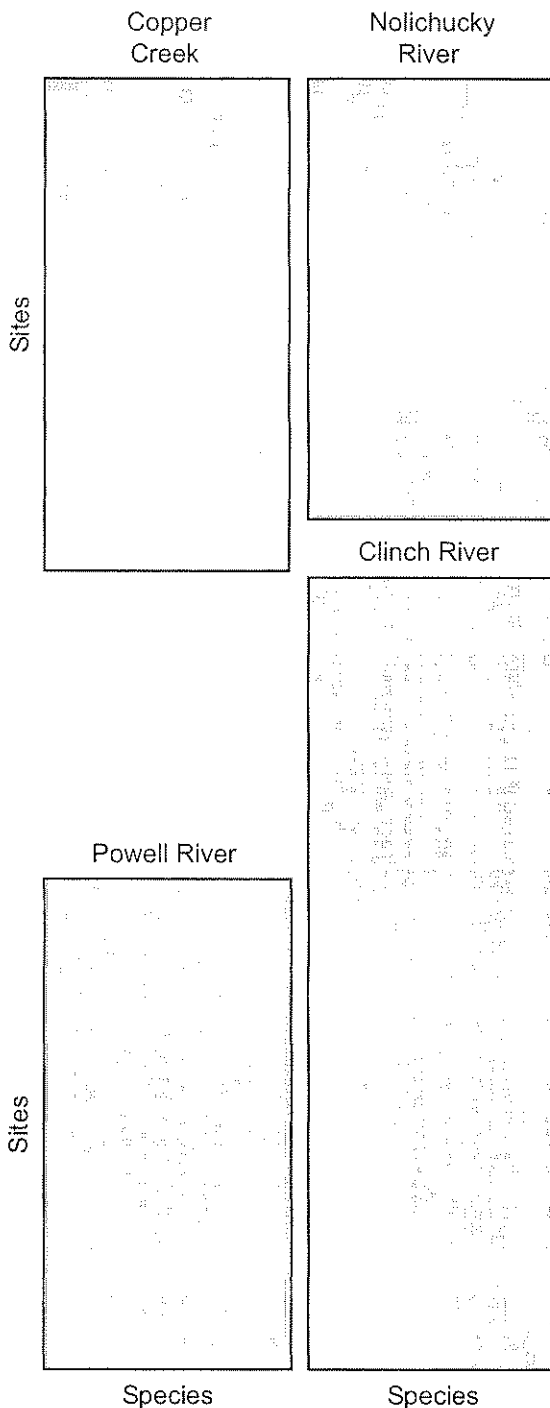


Figure 3. Matrices of sites and mussel species sorted by the scores of the first ordination axis in reciprocal averaging. These matrices tend to exhibit nestedness (upper right triangular) as opposed to turnover (species occurrences only along the diagonal), except for the Nolichucky River.

More diverse sites tend to support significantly higher, rather than lower, average abundance of mussels, as shown by significant positive relationships between diversity and average abundance for three of the four rivers (Table 2). That is, species-rich sites have larger populations, and are therefore useful conservation targets.

Mechanisms behind nestedness

Correlation of mussel diversity with isolation was only significant for Copper Creek (Table 2). This correlation was negative, as would be expected if isolated patches were less diverse due to reduced immigration. All of the correlations of mussel diversity with river kilometer were significant and negative, indicating that mussel diversity decreases with distance upstream (Table 2). These correlation coefficients were moderate, with absolute values in the range of 0.29–0.44.

There was no relationship between the number of sites at which a mussel species was found (summed across the four rivers) and the number of hosts used by that mussel species ($r^2 = 0.005$). That is, rare mussel species do not use fewer fish hosts than common mussel species. Only 49 of the 72 fish species collected in the four rivers were used as hosts. It appeared that most mussel species use common fish hosts: the fish species used as hosts were more widely distributed across the four rivers (mean of 3.0 rivers) than the fish species that were not used as hosts (mean of 2.0 rivers, $F = 11.4$, $Pr > F 0.0012$).

