

Evaluating regional differences in macroinvertebrate communities from forested depressional wetlands across eastern and central North America

DAROLD P. BATZER¹

Department of Entomology, University of Georgia, Athens, Georgia 30602 USA

SUSAN E. DIETZ-BRANTLEY²

Department of Entomology, University of Georgia, Athens, Georgia 30602 USA and Savannah River Ecology Laboratory, Aiken, South Carolina 29802 USA

BARBARA E. TAYLOR³ AND ADRIENNE E. DEBIASE⁴

Savannah River Ecology Laboratory, Aiken, South Carolina 29802 USA

Abstract. Forested depressional wetlands are an important seasonal wetland type across eastern and central North America. Macroinvertebrates are crucial ecosystem components of most forested depressional wetlands, but community compositions can vary widely across the region. We evaluated variation in macroinvertebrate faunas across eastern and central North America using 5 published taxa lists from forested depressional wetlands in Michigan, Ontario, Wisconsin, Florida, and Georgia. We supplemented those data with quantitative community descriptions generated from 17 forested depressional wetlands in South Carolina and 74 of these wetlands in Minnesota. Cluster analysis of presence/absence data from these 7 locations indicated that distinct macroinvertebrate communities existed in northern and southern areas. Taxa characteristic of northern forested depressional wetlands included Sphaeriidae, Lumbriculidae, Lymnaeidae, Physidae, Limnephilidae, Chirocephalidae, and Hirudinea (Glossophoniidae and/or Erpobdellidae) and taxa characteristic of southern sites included Asellidae, Crangonyctidae, Noteridae, and Cambaridae. Quantitative sampling in South Carolina and Minnesota indicated that regionally characteristic taxa included some of the most abundant organisms, with Sphaeriidae being the 2nd most abundant macroinvertebrate in Minnesota wetlands and Asellidae being the 2nd most abundant macroinvertebrate in South Carolina wetlands. Mollusks, in general, were restricted to forested depressional wetlands of northern latitudes, a pattern that may reflect a lack of Ca needed for shell formation in acidic southern sites. Differences in community composition probably translate into region-specific differences in the ecological functions performed by macroinvertebrates in forested depressional wetlands.

Key words: fingernail clams, hydroperiod, invertebrates, Isopoda, latitude, Mollusca, seasonal ponds, vernal ponds, wetland.

The character of seasonal wetland habitats varies widely across North America, and these differences undoubtedly affect resident macroinvertebrates (Batzer et al. 1999). Wissinger (1999) maintained that various aspects of hydroperiod including variation in water permanence, flood predictability, phenology of drying and filling, and harshness of dry and wet phases all influence aquatic invertebrate community compositions in seasonal wetlands. He proposed that an important difference between seasonal

wetlands of eastern and western North America is that the dry phase is harsher for invertebrates in the arid west than in the more humid east. Consequently, western seasonal wetlands (Batzer and Resh 1992, Anderson et al. 1999, Hall et al. 2004) support relatively few invertebrates with desiccation-resistant strategies and relatively more invertebrates that are cyclic colonizers (organisms that migrate between permanent and temporary waters to complete their life cycle, sensu Batzer and Wissinger 1996). In contrast, eastern seasonal wetlands support many taxa with desiccation resistance (Wiggins et al. 1980, Wissinger and Gallagher 1999, Dietz-Brantley et al. 2002).

We have been working in various seasonal de-

¹ E-mail addresses: dbatzer@bugs.ent.uga.edu

² sebrantley1@yahoo.com

³ taylor@srel.edu

⁴ debiase@srel.edu

pressional wetlands across the forested portions of eastern and central North America including Minnesota (Palik et al. 2001, Batzer et al. 2004), New York (Batzer and Sion 1999), South Carolina (Leeper and Taylor 1998, Taylor et al. 1999, Dietz-Brantley et al. 2002, DeBiase and Taylor 2003), and Georgia (Batzer et al. 2000), and we have observed that macroinvertebrate faunas vary widely among these locations. For example, we found that fingernail clams (*Sphaeriidae*) were very abundant in forested depressional wetlands in Minnesota and New York, but not in South Carolina or Georgia. We hypothesized that, like macroinvertebrate community differences along the east-west longitudinal gradient, macroinvertebrate community compositions might differ between seasonal wetlands in northern and southern latitudes.

Forested depressional wetlands are a kind of seasonal wetland that occurs across most of the eastern and central North American forest (Batzer et al. 1999, Palik et al. 2003). They have been called an assortment of names. In the north, they are called temporary or seasonal woodland ponds, vernal ponds, or autumnal ponds. In the south, they are called cypress domes, gum ponds, forested Carolina bays, or forested limesinks. We use the name, forested depressional wetland, to emphasize the importance of hydrologic isolation and a forested setting, but the seasonal hydroperiod of these wetlands also is a crucially important feature. Forested floodplain habitats and nonforested seasonal marshes do not fit the category and are not addressed in our paper. Forested depressional wetlands across eastern and central North America vary in terms of climate and geology, but they share many common traits including small size, a seasonal precipitation-based hydrology, hydrologic isolation in terms of surface flow from other water bodies (lakes, rivers, streams), and the presence of trees in or around the basins. We gathered published faunal lists from forested depressional wetlands from across eastern and central North America (Michigan, Ontario, Wisconsin, Florida, and Georgia), and supplemented this database with our own collections from South Carolina and Minnesota wetlands. We used all of these data to evaluate whether predictable patterns in macroinvertebrate community composition existed across this region.

