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# Nested-subset structure of larval odonate assemblages in the Enoree River basin, USA

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## Abstract

Communities have a nested-subset structure if the species found in species-poor assemblages are also found in progressively more species-rich assemblages. This nested-subset structure can be caused by differential colonization rates among species, differential extinction rates among species, or nested niche space. In this study, the assemblages of larval odonates in the Enoree River of South Carolina (USA) and nine of its tributaries were found to have statistically significant nested-subset structure. In addition, the degree of nestedness in these ten streams correlated with several chemical and physical variables. Nestedness was correlated with pH, turbidity, and concentrations of silica, bicarbonate, and calcium; suggesting that differential extinction in response to environmental stress may play a role in structuring these assemblages. However, nestedness also correlated with a crude measure of habitat homogeneity. Drainages with a heterogeneous mix of substrate types (cobbles and sand) maintained different sets of species from site to site, and had the lowest nestedness scores. Drainages with exclusively sandy substrates were dominated by burrowing species at all sites, and showed the strongest nested-subset patterns. As such, nested-subset structure in these assemblages is related to both chemical and physical parameters.

## Introduction

Many species assemblages exhibit a particular pattern of community composition called ‘nested-subset structure’. Assemblages are ‘nested’ if the species found in depauperate communities are also found in progressively more species-rich assemblages (Patterson & Atmar 1986). This pattern can result from differential colonization or extinction rates among species, or nested niche space (Patterson & Atmar 1986; Kodric-Brown & Brown 1992). The most vagile, tolerant, and abundant species will probably occur in most habitats, whereas the least vagile, most sensitive, and least abundant species will only be found in the few habitats that they can reach, tolerate, and maintain a population. As such, species-poor assemblages will probably contain a particular non-random subset of tolerant, vagile, or abundant species, and rare species will probably occur on the largest fragments with the greatest species diversity.

Nestedness has important consequences for conservation biology (Patterson 1987; Simberloff & Martin 1991; Doak & Mills 1994; Lomolino 1994; Cook 1995; Sahlén & Ekestubbe 2001). As an ecosystem is fragmented into a set of habitat 'islands', extinctions will occur on these islands in a manner consistent with the species-area relationship (MacArthur & Wilson 1967). However, when sensitive, sedentary, or extinction-prone species are lost from smaller habitat fragments, these assemblages may decay to the same redundant subset of tolerant species (Worthen et al. 1998; Fernandez-Juricic 2002). Across a range of fragments of different size, we should expect both a species-area relationship and a pattern of nested assemblages.

These changes occur because reduction in habitat size imposes a number of important ecological stresses on natural communities; from changes in abiotic conditions to changes in disturbance frequency to changes in productivity and trophic structure (Laurance et al. 2002). Only species that can tolerate all of these changes will persist. Other generalized environmental stressors should elicit a similar pattern, regardless of whether there is a change in the size of the habitat or not. Human activity now represents the primary stress experienced by most natural systems. Although the primary anthropogenic stress is habitat reduction, other effects are also important; from direct hunting pressure on single species, to the release of toxins into the environment, to the reduction of habitat heterogeneity. These stresses are usually not equivalent across the landscape, and they probably have complex cumulative effects. Nonetheless, even initially unnested assemblages can decay to nested communities as a function of differential species tolerances to anthropogenic stress (Worthen et al. 1998; Fernandez-Juricic 2002). And, the degree of nestedness should correlate with the variables (or a derivative) contributing most to this non-random pattern of species extinction. As such, nested-subset analysis might be used to identify variables that are important determinants of community structure (Worthen 1996).

Larval odonate assemblages provide an appropriate system to test this hypothesis. The primary anthropogenic impact on aquatic systems is not habitat fragmentation; rather, humans affect these systems by changing the chemical and physical properties of the aquatic environment (Beavan et al. 2001). In the most direct case, the direct input of a particular toxin may select for particular tolerant species (Wallace et al. 1991). However, it is also likely that the interactive, cumulative effects of multiple chemical inputs are also important. And, even tolerant odonates may be indirectly affected by changes in water quality if important prey or predator species are sensitive. Anthropogenic impacts on the physical attributes of streams may be even more important to odonate assemblages than chemical changes in water quality, given the specific larval habitat requirements of many odonate species (Schridde & Suhling 1994). By channelizing streams, building dams, cutting forests, and increasing the coverage of impervious surface, humans alter stream flow dynamics and disturbance regimes, increase runoff , and increase siltation. These changes tend to reduce habitat heterogeneity and increase the variance in stream discharge. The structure of odonate assemblages should respond to these cumulative anthropogenic effects (Clark & Samways 1996; Corbet 1999: 204).