The host-mussel matrix was significantly nested using BINMAT null model 3 ($T_{obs} = 10.3$, $T_{null} = 16.7$, $p = 0.0010$, Fig. 4a). However, the ordination analysis shows definite indication of both turnover and clumping, as described by Leibold and Mikkelson (2002) (Fig. 4b, $\lambda_1 = 0.87$). In this figure, three clumps, or groups, can be separated visually. The first 11 mussel species form an upper left group that includes species from all of the mussel tribes using several fish families – predominantly Centrarchidae, Ictaluridae, and Catostomatidae – as hosts. The next 13 mussel species form a center group dominated by the Pleurobemini mussel tribe (54%) using Cyprinidae fish hosts (74%). The group on the bottom right is predominantly the Lampsilini mussel tribe (91%) using Percidae fish hosts (92%).

ECOSIM indicated that there was significantly more niche overlap in the host-use matrix than expected ($p < 0.0001$), but significantly lower overlap in host use among the three groups in Fig. 4b than expected by chance ($p < 0.0001$). There was no difference in the mean number of sites occupied by mussel species in these three groups shown in Fig. 4b ($F = 2.45$, $p = 0.1015$), but there is a difference in conservation status: the center and lower right groups contain significantly more threatened/ endangered mussel species than the upper left group ($F = 9.3$, $p = 0.0006$).

Discussion

The finding of significant nestedness in mussel communities is not surprising; nestedness is often found in nature (Wright et al. 1998). Only one other study has examined nestedness in freshwater mussels: Vaughn and Taylor (1999) tested for nestedness of freshwater mussel communities in two sections of an Oklahoma river downstream of a dam, and they found nestedness in the section directly below the dam but not in the section further downstream. Layzer and Madison (1995) found that the numbers of most mussel species in 23 sites along Horse Lick Creek in

Table 2. Results from selected correlations for four rivers in the Upper Tennessee River basin.

Pearson correlations	Copper Creek (n = 36)	Nolichucky River (n = 38)	Powell River (n = 73)	Clinch River (n = 135)
Reciprocal averaging site scores and mussel species richness	r = 0.55 p = 0.0005	r = 0.06 p = 0.7272	r = 0.34 p = 0.0034	r = 0.24 p = 0.0045
Site species richness and average abundance	r = -0.05 p = 0.7570	r = 0.48 p = 0.0024	r = 0.37 p = 0.0015	r = 0.38 p < 0.0001
Site isolation and mussel species richness	r = -0.33 p = 0.0490	r = 0.09 p = 0.5807	r = -0.02 p = 0.8024	r = -0.17 p = 0.0513
Site location (river km upstream of confluence) and mussel species richness	r = -0.44 p = 0.0077	r = -0.33 p = 0.0403	r = -0.25 p = 0.0326	r = -0.29 p = 0.0008

Kentucky were positively correlated with each other. Nested patterns have also been identified in communities of freshwater fish (Taylor and Warren 2001, Cook et al.

2004). Taylor and Warren (2001) attributed nestedness in fish communities to differences in immigration and extinction rates, which were related to abundance. Nestedness has also been found for stream macroinvertebrates (Malmqvist and Hoffsten 2000), so it appears to be a common pattern in aquatic systems.

Correlation results indicated minimal support for the role of isolation, and only partial support for the role of extinction, in promoting nestedness for mussels. The lack of relationship of diversity with isolation indicates that differences in immigration are not important; however, this analysis only considered isolation among mainstem sites – it is possible that immigration occurs from the tributaries (Jenkinson pers. comm.). Another consideration is that this analysis relied on the assumption that equal sampling effort was expended at each site, such that sites could be considered comparable, which may not be the case (Gotelli and Colwell 2001). The significant correlations of mussel species diversity with river kilometer give some support for the hypothesis that nestedness is driven by differences in extinction among mussel species, but the variation in these relationships implied that there were other differences among sites.