Study Sites and Methods

Michigan, Ontario, Wisconsin, Florida, and Georgia forested depressional wetlands

We reviewed the published literature and found 5 studies (Michigan: Kenk 1949, Ontario: Wiggins et al. 1980, Wisconsin: Schneider and Frost 1996, Florida: Leslie et al. 1997, and Georgia: Golladay et al. 1999) that provided complete descriptions of macroinvertebrate communities in forested depressional wetlands in eastern or central North America. We compiled presence/absence taxa lists for each of the 5 locations, but could not quantify relative abundances because some sources did not report densities. These 5 locations provided a reasonable cross-section of eastern North America, but we decided to supplement the qualitative data sets with quantitative data from forested depressional wetlands in South Carolina and Minnesota.

South Carolina and Minnesota forested depressional wetlands

In South Carolina, we sampled 17 forested depressional wetlands (Carolina bays and other depressional wetlands) on the Savannah River Site in Aiken and Barnwell Counties (lat 33°N, long 81°W). Carolina bay wetlands are elliptical, seasonal wetlands that are common on the Atlantic Coastal Plain, and many are forested (Taylor et al. 1999). The 17 wetlands in our study ranged from 0.3 ha to 3.3 ha. Hydroperiods depended primarily on precipitation and evapotranspiration, and these habitats lacked surface-water connections to streams, rivers, or permanent wetlands. Typically, these wetlands fill in late autumn to early winter and dry in late spring or early summer, with the possibility of additional short flooded periods after summer storms (although longer- and shorter-duration hydroperiods occur commonly). Wetland waters were moderately to heavily colored, and pH ranged from 3.5 to 6.5. Trees of the basins included red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), pondcypress (*Taxodium distichum* var. *nutans*), black gum (*Nyssa sylvatica biflora*), and loblolly pine (*Pinus taeda*) (Barton and Singer 2001). Surrounding uplands supported mixed pine/hardwood forests.

In Minnesota, we sampled 74 forested depressional wetlands located in the Chippewa

National Forest in Cass and Itasca counties (lat 47°N, long 94°W). Dominant glacial landforms of the study area include ground moraine (till plain), outwash plain, end moraine, and lake plain. These wetlands also were isolated hydrologically from other water bodies, and seasonal hydroperiods depended primarily on precipitation (snowmelt and autumn and spring rains) and evapotranspiration. Most wetlands filled in late autumn or early spring and typically dried for variable periods in the summer (Batzer et al. 2004). Wetland areas ranged from 0.02 to 0.5 ha, and most were smaller than the South Carolina wetlands. Minnesota wetlands were less acidic than South Carolina wetlands, with pH ranging from 5.5 to 7.5 from CaCO₃ alkalinity (Batzer et al. 2004). Trees in the basins included black ash (*Fraxinus nigra*) and red maple, and surrounding uplands supported mixed pine/hardwood forests.

We used similar methods to sample macroinvertebrates from South Carolina and Minnesota habitats to enable assessment of relative abundances of taxa between locations. We used a D-frame net (30-cm width, 1-mm mesh) to collect macroinvertebrates because it samples macroinvertebrate communities from wetlands efficiently and precisely (Cheal et al. 1993, Batzer et al. 2001). The net mesh was small enough to retain most macroinvertebrates but large enough to prevent excessive clogging by fine sediments (Batzer et al. 2001). For each wetland sample, we collected the macroinvertebrates in three 1-m sweep samples; the 1st sweep was along the edge of the wetland, the 2nd was from the deepest area of the wetland, and the 3rd was from a midpoint location or a subhabitat not sampled in the first 2 sweeps. We scraped the net along the bottom of the wetland, regardless of depth. We pooled the contents of the 3 sweeps into a single composite sample. In the South Carolina wetlands, we sampled macroinvertebrates every 2 mo from February 1998 to December 2000 if the wetlands held water (except August and October 1998); most samples were collected in winter or spring because only a few sites held water in the summer and autumn months. We collected 91 samples in South Carolina. In the Minnesota wetlands, we restricted our sampling to early May and late June 1998 and 1999 (Batzer et al. 2004). This period encompassed the primary activity period for macroinverte-

brates in Minnesota, with the early May sample occurring soon after the ice cover melted and the late June sample occurring as most wetlands were drying. We collected 257 samples in Minnesota. Ethanol-preserved samples were sorted in the laboratory, and macroinvertebrates were identified using keys in Ward and Whipple (1945), Pennak (1989), Thorp and Covich (1991), and Merritt and Cummins (1996).

Statistical analyses

We used multivariate analyses to assess patterns in composition of macroinvertebrate assemblages among forested depressional wetlands of eastern and central North America and between wetlands of South Carolina and Minnesota. We used S-Plus 6.1 (Insightful Corporation, Seattle, Washington) for all multivariate procedures.

For the regional assessment, we did cluster analysis using a divisive hierarchical algorithm on the matrix of dissimilarities among 7 geographic locations (South Carolina, Minnesota, Michigan, Ontario, Wisconsin, Florida, and Georgia). We computed dissimilarity using the Jaccard dissimilarity metric, which measures the proportion of unshared species between assemblages *i* and *j*, such that

$$d_{ij} = \frac{\text{count of taxa in } i \text{ or } j \text{ but not both}}{\text{count of taxa in } i \text{ or } j \text{ or both}}$$

We excluded taxa common to all assemblages from the computation. We assessed whether a taxon was an indicator of a particular geographic cluster by contrasting its presence or absence in groups using simple χ^2 tests.

We compared wetland assemblages in Minnesota and South Carolina using nonmetric multidimensional scaling (NMDS) on the matrix of Jaccard dissimilarities among pairs of wetlands. Basing the ordination on presence or absence rather than average abundance enhanced the influence of taxa that were large, rare, or seasonally restricted in occurrence. We did the analysis using functions from the MASS library in S-Plus (Venables and Ripley 2002), implemented with a function from the Laboratory for Dynamic Synthetic Vegetation Phenomenology (D. Roberts, Utah State University, Logan, Utah; <http://labdsv.nr.usu.edu/>).