The Enoree River and its tributaries in South Carolina (USA) drain a variety of habitats, from a state park and a national forest to rural, suburban, and urban areas. These tributaries vary in their chemical and physical attributes, largely as a function of anthropogenic impact and differences in underlying geology (Andersen et al. 2001; Worthen et al. 2001a, 2001b). Kings Creek and Indian Creek are notably different than the other streams, with significantly higher concentrations of silica, bicarbonate, calcium, and magnesium (Andersen et al. 2001; Worthen et al. 2001a). In addition, these two drainages have sandy substrates throughout, whereas the other streams have a greater variety of substrate types (Worthen et al. 2001a). Previous research demonstrated that the odonate assemblages in these streams were dominated by a group of eight species that often co-occur (Worthen 2002). These species fill different, complementary ecological niches (Corbet 1999: 150), suggesting that these assemblages are non-randomly structured. *Boyeria vinosa* (Say) is a clasper, *Hagenius brevistylus* Selys is a hider, *Macromia illinoiensis* Walsh is a sprawler, and *Ophiogomphus mainensis* Packard, *Cordulegaster maculata* Selys, *Gomphus cavillaris* Needham, *Progomphus obscurus* (Rambur) and *Stylurus scudderi* (Selys) are burrowers (Corbet 1999: 620). The abundance, species richness, and diversity of larval odonate assemblages correlate with several chemical and physical properties of these streams (Worthen et al. 2001a; Worthen 2002). As such, it seems that the structure of these odonate assemblages responds to anthropogenic disturbance in these watersheds. In this study, the relationship between the nested-subset structure of these assemblages and the chemical and physical properties of these streams is described.

## Methods

The Enoree River Basin is a 1,193 km² sixth-order watershed in the piedmont of South Carolina, USA, with 170 km of perennial streams (Worthen et al. 2001b: fig. 1). The southern half of the watershed is a patchwork of agricultural fields and forests, including portions of Sumter National Forest. The northern third of the watershed is dominated by the Greenville-Spartanburg metropolitan area. In 1999-2000, The River Basins Research Initiative of Furman University conducted a chemical and biological inventory of the Enoree River and nine of its tributaries to describe the impact of suburban development on water quality.

A total of 127 sites were sampled in May-July 1999 (63 sites) and May-July 2000 (64 sites). Sampling sites were selected by locating bridge crossings and streams with road access on USGS topographic maps. When possible, sampling was conducted upstream from bridge crossings to reduce the effect of roadway runoff. A water sample was collected each week from each site for seven weeks, and the following parameters were measured: pH, temperature, conductivity, dissolved oxygen, the concentration of major cations (aluminum, calcium, iron, magnesium, manganese, potassium, silicon, sodium, and zinc), the concentration of major anions (phosphate, nitrate, fluorine, bromine, chlorine, and nitrite) alkalinity, and turbidity. For a complete description of the methods used to quantify these parameters, see Worthen et al. (2001a).

Odonates were sampled once at each site by electrofishing with a Smith-Root® Backpack Electrofisher. Electrofishing provides accurate estimates of population size and diversity (Taylor et al. 2001). Sampling was standardized by electrofishing for a total of 8 min at each site. Sampling was conducted in the following manner. A short reach of 5-6 m was electroshocked for 1-2 min. The substrate was kicked during this shocking period to dislodge organisms, which were collected downstream in a seine (1.5 m × 3.3 m; mesh size = 3.0 mm) and dip nets. After removing invertebrates from the seine, another short reach was electroshocked further upstream. In this way, four to six different microhabitats were electroshocked at each site during the total 8 min electroshocking period. Typically, these microhabitats were distributed within a reach 50-100 m in length. All specimens were sorted, counted, and preserved; odonate larvae were preserved in 75% EtOH and identified to species, if possible, using the taxonomic keys of Huggins & Brigham (1982), Merritt & Cummins (1996), Westfall & May (1996), and Needham et al. (2000).