The general pattern of a downstream increase in diversity of aquatic fauna has often been identified for riverine systems (Schlosser 1987). Available space and food increase in the downstream direction, but these resources do not appear to be limiting to freshwater mussels (Fuller 1980, Strayer 1993). Downstream sites are typically considered to be more stable; however, Cook et al. (2004) found no evidence that higher elevation streams in Virginia experienced more variable flow or higher rates of fish extinction than downstream sites. Fish diversity does increase downstream in this region (Angermeier and Winston 1997), so the increase in downstream mussel diversity in this study may be related to more diverse downstream fish faunas (Jenkinson and Heuer 1986).

Nestedness of mussel species may reflect fish host diversity patterns in combination with differences in mussel species' niche breadth (Fleishman et al. 2002, Heino 2005). One possibility is that mussel species with narrower niches (using fewer species of fish as hosts) may be rarer. Since more fish species occur downstream, the rarer mussel species would be more likely to find suitable hosts there. Although complete host-mussel relationships are unknown, available host-use data did not support this hypothesis. Similarly, Layzer and Madison (1995) found no relationship between mussel species' abundance and the number of their fish hosts in Horse Lick Creek, Kentucky. A second

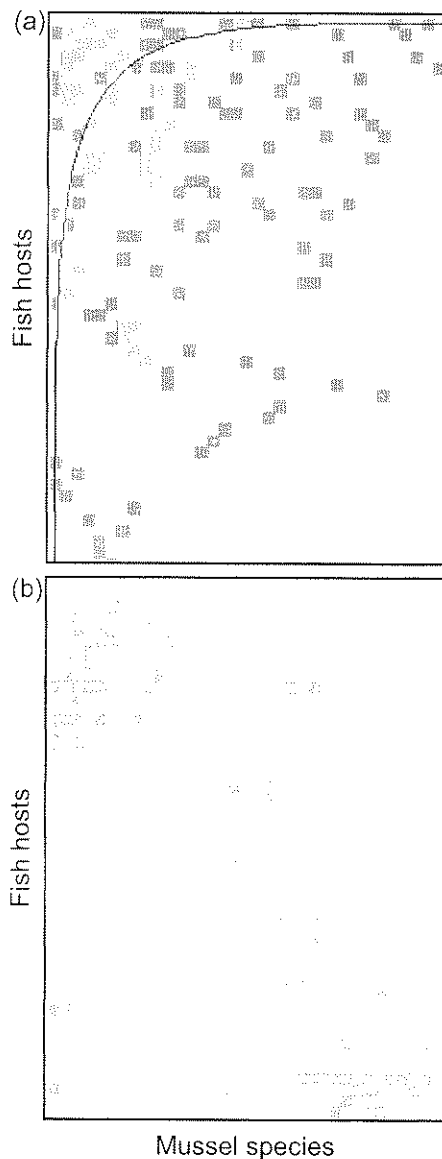


Figure 4. Host-use matrix sorted (a) to show nestedness, where a filled-square indicates that a particular mussel species uses that fish host, and the curved line represents the isocline of perfect nestedness; and (b) by the scores of the first ordination axis in reciprocal averaging.

possibility is that rare mussel species are using rarer fish hosts – if so, these mussels would only occur on the patches where their hosts were found, and would therefore mirror the nested pattern of fish communities (Cook et al. 2004). However, most mussel species in this study appeared to be overlapping on common fish hosts. It is likely that these more common fish hosts provide a more predictable resource than do rare host species (Vazquez and Aizen 2004).