To assess family-specific differences between

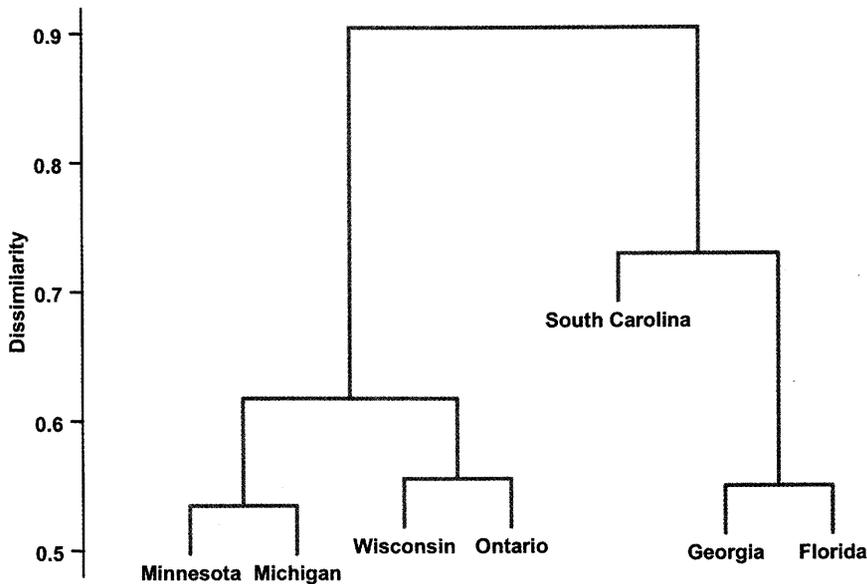


FIG. 1. Similarities in composition of macroinvertebrates from forested depressional wetlands across eastern North America. Sources were: Minnesota (our study), South Carolina (our study), Michigan (Kenk 1949), Ontario (Wiggins et al. 1980), Wisconsin (Schneider and Frost 1996), Florida (Leslie et al. 1997), and Georgia (Golladay et al. 1999). Cluster analysis was done on presence/absence data presented in the Appendix.

the South Carolina and Minnesota wetlands, we calculated average abundances per wetland for each family of macroinvertebrates and used those values to calculate the family average abundance and 95% confidence interval (CI) for both areas. We then determined the 20 most abundant macroinvertebrate families for South Carolina and Minnesota and assessed whether any of these families occurred exclusively in one location or the other (families that were abundant in one location but occurred in even very low numbers in the other did not meet this criterion). For families occurring at both locations, we determined whether 95% CIs for sample abundances overlapped, and we qualitatively assessed whether those families were dominated by the same or different genera. We could identify only late-stage immatures or adults reliably to genus, so we did not quantify abundances of genera. Instead, we identified cases where 1 or 2 genera dominated collections (made up >90% of identified individuals) for a particular family, and we used that information to determine if families common in both South Carolina and Minnesota were dominated by similar or different genera.

Results

Regional patterns

Cluster analysis of macroinvertebrate presence and absence revealed 2 distinct groups (Fig. 1). Forested depressional wetlands from Minnesota, Michigan, Ontario, and Wisconsin (northern latitudes) made up one group, whereas forested depressional wetlands from South Carolina, Florida, and Georgia (southern latitudes) made up the second. Macroinvertebrates indicative of northern habitats (taxa that occurred in at least 3 of the 4 northern sites, and none of the 3 southern sites; χ^2 tests, $p < 0.05$) included Sphaeriidae, Lumbriculidae, Lymnaeidae, Physidae, Limnephilidae, Chirocephalidae, Leptoceridae, Nepidae, and Hirudinea (Glossophoniidae and/or Erpobdellidae) (Appendix). Macroinvertebrate taxa indicative of southern sites (taxa that occurred at all 3 southern sites and ≤ 1 of the 4 northern sites) included Asellidae, Crangonyctidae, Noteridae, and Cambaridae (Appendix). The South Carolina location, which was the most northerly site in the southern cluster, held a somewhat intermediate position in the cluster analysis (Fig. 1). The Mich-

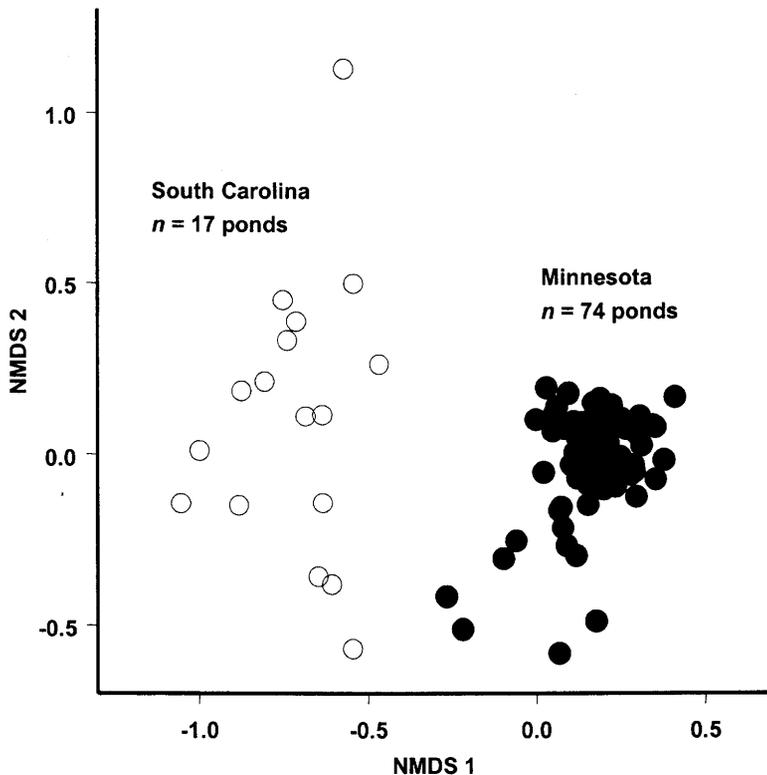


FIG. 2. Patterns in composition of macroinvertebrate assemblages among forested depressional wetlands in South Carolina and Minnesota. Nonmetric multidimensional scaling (NMDS) ordination was done on a matrix of Jaccard dissimilarities in taxonomic composition.

igan location, which was the most southerly site in the northern cluster, was the only site that contained both northern (sphaeriids, lumbriculids, lymnaeids, physids, limnephilids, leeches) and southern taxa (asellids, crangonyctids, cambarids) (Appendix).