There are several shortcomings to this methodology. First, by sample each site only once and by beginning in May, all samples may have missed early univoltine species such as *Tetragoneuria cynosura* (Say), which completes emergence by May (Smock 1988). Second, the degree to which early instar larva could be identified to species varied as a function of the size of the larva and the taxon to which it belonged. For instance, *Hagenius brevistylus* larvae can be unambiguously identified at any size, but early instars of many *Gomphus* species are particularly difficult to discriminate. As such, it is quite possible that species-specific sampling bias was present in this survey. However, this bias is assumed to be uniform across the data set.

A nestedness score for the Enoree River and each of the nine tributary systems was computed using the nestedness index $N_c$ and the standardized $C$ index of Wright & Reeves (1992). The primary advantage of this metric over those of Patterson & Atmar (1984) or Atmar & Patterson (1993) is that the standardized metric $C$ is independent of the size of the 'species x habitat' matrix. Therefore, nestedness values can be compared across matrices and communities. The relative merits of these metrics, and others, have been discussed elsewhere (Wright et al. 1998). In this study, the Wright & Reeves (1992) nestedness scores were calculated and correlated with the mean values of the chemical and physical parameters in the Enoree River and its nine tributaries, and with discriminant functions that summarized chemical differences (Worthen et al. 2001a).

## Results

The odonate assemblages in the Enoree River and nine of its tributaries were all significantly nested using the Wright & Reeves (1992) nestedness index, $N_c$ ($p < 0.01$, Table 1). The standardized nestedness index, $C$, was calculated for each assemblage. These standardized nestedness values were directly correlated with pH, turbidity, and mean concentrations of silica, bicarbonate, and calcium (Table 2). The standardized metric, $C$, was also significantly correlated with centroid scores from Discriminant Function 1 (DFA1, Table 2); a variable derived from all chemical measurements (Worthen et al. 2001a). DFA1 accounted for 72.4% of the variance among streams, and was significantly correlated with silica and bicarbonate concentrations (Worthen et al. 2001a). Also, $C$ correlated with the percentage of sandy sites within a drainage. However,

Table 1. Nestedness indices for larval odonate assemblages in the Enoree River and nine of its tributaries. Tributaries listed from north to south are BD: Beaverdam Creek; UE: Upper Enoree; MC: Mountain Creek; BC: Brushy Creek; RC: Rocky Creek; GC: Gilder Creek; DC: Durbin Creek; IC: Indian Creek; KC: Kings Creek; ER: main channel of the Enoree River; *n*: number of sites sampled; *R*: total number of odonate species collected. Nestedness indices are computed after Wright & Reeves (1992), and are *Nc*: observed nestedness score; *E(Nc)*: expected nestedness score based on species incidences; *Max(Nc)*: maximum nestedness score based on species incidences; *C*: standardized nestedness metric; the *z* value; and *p*: statistical significance of the nestedness score, *Nc*.

| Stream (*n*, *R*) | $N_c$ | $E(N_c)$ | $Max(N_c)$ | *C* | *z* | *p* |
|---|---|---|---|---|---|---|
| BD (10, 13) | 144 | 107.2 | 199 | 0.401 | 9.85 | 0.0001 |
| UE (11, 12) | 95 | 58.8 | 134 | 0.481 | 7.26 | 0.0001 |
| MC (13, 14) | 148 | 119.0 | 235 | 0.250 | 4.85 | 0.0001 |
| BC (11, 11) | 73 | 44.1 | 119 | 0.386 | 6.03 | 0.0001 |
| RC (12, 9) | 85 | 60.9 | 134 | 0.330 | 4.79 | 0.0001 |
| GC (14, 14) | 314 | 219.3 | 383 | 0.578 | 12.41 | 0.0001 |
| DC (15, 15) | 417 | 302.1 | 544 | 0.475 | 12.57 | 0.0001 |
| IC (9, 10) | 110 | 95.8 | 136 | 0.546 | 3.49 | 0.001 |
| KC (7, 13) | 123 | 88.8 | 140 | 0.668 | 8.28 | 0.0001 |
| ER (15, 24) | 365 | 196.3 | 548 | 0.480 | 17.25 | 0.0001 |

standardized nestedness values did not correlate with either mean odonate species richness or Simpson's diversity.