Nestedness of freshwater mussel species may be driven by differences in the abundances of the fishes commonly used as hosts across the sites, coupled with differences in mussel species' ability to attract and infect hosts. Haag and Warren (1998) found a correlation between mussel abundance and fish host abundance for two species in two rivers in Alabama. Higher host fish abundance would allow mussels that are poorer competitors (e.g. worse at attracting/infecting shared hosts) to survive (Rashleigh and DeAngelis 2007). This is consistent with the "nested habitat quality" hypothesis of Hylander et al. (2005) where all species in an assemblage increase in abundance along the same gradient, but differ in tolerance. This is also similar to the finding of Selva and Fortuna (2007) where a nested pattern in scavenger communities was related to the array of different quality resources, coupled with differential abilities of species. This hypothesis bridges two existing hypotheses – the role of species extinction and the distribution of resources – in explaining the pattern of nestedness for freshwater mussel communities. Future study is needed to relate patterns within groups of interacting mussel species to the abundance and distribution of their shared hosts.

An understanding of nestedness can support conservation efforts. For example, within a nested structure, sites with high diversity should be protected (Baber et al. 2004), and species occurring only at the most species-rich sites can be used as indicators of species diversity (Kerr et al. 2000, Fleishman et al. 2002, Hylander et al. 2005). Copper Creek, one of the rivers in this study, was resurveyed in 1998, and seven of the eleven rarest species appeared to be extirpated from the river (Fralei and Ahlstedt 1999). This analysis showed that the mussels' use of fish host resources was related to phylogeny, which has also been noted by Dillon (2000). Rezende et al. (2007) found that when resource use follows a phylogenetic pattern developed through coevolution, coextinctions may also follow this pattern. This is consistent with the differences in conservation status among groups of mussels in different tribes using different sets of fish hosts. Conservation activities are crucial because over seventy percent of North American freshwater mussel species are in decline, threatened, or extinct (Williams et al. 1992). Understanding the dynamics of fish hosts, site quality, and mussel diversity can support these conservation efforts.

Acknowledgements – I am grateful to Jim Drake, Dave Etnier, Mark Kot, and Michael Huston for helpful reviews on an earlier draft, and I thank Jeff Powell, Mike Cyterski, Wade Worthen, and Gary Grossman for useful discussions. I especially thank Steve Ahlstedt for mussel help and guidance. Thanks also to Tom Purucker and three anonymous referees for helpful reviews; Lourdes Prieto for GIS assistance; and Christian Hennig for assistance with R. This paper has been reviewed in accordance with the U.S.

Environmental Protection Agency's peer and administrative review policies and approved for publication. Mention of trade names or commercial products does not constitute endorsement or recommendation for use.