South Carolina and Minnesota forested depressional wetland faunas

The NMDS ordination showed a distinct separation between macroinvertebrate assemblages in South Carolina and Minnesota ponds (Fig. 2). The correlation coefficient between ordination distances (in 2 dimensions) and Jaccard dissimilarities was 0.925. The analysis also showed substantial variation among assemblages within each of the 2 locations.

An examination of the 20 most abundant families in South Carolina and Minnesota (Table 1) showed that the lists included several of the families characteristic of southern (Aselli-

dae, Crangonyctidae, Noteridae) or northern (Sphaeriidae, Lumbriculidae, Lymnaeidae, Physidae, Limnephilidae, Chirocephalidae) forested depressional wetlands. The 2nd most abundant macroinvertebrates in South Carolina (Asellidae) and Minnesota (Sphaeriidae) were characteristic of southern and northern forested depressional wetlands, respectively. Several other macroinvertebrates associated with northern regions also were very abundant in the Minnesota wetlands (Lumbriculidae: 4th, Physidae: 6th, Limnephilidae: 8th, Lymnaeidae: 10th). Although never particularly abundant, 2 leech families, Erpobdellidae and Glossophoniidae, were among the largest macroinvertebrates encountered in our study. Leeches were a characteristic northern taxon, and they occurred in 61% of the Minnesota wetlands, but were never collected from the South Carolina wetlands. Some compositional differences were evident only at the generic level. For example, Chaoboridae held similar relative abundance

TABLE 1. Mean numbers ($\pm 95\%$ confidence interval [CI] per wetland (/1-m sweep; roughly equivalent to 0.3 m²) of the 20 most abundant macroinvertebrate families collected from South Carolina and Minnesota forested depressional wetlands. * indicates families that were collected only in that location.

Rank	South Carolina ($n = 17$)			Minnesota ($n = 74$)		
	Family	Mean ($\pm 95\%$ CI)	% occurrence	Family	Mean ($\pm 95\%$ CI)	% occurrence
1	Chironomidae	14.2 (5.0)	100	Chironomidae	57.3 (14.4)	100
2	Asellidae*	3.12 (2.70)	41	Sphaeriidae*	53.9 (11.8)	95
3	Lynceidae	0.76 (1.50)	18	Culicidae	11.7 (10.0)	81
4	Dytiscidae	0.70 (0.48)	88	Lumbriculidae*	10.7 (4.0)	100
5	Culicidae	0.44 (0.36)	65	Lynceidae	8.84 (5.84)	51
6	Notonectidae	0.37 (0.18)	76	Physidae*	6.32 (2.06)	89
7	Corixidae	0.27 (0.18)	59	Planorbidae*	5.58 (2.46)	82
8	Chaoboridae	0.18 (0.14)	41	Limnephilidae*	3.64 (0.96)	78
9	Hydrophilidae	0.11 (0.10)	35	Chaoboridae	2.52 (0.66)	90
10	Gyrinidae	0.08 (0.14)	12	Lymnaeidae*	1.81 (0.98)	55
11	Naucoridae*	0.06 (0.06)	29	Chirocephalidae*	1.66 (2.26)	32
12	Gammaridae*	0.05 (0.08)	18	Dytiscidae	0.95 (0.22)	90
13	Crangonyctidae*	0.04 (0.08)	6	Ceratopogonidae	0.90 (0.42)	65
14	Coenagrionidae	0.03 (0.04)	12	Haliplidae	0.79 (0.26)	77
15	Noteridae*	0.03 (0.04)	12	Corixidae	0.77 (0.60)	39
16	Gerridae	0.03 (0.04)	12	Libellulidae	0.62 (0.32)	72
17	Lestidae	0.02 (0.04)	12	Lumbriculidae*	0.57 (0.46)	38
18	Libellulidae	0.02 (0.04)	12	Hydrophilidae	0.55 (0.60)	74
19	Tabanidae	0.02 (0.04)	6	Dixidae*	0.43 (0.18)	60
20	Tubificidae*	0.02 (0.02)	12	Lestidae	0.30 (0.20)	37

rankings in South Carolina (8th) and Minnesota (9th), but most individuals in South Carolina were *Chaoborus*, whereas most individuals in Minnesota were *Mochlonyx*.

Some families were ubiquitous across the 7 study locations (Appendix), but quantitative comparisons between South Carolina and Minnesota indicated that relative abundances varied. Chironomidae (primarily *Chironomus* and *Polypedilum*) was the most abundant family in both South Carolina and Minnesota forested depressional wetlands. Chironomid relative abundance was 4 \times greater in Minnesota than South Carolina (and 95% CIs did not overlap, Table 1), although midges actually made up a greater % of the community in the South Carolina wetlands than the Minnesota wetlands (Table 1). Culicidae (mostly *Aedes*) was among the 5 most abundant macroinvertebrates in both South Carolina and Minnesota wetlands, but relative abundance was greater in Minnesota than South Carolina (Table 1). The Notonectidae (*Notonecta*) was the sole ubiquitous family (ranked 6th in South Carolina and unranked in Minnesota) that had a greater relative abundance in the South Carolina wetlands (South Carolina: 0.37

individuals/sweep \pm 0.18 [95% CI] vs Minnesota: 0.04 individuals/sweep \pm 0.06 [95% CI]). Because a variety of sampling methods were used by the researchers in Michigan, Ontario, Wisconsin, Florida, and Georgia, and not all studies reported abundance data, we could not assess whether abundance differences between South Carolina and Minnesota reflected a regional pattern.