Kings Creek had the highest standardized nestedness score (*C* = 0.668, Table 1). All sites sampled had the burrowing species ***Progomphus obscurus***, ***Cordulegaster maculata***, ***Gomphus cavillaris***, and ***Ophiogomphus mainensis*** (Table 3). The other five species found in this drainage were: ***Aeshna umbrosa*** Walker, ***Dromogomphus spinosus*** Selys, ***Gomphus parvidens*** Currie, ***Stylogomphus albistylus*** (Hagen), and ***Stylurus spiniceps*** (Walsh). These rare species occupied progressively more species-rich sites, consistent with the high nestedness score. In contrast, Mountain Creek had the lowest standardized nestedness score (*C* = 0.250, Table 1). There was fairly equal ecological representation among the most frequent species, with a sprawler (***Macromia illinoiensis***), a burrower (***P. obscurus***), a clasper (***Boyeria vinosa***), and a hider (***Hagenius brevistylus***) occurring at seven, eight, or nine sites (Table 4). Rare species, including ***Argia fumipennis*** (Burmeister), ***Calopteryx maculata*** (Beauvois), ***Cordulegaster erronea*** Hagen, and ***Lanthus parvulus*** (Selys), were more haphazardly distributed across sites, creating a lower nestedness score (Table 4).

Table 2. Correlations between the standardized nestedness metric, *C*, for larval odonate assemblages in the Enoree River and nine of its tributaries, and mean values for chemical, physical, and biological descriptors; $n = 10$ for each correlation; *: statistically significant relationships. DFA1, DFA2: Discriminant Function variables derived from the chemical data (Worthen et al. 2001a). % sand: percentage of sampled sites with primarily sandy substrates; Richness: odonate species richness per site; Diversity: mean Simpson's diversity of odonates per site.

| Variable | *r* | *p* | Variable | *r* | *p* |
|---|---|---|---|---|---|
| pH | 0.639 | 0.047* | $PO_4^{3-}$ (mg/L) | 0.143 | 0.694 |
| Conductivity | 0.593 | 0.071 | F (mg/L) | 0.237 | 0.509 |
| DO (mg/L) | –0.421 | 0.225 | $Si^{4+}$ (mg/L) | 0.740 | 0.014* |
| Turbidity | 0.774 | 0.009* | $Zn^{2+}$ (mg/L) | 0.054 | 0.883 |
| $Na^{1+}$ (mg/L) | 0.420 | 0.227 | $Mn^{2+}$ (mg/L) | 0.361 | 0.306 |
| $K^{1+}$ (mg/L) | 0.213 | 0.555 | $Al^{2+}$ (mg/L) | 0.307 | 0.388 |
| $Ca^{2+}$ (mg/L) | 0.693 | 0.029* | $Fe^{2+}$ (mg/L) | 0.542 | 0.106 |
| $Mg^{2+}$ (mg/L) | 0.557 | 0.095 | DFA1 | 0.699 | 0.024* |
| $Cl^-$ (mg/L) | 0.145 | 0.690 | DFA2 | 0.205 | 0.571 |
| $SO_4^{2-}$ (mg/L) | 0.085 | 0.815 | % sand | 0.668 | 0.035* |
| $HCO_3^-$ (mg/L) | 0.640 | 0.046* | Richness | 0.563 | 0.275 |
| $NO_3^-$ (mg/L) | –0.020 | 0.957 | Diversity | 0.261 | 0.467 |
| $NO_2$ (mg/L) | 0.501 | 0.141 | | | |

## Discussion

The odonate assemblages in all ten drainages exhibited statistically significant nested-subset structure. The standardized metric, *C*, varied from 0.250 in Mountain Creek to 0.668 in Kings Creek. This range is consistent with values found in other surveys (Wright & Reeves 1992; Worthen & Rhode 1996). The standardized nestedness metric correlated with several chemical parameters, including pH, turbidity, and the concentrations of silica, magnesium and calcium. This metric also correlated with the first discriminant function derived from the chemical variability among these streams. In addition, nestedness correlated with homogeneity in substrate type, measured as the percentage of sites in a drainage with sandy substrates. As such, there is ample evidence that the nested-subset structure of these assemblages correlates with the chemical and physical characteristics of these streams.