References

- Ahlstedt, S. A. 1986. Cumberlandian Mollusk Conservation Program Activity 1: mussel distribution surveys. – TVA/ONRED/AWR-86/15, Office of Natural Resources and Economic Development, Tennessee Valley Authority, Knoxville, TN.
- Angermeier, P. L. and Winston, M. R. 1997. Assessing conservation value of stream communities: a comparison of approaches based on centres of diversity and species richness. – *Freshwater Biol.* 37: 699–710.
- Atmar, W. and Patterson, B. D. 1993. On the measure of order and disorder in the distribution of species on archipelagos. – *Oecologia* 96: 373–382.
- Baber, M. J. et al. 2004. The relationship between wetland hydroperiod and nestedness patterns in assemblages of larval amphibians and predatory macroinvertebrates. – *Oikos* 107: 16–27.
- Barr, W. C. et al. 1993–1994. Cumberlandian Mollusk Conservation Program Activity 8: analysis of macrofauna factors. – *Walkerana* 7: 159–224.
- Bascompte, J. et al. 2003. The nested assembly of plant-animal mutualistic networks. – *Proc. Nat. Acad. Sci. USA* 100: 9383–9387.
- Bates, J. M. and Dennis, S. D. 1978. The mussel fauna of the Clinch River, Tennessee and Virginia. – *Sterkiana* 69–70: 3–23.
- Cook, R. R. et al. 2004. Geographic variation in patterns of nestedness among local stream fish assemblages in Virginia. – *Oecologia* 140: 639–649.
- Culp, J. J. et al. 2006. New host fish identifications for the pyramid pigtoe, *Pleurobema rubrum*. – *Ellipsaria* 8: 5–6.
- Dillon Jr, R. T. 2000. The ecology of freshwater mollusks. – Cambridge Univ. Press.
- Ficetola, G. F. and DeBernardi, F. 2004. Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. – *Biol. Conserv.* 119: 219–230.
- Fischer, J. and Lindenmayer, D. B. 2005a. Nestedness in fragmented landscapes: a case study on birds, arboreal marsupials and lizards. – *J. Biogeogr.* 32: 1737–1750.
- Fischer, J. and Lindenmayer, D. B. 2005b. Perfectly nested or significantly nested – an important difference for conservation management. – *Oikos* 109: 485–494.
- Fleishman, E. et al. 2002. Nestedness analysis and conservation planning: the importance of place, environment, and life history across taxonomic groups. – *Oecologia* 133: 78–89.
- Fralei, S. J. and Ahlstedt, S. A. 1999. The recent decline of the native mussels (Unionidae) of Copper Creek, Russell and Scott Counties, Virginia. – In: Ohio Biological Survey (ed.), Proceedings of the Fish Freshwater Mollusk Conservation Society Symp., pp. 189–195.
- Fuller, S. L. H. 1980. Freshwater mussels (Mollusca: Bivalvia: Unionidae) of the upper Mississippi River: observation at selected sites within the 9-foot navigation channel project for the St. Paul District, United States Army Corps of Engineers, 1977–1979. – Academy of Natural Sciences of Philadelphia, Division of Limnology and Ecology, Report no. 79-24F, Philadelphia, PA, USA.
- Gotelli, N. J. and Colwell, R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. – *Ecol. Lett.* 4: 379–391.