Discussion

Compositional differences between northern and southern forested depressional wetlands

Clear compositional differences existed between macroinvertebrate communities of southern and northern forested depressional wetlands (Fig. 1, Appendix). The fauna at our South Carolina sites resembled the communities in forested depressional wetlands at other southern locations (Georgia, Florida), and the fauna in Minnesota resembled the communities at other northern locations (Michigan, Wisconsin, and Ontario). Quantitative sampling in South Carolina and Minnesota suggested that many of the

taxa differing between regions were not ecologically incidental forms, but included some of the largest and most abundant organisms present in these ecosystems (e.g., Asellidae, Cambaridae, Sphaeriidae, Lumbriculidae, Physidae, Planorbidae, Limnephilidae, Hirudinea). For some of the less common organisms, varying sampling intensities and sampling methods among studies might have influenced detection and so those differences should be viewed with caution. We focus our discussion on those taxa that differed most dramatically between the southern and northern sites.

We suspected that different environmental conditions between regions affected macroinvertebrate distributions. However, southern and northern locations differed in many ways (climate, geology, hydrology, vegetation), and isolating the mechanisms for variation in macroinvertebrate distributions would have been difficult. Furthermore, we lacked comprehensive water chemistry and environmental data from the other published studies used for our regional faunal comparisons, so quantitative regional analyses could not be conducted. However, certain features of southern and northern areas merit discussion.

The most striking faunal difference between southern and northern forested depressional wetlands occurred within the Mollusca. Sphaeriidae, Physidae, and Lymnaeidae were found at every northern habitat and these families were among the most abundant and widely distributed invertebrates in the Minnesota wetlands. However, these mollusks were not detected in any of the southern wetlands. We suspect that water chemistry plays a role in limiting distributions of mollusks in the southern habitats. Forested depressional wetlands across the southeastern US are typically acidic (pH <5; Leslie et al. 1997, Batzer et al. 2000, Entrekin et al. 2001, our study), primarily because they lack buffering capacity. In contrast, northern forested depressional wetlands tend to be less acidic because alkalinity (in the form of CaCO_3) is relatively high (Batzer et al. 2004). Mollusks require sufficient Ca concentration for shell development (Pennak 1989, Brown 1991, McMahon 1991), and in the absence of significant Ca, snails and clams may be physiologically unable to thrive in southern forested depressional wetlands (Taylor et al. 1999). This water chemistry link is further supported because snails and

clams are very rare in other acidic, precipitation-based wetlands of the south (other than forested depressional wetlands) including flatwoods marshes of Florida (Evans et al. 1999) and the Okefenokee Swamp of Georgia (Kratzer 2003). In contrast, snails and clams are common in southern wetlands that receive significant input from more Ca-rich groundwater or river floodwater including the Florida Everglades (Rader 1999) and some river floodplains (Merritt et al. 1999, Smock 1999, Reese 2004). Like the mollusks, leeches of northern forested depressional wetlands are intolerant of acid conditions (Pennak 1989), and they also may be chemically excluded from many southern forested depressional wetlands.

Different phenologies of flooding between regions might help explain why limnephilid caddisflies were restricted to northern sites. Wiggins (1996) reported that reproductive maturity of limnephilid adults was delayed by diapause until late summer and early autumn when many northern depressional wetlands begin to refill. However, forested depressional wetlands in southern locations typically are driest during this time period, so even if Limnephilidae occurred in the vicinity of these habitats, they would have few opportunities to oviposit.

Some invertebrates were characteristic of southern forested depressional wetlands. Asellidae and Crangonyctidae were collected mostly from southern wetlands, but geology or geography per se probably did not limit their distributions. These crustaceans have been collected from previously glaciated portions of western New York (Batzer and Sion 1999) and southern Michigan (Kenk 1949, Higgins and Merritt 1999). In their New York study, Batzer and Sion (1999) proposed that old-growth deciduous forest conditions (intense shading and abundant leaf litter) made drought conditions less harsh for asellids and crangonyctids, which do not have well developed desiccation-resistant stages (Wiggins et al. 1980). Latitudinal changes in forest communities might affect the environmental conditions in embedded depressional wetlands and, in turn, the distributions of macroinvertebrates.

Those taxa with the most pronounced regional differences tended to be flightless forms such as mollusks (clams and snails), annelids (worms and leeches), and crustaceans (isopods and amphipods). Organisms that lack efficient dispers-

al may specialize on narrower sets of environmental conditions and have more restricted distributions than organisms that disperse efficiently. Flying insect families typically were ubiquitous, although genera and species probably varied among locations.

Additional data on taxonomic patterns in forested depressional wetlands

The data available cannot generate a complete picture of the geographic variation in macroinvertebrate communities among wetlands of eastern and central North America. Published descriptions of macroinvertebrate communities are unavailable for extensive portions of the region, including south-central states (Alabama, Mississippi, Tennessee), mid-latitude states (Virginia, North Carolina, Ohio, Kentucky), New England and the eastern provinces of Canada, and northern Canada. However, population-level and partial-community descriptions can provide some information. In Massachusetts, Brooks (2000) collected unknown mollusk and leech families, a composition that suggests northern characteristics. As in Minnesota, Sphaeriidae was among the most abundant macroinvertebrates in wetlands of western New York (Batzer and Sion 1999). Most of the typical northern taxa (Sphaeriidae, Lymnaeidae, Physidae, Limnephilidae, Hirudinea), but no typical southern taxa, were collected in wetlands in western Pennsylvania (C. R. Orr and S. A. Wisinger, Allegheny College, Meadville, Pennsylvania, unpublished data). Limnephilids have been collected from a wetland in West Virginia (Stout and Stout 1989), extending the known distribution of that family in forested depressional wetlands further south than Pennsylvania. In a preliminary survey of 13 forested depressional wetlands of North Carolina and Virginia, we (DPB, SED-B, BET, and AED, unpublished data) found leeches and asellids, but not mollusks, a composition that suggests a mixture of northern and southern characteristics. In 12 forested depressional wetlands of east-central Georgia, asellids and crangonyctids were common, and mollusks were absent (Batzer et al. 2000, Batzer, unpublished data), a composition that resembles the pattern in surrounding southern areas. Leeches (Leeper and Taylor 1998) and chirocephalid fairy shrimp (DeBiase and Taylor 2003), both primarily northern taxa,