The strong correlations between nestedness and turbidity, silica concentration, and the percentage of sites with sandy substrates may indicate that the assemblages are responding to anthropogenic impact. Increased runoff associated with increases in

Table 3. Species occurrence matrices for Kings Creek, the tributary of the Enoree River with the highest standardized nestedness score. Sites are ordered by species richness values (*R*); species are ordered by the number of sites occupied (frequency).

| | Site: | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|
| Species (frequency) | *R*: | 9 | 9 | 8 | 7 | 7 | 6 | 6 |
| *Cordulegaster maculata* (7) | | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Gomphus cavillaris* (7) | | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Ophiogomphus mainensis* (7) | | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Progomphus obscurus* (7) | | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Boyeria vinosa* (6) | | 1 | 1 | 1 | 1 | 1 | 1 | — |
| *Macromia illinoiensis* (6) | | 1 | 1 | 1 | 1 | 1 | — | 1 |
| *Hagenius brevistylus* (4) | | — | 1 | 1 | 1 | 1 | — | — |
| *Stylurus scudderi* (3) | | 1 | 1 | — | — | — | — | 1 |
| *Aeshna umbrosa* (1) | | — | — | — | — | — | 1 | — |
| *Dromogomphus spinosus* (1) | | — | 1 | — | — | — | — | — |
| *Gomphus parvidens* (1) | | 1 | — | — | — | — | — | — |
| *Stylogomphus albistylus* (1) | | — | — | 1 | — | — | — | — |
| *Stylurus spiniceps* (1) | | 1 | — | — | — | — | — | — |

impervious surface cover and decreased forest cover in a watershed causes increased erosion, increased storm flow, and increased siltation. This would increase turbidity, and could change a heterogeneous mix of pool, riffle, and run microhabitats with a diverse substrate of sand and cobbles to a homogeneous habitat with only sandy substrate. Homogenization of habitat is likely to lead to a homogenization of resident assemblages and increased nested-subset structure, as the assemblages decay to the same redundant subset of tolerant species (Worthen et al. 1998).

For instance, Kings Creek, Gilder Creek, and Indian Creek had the most highly nested larval odonate assemblages in the Enoree River basin. Kings and Indian Creeks were the southernmost tributaries sampled; they have a different underlying geology (Andersen et al. 2001) that contributes to the high concentration of silica and uniformity in substrate type (100% of the sites have sandy substrates; Worthen et al. 2001a). However, Kings Creek also drains the Sumter National Forest, where logging may contribute to siltation and raise turbidity levels. Siltation from forestry activity has been shown to eliminate intolerant odonate species from other aquatic systems (Rith-Najarian 1998; Sahlén 1999). Gilder Creek drains the southern rim of the greater Greenville area, a region of rapid development where agricultural lands are being converted to suburban developments. Increased runoff could increase erosion and sediment load, and could be responsible for increased turbidity and siltation in this tributary. The odonate assemblages at

Table 4. Species occurrence matrices for Mountain Creek, the tributary of the Enoree River with the lowest standardized nestedness score. Sites are ordered by species richness values (*R*); species are ordered by the number of sites occupied (frequency).