- Gotelli, N. J. and Entsminger, G. L. 2001. EcoSim: null models software for ecology, ver. 7.0. – Acquired Intelligence and Kesey-Bear, <<http://homepages.together.net/~gentsmin/ecosim.htm>>.
- Graf, D. L. and Cummings, K. S. 2006. Palaeoheterodonta diversity (Mollusca: Trigonioidea + Unionoidea): what we know and what we wish we knew about freshwater mussel evolution. – *Zool. J. Linn. Soc.* 148: 343–394.
- Haag, W. R. and Warren Jr, M. L. 1998. Role of ecological factors and reproductive strategies in structuring freshwater mussel communities. – *Can. J. Fish. Aquat. Sci.* 55: 297–306.
- Hausdorf, B. and Hennig, C. 2007. Null model tests of clustering of species, negative cooccurrence patterns and nestedness in metacommunities. – *Oikos* 116: 818–828.
- Heino, J. 2005. Positive relationship between regional distribution and local abundance in stream insects: a consequence of niche breadth or niche position? – *Ecography* 28: 345–354.
- Hylander, K. et al. 2005. Differences in habitat quality explain nestedness in a land snail meta-community. – *Oikos* 108: 351–361.
- Jenkinson, J. J. and Heuer, J. H. 1986. Cumberlandian Mollusk Conservation Program Activity 9: selection of transplant sites and habitat characterization. – TVA/ONRED/AWR-86/23, Tennessee Valley Authority, Knoxville, TN.
- Kadmon, R. 1995. Nested species subsets and geographic isolation: a case study. – *Ecology* 76: 458–465.
- Kerr, J. T. et al. 2000. Indicator taxa, rapid biodiversity assessment, and nestedness in an endangered ecosystem. – *Conserv. Biol.* 14: 1726–1734.
- Layzer, J. B. and Madison, L. M. 1995. Microhabitat use by freshwater mussels and recommendations for determining their instream flow needs. – *Regul. Rivers: Res. Manage.* 10: 329–345.
- Leibold, M. A. and Mikkelsen, G. M. 2002. Coherence, species turnover, and boundary clumping: elements of meta-community structure. – *Oikos* 97: 237–250.
- Malmqvist, B. and Hoffsten, P. O. 2000. Macroinvertebrate taxonomic richness, community structure, and nestedness in Swedish streams. – *Arch. Hydrobiol.* 150: 29–54.
- McAbendroth, L. et al. 2005. Unraveling nestedness and spatial pattern in pond assemblages. – *J. Anim. Ecol.* 74: 41–49.
- McCune, B. and Medford, M. J. 1999. PC-Ord software ver. 4.10: multivariate analysis of ecological data. – MJM Software, Gleneden Beach, OR.
- Neves, R. J. and Angermeier, P. L. 1990. Habitat alteration and its effects on native fishes in the upper Tennessee River system, east-central U.S.A. – *J. Fish Biol.* 37: 45–52.
- O'Brien, C. and Lyttle, M. 2004. Reproductive biology of *Elliptio complanata*, *Lampsilis ovata*, *Lampsilis radiata*, and *Potamilus alatus* (Bivalvia: Unionidae) from the Poultney River, Vermont. – The Nature Conservancy, Southern Lake Champlain Valley Field Office, West Haven, VT.
- Rashleigh, B. and DeAngelis, D. L. 2007. Conditions for coexistence of freshwater mussel species via partitioning of fish host resources. – *Ecol. Model.* 20: 171–178.
- Rezende, E. L. et al. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. – *Nature* 448: 925–928.
- Rodríguez-Gironés, M. A. and Santamaría, L. 2006. A new algorithm to calculate the nestedness temperature of presence-absence matrices. – *J. Biogeogr.* 33: 924–935.
- Schlosser, I. J. 1987. A conceptual framework for fish communities in small warmwater streams. – In: Matthews, W. J. and Heins, D. C. (eds), *Community and evolutionary ecology of North American stream fishes*. Univ. of Oklahoma Press, pp. 17–24.
- Selva, N. and Fortuna, M. A. 2007. The nested structure of a scavenger community. – *Proc. R. Soc. B.* 274: 1101–1108.
- Strayer, D. L. 1993. Macrohabitats of freshwater mussels (Bivalvia: Unionacea) in streams of the northern Atlantic Slope. – *J. North Am. Benthol. Soc.* 12: 236–246.
- Taylor, C. M. and Warren Jr, M. L. 2001. Dynamics in species composition of stream fish assemblages: environmental variables and nested subsets. – *Ecology* 82: 2320–2330.
- Ulrich, W. and Gotelli, N. J. 2007. Disentangling community patterns of nestedness and species co-occurrence. – *Oikos* 116: 2053–2061.
- Vaughn, C. C. and Taylor, C. M. 1999. Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. – *Conserv. Biol.* 13: 912–920.
- Vázquez, D. P. and Aizen, M. A. 2004. Asymmetric specialization: a pervasive feature of plant-pollinator interactions. – *Ecology* 85: 1251–1257.
- Watters, G. T. 1992. Unionids, fishes, and the species-area curve. – *J. Biogeogr.* 19: 481–490.
- Watters, G. T. 1994. An annotated bibliography of the reproduction and propagation of the Unionoidea (primarily of North America). – *Ohio Biol. Surv. Misc. Cont. No.* 1.
- Williams, J. D. et al. 1992. Conservation status of freshwater mussels of the United States and Canada. – *Fisheries* 18: 6–22.
- Worthen, W. B. 1996. Community composition and nested-subset analyses: basic descriptors for community ecology. – *Oikos* 76: 417–426.
- Worthen, W. B. et al. 1998. Community structure and environmental stress: desiccation promotes nestedness in mycophagous fly communities. – *Oikos* 81: 45–54.
- Wright, D. H. and Reeves, J. H. 1992. On the meaning and measurement of nestedness of species assemblages. – *Oecologia* 92: 416–428.
- Wright, D. H. et al. 1998. A comparative analysis of nested subset patterns of species composition. – *Oecologia* 113: 1–20.