were found in forested depressional wetlands in South Carolina (near our study sites), but they were not particularly common. These population and partial-community studies indicate that the northern and southern distributions proposed in our paper probably have general applicability, but the distributions clearly are not absolute. As more complete community descriptions become available from forested depressional wetlands across eastern and central North America, wetland ecologists will be able to test and refine the distributional and functional framework proposed in our study.

Ecological roles of macroinvertebrates in forested depressional wetlands

The ecological roles of macroinvertebrates in forested depressional wetlands appeared to differ regionally. We found that overall macroinvertebrate numbers in Minnesota wetlands dwarfed those in South Carolina (Table 1) and this difference in abundance may have reflected a productivity difference; unfortunately, density data were not available from the other northern and southern locations, so we could not determine if the difference was regional. However, the trophic structure of invertebrate communities in southern and northern sites was clearly different. Scrapers (Physidae, Planorbidae, Lymnaeidae) and shredders (Limnephilidae) were widespread and abundant only in the northern habitats, so these macroinvertebrate functions probably were more important in northern than southern forested depressional wetlands. Asellidae, which were abundant in many southern habitats, consume a wide variety of foods including macrophyte detritus and algae (Pennak 1989), and they may partially fill those niches in southern wetlands; the feeding ecology of this important group needs to be more thoroughly assessed. The southern and northern wetlands shared many common collector taxa, but only collector-gatherers (Chironomidae, Culicidae, Lyncidae) were ubiquitous, and collector-filterers (Sphaeriidae) were common only in northern habitats. Macroinvertebrate predators were also ubiquitous, but the hemipterans, especially the Notonectidae, were a more important component of the predator complex in South Carolina wetlands than those in Minnesota. Because Hemiptera differ from other macroinvertebrate predators (Odonata, Coleoptera, Diptera) in

terms of feeding mode (piercing-sucking vs engulfing) and hunting behavior (chase-and-subdue vs ambush), the kinds of prey selected by macroinvertebrate predators may differ regionally. Bottom-up and top-down pathways of energy flow through macroinvertebrates in food webs of forested depressional wetlands probably differ regionally (see discussion in Wissinger 1999), and it will be important to account for such regional characteristics when studying the ecology of these ecosystems.

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Literature Cited

- ANDERSON, C. R., B. L. PECKARSKY, AND S. A. WISSINGER. 1999. Tinajas of southeastern Utah: invertebrate reproductive strategies and the habitat template. Pages 791-810 in D. P. Batzer, R. B. Rader, and S. A. Wissinger (editors). *Invertebrates in freshwater wetlands of North America: ecology and management*. John Wiley and Sons, New York.
- BARTON, C., AND J. SINGER. 2001. Carolina bay restoration: SRS wetland mitigation bank documentation. Center for Forested Wetlands Research, Charleston, South Carolina. (Available from: Center for Forested Wetland Research, 2730 Savannah Highway, Charleston, South Carolina 29414 USA.)
- BATZER, D. P., C. R. JACKSON, AND M. MOSNER. 2000. Influences of riparian logging on plants and invertebrates in small, depressional wetlands of Georgia, U.S.A. *Hydrobiologia* 441:123-132.
- BATZER, D. P., B. J. PALIK, AND R. BUECH. 2004. Relationships between environmental characteristics and macroinvertebrate communities in seasonal woodland ponds of Minnesota. *Journal of the North American Benthological Society* 23:50-68.
- BATZER, D. P., R. B. RADER, AND S. A. WISSINGER (EDITORS). 1999. *Invertebrates in freshwater wetlands of North America: ecology and management*. John Wiley and Sons, New York.
- BATZER, D. P., AND V. H. RESH. 1992. Macroinvertebrates of a California seasonal wetland and responses to experimental habitat manipulation. *Wetlands* 12:1-7.
- BATZER, D. P., A. S. SHURTLEFF, AND R. B. RADER. 2001. Sampling invertebrates in wetlands. Pages 339-354 in R. B. Rader, D. P. Batzer, and S. A. Wissinger (editors). *Bioassessment and management of North American freshwater wetlands*. John Wiley and Sons, New York.
- BATZER, D. P., AND K. SION. 1999. Autumnal woodland pools of western New York: temporary habitats that support permanent water invertebrates. Pages 319-332 in D. P. Batzer, R. B. Rader, and S. A. Wissinger (editors). *Invertebrates in freshwater wetlands of North America: ecology and management*. John Wiley and Sons, New York.
- BATZER, D. P., AND S. A. WISSINGER. 1996. Ecology of insect communities in nontidal wetlands. *Annual Review of Entomology* 41:75-100.
- BROOKS, R. T. 2000. Annual and seasonal variation and the effects of hydroperiod on benthic macroinvertebrates of seasonal forest ("vernal") ponds in central Massachusetts, USA. *Wetlands* 20:707-715.
- BROWN, K. M. 1991. Mollusca: Gastropoda. Pages 285-314 in J. H. Thorp and A. P. Covich (editors). *Ecology and classification of North American freshwater invertebrates*. Academic Press, New York.
- CHEAL, F., J. A. DAVIS, J. E. GROWNS, J. S. BRADLEY, AND F. H. WHITTLES. 1993. The influences of sampling method on the classification of wetland macroinvertebrate communities. *Hydrobiologia* 257:47-56.
- DEBIASE, A. E., AND B. E. TAYLOR. 2003. New reports of fairy shrimps (Crustacea: Anostraca) and clam shrimps (Crustacea: Laevicaudata and Spinicaudata) from South Carolina. *Southeastern Naturalist* 2:207-216.
- DIETZ-BRANTLEY, S. E., B. E. TAYLOR, D. P. BATZER, AND A. E. DEBIASE. 2002. Invertebrates that aestivate in dry basins of Carolina bay wetlands. *Wetlands* 22:767-775.
- ENTREKIN, S. A., S. W. GOLLADAY, AND D. P. BATZER. 2001. The influence of plant community on chironomid secondary production in two wetland types: cypress-gum swamps and grass-sedge marshes. *Archiv für Hydrobiologie* 152:369-394.
- EVANS, D. L., W. J. STREEVER, AND T. L. CRISMAN. 1999. Natural flatwoods marshes and created freshwater marshes of Florida: factors influencing aquatic