| | Site: | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species (frequency) | *R*: | 10 | 9 | 6 | 6 | 6 | 6 | 5 | 5 | 2 | 2 | 2 | 1 | 1 |
| *Macromia illinoiensis* (9) | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | — | — | — | 1 | — |
| *Boyeria vinosa* (8) | | 1 | 1 | — | 1 | 1 | 1 | 1 | 1 | — | — | 1 | — | — |
| *Progomphus obscurus* (8) | | 1 | 1 | 1 | 1 | 1 | 1 | — | 1 | 1 | — | — | — | — |
| *Hagenius brevistylus* (7) | | 1 | 1 | — | 1 | — | 1 | 1 | 1 | 1 | — | — | — | — |
| *Cordulegaster maculata* (5) | | 1 | 1 | 1 | — | 1 | 1 | — | — | — | — | — | — | — |
| *Ophiogomphus mainensis* (4) | | 1 | 1 | — | — | 1 | 1 | — | — | — | — | — | — | — |
| *Stylogomphus albistylus* (4) | | 1 | 1 | 1 | — | — | — | — | — | — | 1 | — | — | — |
| *Argia fumipennis* (3) | | — | — | — | — | — | — | — | 1 | — | — | 1 | — | 1 |
| *Dromogomphus spinosus* (3) | | 1 | — | — | 1 | — | — | 1 | — | — | — | — | — | — |
| *Gomphus cavillaris* (3) | | — | 1 | — | — | 1 | — | 1 | — | — | — | — | — | — |
| *Stylurus scudderi* (3) | | 1 | 1 | — | 1 | — | — | — | — | — | — | — | — | — |
| *Cordulegaster erronea* (2) | | 1 | — | 1 | — | — | — | — | — | — | — | — | — | — |
| *Calopteryx maculata* (1) | | — | — | 1 | — | — | — | — | — | — | — | — | — | — |
| *Lanthus parvulus* (1) | | — | — | — | — | — | — | — | — | — | 1 | — | — | — |

the sites in Kings Creek were very similar, and were dominated by burrowing species such as, *Cordulegaster maculata, Gomphus cavillaris, Ophiogomphus mainenesis,* and *Progomphus obscurus. C. maculata* is a niche generalist, but *G. cavillaris* and *P. obscurus* are more dependent on silt and sandy-bottom microhabitats (Burcher & Smock 2002). So, it seems likely that that homogenization of the substrate type causes homogenization of the odonate assemblages and greater nested-subset structure. However, whether habitat homogenization is due to anthropogenic effects, geology, or a combination of these variables is unknown.

In contrast, Mountain Creek had the 'least nested' assemblages, with a *C* value of 0.250. Mountain Creek originates on Paris Mountain, a monadnock north of Greenville, SC. The headwaters lie within Paris Mountain State Park. Many sites within this drainage represent the most pristine sites within the entire sampling area, and have relatively undisturbed, heterogenous pattern of cobble and sand substrates (only 21% of the sites in Mountain Creek had sandy substrates; Worthen et al. 2001). The odonate assemblages at sites in this drainage were much more heterogeneous, with hiders, claspers, sprawlers, and burrowers represented in the group of frequently encountered species.

So, although there are several chemical correlates with the degree of nestedness in these systems (pH and concentrations of calcium and bicarbonate), it appears that characteristics of the physical environment, and the degree of habitat heterogeneity within a watershed, may have a more direct relationship with species composition and the nested-subset structure of odonate assemblages. In addition, nestedness did not correlate with either odonate species richness or Simpson's diversity. The Upper Enoree, Brushy Creek, and Rocky Creek had the lowest mean diversity and richness values (Worthen 2002). These watersheds are areas of known industrial contamination (Worthen et al. 2001b) or heavy suburban development, yet they had intermediate nestedness values. These sites also have a mixture of sand and cobble, and this heterogeneity may be responsible for their intermediate nestedness scores. This also supports the contention that habitat heterogeneity may be a stronger determinant of nested-subset structure than chemical composition.

In conclusion, nestedness in larval odonate assemblages correlated with several physical and chemical variables in the Enoree River basin. The most highly nested assemblages were found in streams where natural and anthropogenic effects likely contribute to habitat homogeneity. Like the more fundamental effects of habitat fragmentation, the general effects of anthropogenic stress can cause non-random extinction, homogenization of habitats and species assemblages, and an increase in the degree of nested-subset structure (Worthen 1998). This study suggests that these homogenizing effects may be affecting the structure of larval odonate assemblages in the Enoree River basin.

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