- invertebrate distribution and comparisons between natural and created marsh communities. Pages 81–104 in D. P. Batzer, R. B. Rader, and S. A. Wissinger (editors). *Invertebrates in freshwater wetlands of North America: ecology and management*. John Wiley and Sons, New York.
- GOLLADAY, S. W., S. ENTREKIN, AND B. W. TAYLOR. 1999. Forested limesink wetlands of southwest Georgia: invertebrate habitat and hydrologic variation. Pages 197–216 in D. P. Batzer, R. B. Rader, and S. A. Wissinger (editors). *Invertebrates in freshwater wetlands of North America: ecology and management*. John Wiley and Sons, New York.
- HALL, D. L., M. R. WILLIG, D. L. MOORHEAD, R. W. SITES, E. B. FISH, AND T. R. MOLLHAGEN. 2004. Aquatic macroinvertebrate diversity of playa wetlands: the role of landscape and island biogeographic characteristics. *Wetlands* 24:77–91.
- HIGGINS, M. J., AND R. W. MERRITT. 1999. Temporary woodland ponds in Michigan: invertebrate seasonal patterns and trophic relationships. Pages 279–297 in D. P. Batzer, R. B. Rader, and S. A. Wissinger (editors). *Invertebrates in freshwater wetlands of North America: ecology and management*. John Wiley and Sons, New York.
- KENK, R. 1949. The animal life of temporary and permanent ponds in southern Michigan. *Miscellaneous Publication 71*. Museum of Zoology, University of Michigan, Ann Arbor, Michigan.
- KRATZER, E. B. 2003. Invertebrate communities of the Okefenokee Swamp. MS Thesis, University of Georgia, Athens, Georgia.
- LEEPER, D. A., AND B. E. TAYLOR. 1998. Abundance, biomass and production of aquatic invertebrates in Rainbow Bay, a temporary wetland in South Carolina, USA. *Archiv für Hydrobiologie* 143: 335–362.
- LESLIE, A. J., T. L. CRISMAN, J. P. PRENGER, AND K. C. EWEL. 1997. Benthic macroinvertebrates of small Florida pondcypress swamps and the influence of dry periods. *Wetlands* 17:447–455.
- MCMAHON, R. F. 1991. Mollusca: Bivalvia. Pages 315–399 in J. H. Thorp and A. P. Covich (editors). *Ecology and classification of North American freshwater invertebrates*. Academic Press, New York.
- MERRITT, R. W., AND K. W. CUMMINS (EDITORS). 1996. *An introduction to the aquatic insects of North America*. 3rd edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.
- MERRITT, R. W., M. J. HIGGINS, K. W. CUMMINS, AND B. VANDENEEDEN. 1999. The Kissimmee river-riparian marsh ecosystem, Florida: seasonal differences in invertebrate functional feeding group relationships. Pages 55–79 in D. P. Batzer, R. B. Rader, and S. A. Wissinger (editors). *Invertebrates in freshwater wetlands of North America: ecology and management*. John Wiley and Sons, New York.
- PALIK, B., D. P. BATZER, R. BUECH, D. NICHOLS, K. CEASE, L. EGELAND, AND D. E. STREBLOW. 2001. Seasonal pond characteristics across a chronosequence of adjacent forest ages in northern Minnesota, U.S.A. *Wetlands* 21:532–542.
- PALIK, B. J., R. BUECH, AND L. EGELAND. 2003. Using an ecological land hierarchy to predict seasonal-wetland abundance in upland forests. *Ecological Applications* 13:1153–1163.
- PENNAK, R. W. 1989. *Fresh-water invertebrates of the United States: Protozoa to Mollusca*. 3rd edition. John Wiley and Sons, New York.
- RADER, R. B. 1999. The Florida Everglades: natural variability, invertebrate diversity, and foodweb stability. Pages 25–54 in D. P. Batzer, R. B. Rader, and S. A. Wissinger (editors). *Invertebrates in freshwater wetlands of North America: ecology and management*. John Wiley and Sons, New York.
- REESE, E. A. 2004. Invertebrate communities along a continuum of floodplains in the Altamaha River Watershed, Georgia. MS Thesis, University of Georgia, Athens, Georgia.
- SCHNEIDER, D. W., AND T. M. FROST. 1996. Habitat duration and community structure in temporary ponds. *Journal of the North American Benthological Society* 15:64–86.
- SMOCK, L. A. 1999. Riverine floodplain forests of the Southeastern United States: invertebrates in an aquatic-terrestrial ecotone. Pages 137–165 in D. P. Batzer, R. B. Rader, and S. A. Wissinger (editors). *Invertebrates in freshwater wetlands of North America: ecology and management*. John Wiley and Sons, New York.
- STOUT, B. M., AND J. S. STOUT. 1989. Northern caddisfly (Trichoptera) fauna in a remnant boreal wetlands of West Virginia. *Entomological News* 100:37–40.
- TAYLOR, B. E., D. A. LEEPER, M. C. MCCLURE, AND A. E. DEBIASE. 1999. Carolina bays: ecology of aquatic invertebrates and perspectives on conservation. Pages 167–196 in D. P. Batzer, R. B. Rader, and S. A. Wissinger (editors). *Invertebrates in freshwater wetlands of North America: ecology and management*. John Wiley and Sons, New York.
- THORP, J. H., AND A. P. COVICH (EDITORS). 1991. *Ecology and classification of North American freshwater invertebrates*. Academic Press, New York.
- VENABLES, W. N., AND B. D. RIPLEY. 2002. *Modern applied statistics with S-Plus*. 4th edition. Springer, Secaucus, New Jersey.
- WARD, H. B., AND G. C. WHIPPLE. 1945. *Fresh-water biology*. John Wiley, New York.
- WIGGINS, G. B. 1996. *Larvae of the North American caddisfly genera*. 2nd edition. University of Toronto Press, Toronto, Canada.

- WIGGINS, G. B., R. J. MACKAY, AND I. M. SMITH. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. *Archiv für Hydrobiologie Supplement* 58:97–206.
- WISSINGER, S. A. 1999. Ecology of wetland invertebrates: synthesis and applications for conservation and management. Pages 1043–1086 in D. P. Batzer, R. B. Rader, and S. A. Wissinger (editors). *Invertebrates in freshwater wetlands of North America: ecology and management*. John Wiley and Sons, New York.
- WISSINGER, S. A., AND L. J. GALLAGHER. 1999. Beaver pond wetlands in northwestern Pennsylvania: modes of colonization and succession after drought. Pages 333–362 in D. P. Batzer, R. B. Rader, and S. A. Wissinger (editors). *Invertebrates in freshwater wetlands of North America: ecology and management*. John Wiley and Sons, New York.

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APPENDIX. Presence (x) and absence (blank) of macroinvertebrates in forested depressional wetlands from 7 locations of eastern North America. Sources, arranged from north to south, were: Minnesota (our study), Wisconsin (Schneider and Frost 1996), Ontario (Wiggins et al. 1980), Michigan (Kenk 1949), South Carolina (our study), Georgia (Golladay et al. 1999), and Florida (Leslie et al. 1997).

Class or order	Family	South							
		Minnesota	Wisconsin	Ontario	Michigan	Carolina	Georgia	Florida	
Hirudinea		x	x	x	x				
Oligochaeta	Enchytraeidae			x					
	Lumbricidae	x		x					
	Lumbriculidae	x		x	x				
	Naididae				x				
Gastropoda	Tubificidae				x	x			
	Ancylidae						x		
	Lymnaeidae	x	x	x	x				
	Physidae	x	x	x	x				
Bivalvia	Planorbidae	x	x	x	x		x		
	Sphaeriidae	x	x	x	x				
Ephemeroptera		x	x	x		x	x	x	
Odonata	Aeshnidae		x			x	x	x	
	Coenagrionidae	x	x		x	x	x	x	
	Corduliidae		x						
	Corethrellidae							x	
	Lestidae	x	x	x	x	x	x	x	
	Libellulidae	x	x	x	x	x	x	x	
	Protoneuridae						x		
	Hemiptera	Corixidae	x	x	x	x	x	x	
		Gerridae	x	x	x	x	x	x	x
		Hydrometridae				x			
Lygaeidae							x		
Mesoveliidae							x	x	
Naucoridae						x			
Nepidae			x	x	x				
Notonectidae		x	x	x	x	x	x	x	
Ortheziiidae							x		
Pleidae		x			x				
Neuroptera	Saldidae						x		
	Veliidae						x	x	
	Sisyridae						x		
Megaloptera	Corydalidae						x		
	Sialidae							x	

APPENDIX. Continued.

Class or order	Family	Minnesota	Wisconsin	Ontario	Michigan	South			
						Carolina	Georgia	Florida	
Trichoptera	Hydroptilidae	x					x	x	
	Leptoceridae	x	x		x				
	Limnephilidae	x	x	x	x				
	Phryganeidae		x	x	x	x			
	Polycentropodidae	x		x					
Lepidoptera	Pyralidae	x					x	x	
Coleoptera	Carabidae							x	
	Chrysomelidae						x	x	
	Dytiscidae	x	x	x	x	x	x	x	
	Gyrinidae	x	x	x		x	x	x	
	Haliplidae	x	x	x	x	x	x	x	
	Histeridae							x	
	Hydraenidae							x	
	Hydrochidae						x		
	Hydrophilidae	x	x	x		x	x	x	
	Noteridae					x	x	x	
	Scirtidae	x						x	
	Staphylinidae	x						x	
	Diptera	Cecidomyiidae						x	x
		Ceratopogonidae	x		x	x		x	x
		Chironomidae	x	x	x	x	x	x	x
		Chaoboridae	x	x	x	x	x	x	x
		Culicidae	x	x	x	x	x	x	x
Dixidae		x			x				
Dolichopodidae					x			x	
Ephydriidae		x			x			x	
Empididae							x		
Muscidae						x			
Psychodidae		x			x			x	
Sciaridae								x	
Sciomyzidae				x					
Stratiomyidae		x		x	x	x			
Syrphidae		x							
Tabanidae		x		x	x	x	x	x	
Tetanoceridae					x				
Tipulidae	x					x	x		
Isopoda	Asellidae				x	x	x	x	
Amphipoda	Crangonyctidae				x	x	x	x	
	Hyalessidae			x					
Conchostraca	Lynceidae	x	x		x	x			
Anostraca	Chirocephalidae	x	x	x	x				
	Streptocephalidae					x			
Notostraca	Triopsidae	x							
Decapoda	Cambaridae				x	x	x	x	