Habitat Variation Among Aquatic Gastropod Assemblages of Indiana, USA

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Abstract: We collected aquatic gastropods at 137 sites in lakes and streams of Indiana and tested for patterns of assemblages with environmental variables. The survey resulted in 32 species with a mean of 2.8 species at each site, and a mean abundance at each site of 144 individuals. Nonmetric multidimensional scaling (NMS) multivariate analyses resulted in watershed drainage area, water conductivity, substrate category frequency, and dissolved oxygen as significant correlates of gastropod assemblage structure. Gastropod assemblages of lakes were not significantly different than assemblages of streams in the ordination. Prosobranch taxa occurred in higher abundances than pulmonate taxa at sites with lower conductivity in larger watersheds. There were no pairs of gastropod species that tended to co-occur more frequently than random. Our analyses resulted in local environmental variables providing explanation of aquatic gastropod assemblage structure.

Keywords: Gastropods, ecological distribution, snails, multivariate analysis, freshwater, assemblage.

INTRODUCTION

Lodge *et al.* [1] reviewed ecological studies of freshwater gastropods and concluded that biogeographical distributions are primarily controlled by physicochemical variables. Calcium is required at a minimum level (~ 5.2 mg Ca / l; [1]). However, there are exceptions to the importance of calcium. For example, several species of British freshwater gastropods require high calcium concentrations [2]. Biotic variables such as predation and competition were more important at local scales. Local gastropod occurrence patterns are under the influence of multiple variables. The architecture of available habitats is important to freshwater gastropods. Brown [3] showed that gastropods have preferences for macrophyte species with broader leaves, and these preferences were present in the field and in lab experiments. Antoine *et al.* [4] found differences in gastropod assemblages in wetlands that differed by type of dominant macrophytes. Macrophytes with the majority of their vegetative structures above water had higher gastropod species richness and higher densities than macrophytes with only underwater structures.

Lake assemblages vary with lake area, spatial position, water chemistry, predators, and competitors [5]. Stream assemblages are controlled by similar variables at regional scales. However, local habitats are predominately controlled by the local flow regime [6]. Thus, fish [7] and macroinvertebrate assemblages [8] respond to local habitat variation in small streams. In large river systems habitat variation is not as obvious to observers, but hydrologic variation provides a strong explanation of fish assemblage variation [6, 9].

The impacts of predation and competition on local assemblages vary with study system. Dillon [10] reviewed predation studies of molluscs. Multiple taxa consume freshwater gastropods, and predator effects vary among gastropod species based on shell shape and strength. Lodge *et al.* [1] found abundant evidence of strong predation effects of fish and crayfish on freshwater gastropods. In addition, invertebrate predators including dragonflies exert strong effects on gastropod species and abundance patterns in ponds that lack fish or crayfish [11]. Variation in shell thickness and strength covaries with risk of predation [12]. Gastropods respond behaviorally to predators, especially fish [12] and crayfish [13]. For example, physid snails hide under cover to avoid exposure to fish [14]. Lodge *et al.* [1] concluded that the presence of predators is a strong control on local gastropod abundance across lake habitats. Competition may structure gastropod assemblages in some situations such as temporary ponds [15]. However, the strength of competition in local assemblages appears to be slight compared to the importance of disturbance and predation [1].

Area effects on gastropod distribution, species richness, and abundance in local habitats are common [1, 16, 17]. Larger streams and larger habitats tend to have higher species richness. Lewis and Magnuson [5] found that the number of lake connections (inlets and outlets that apparently act as dispersal corridors) was correlated with species richness in Northern Highland lakes of Wisconsin and Michigan, USA. Dillon and Benfield [18] showed that pulmonates increased in abundance in larger stream watersheds with higher alkalinity. Area effects are likely important in structuring all gastropod assemblages.

Relatively few studies exist that examine detailed distributions of lotic gastropod assemblages [19]. Gastropod studies in streams have primarily been in small-order streams and tend to be studies of pulmonates (e.g., [18, 20, 21]). An exception is Greenwood and Thorp [19], who found substantial variation in the distributions, diets, and substrate usage among two prosobranch (coenogastropod) gastropods that

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occur in a large river, the Ohio River. Variation was attributed to differences in susceptibility to predation, resulting in the gastropods inhabitating different water depths.

Brown *et al*. [21] reviewed the ecology of pulmonate and prosobranch (= coenogastropod) freshwater gastropods and predicted distribution differences based on shell shape, life history, and physiology. Pulmonates are able to use aerial respiration, have shells with higher drag coefficients, and have life history characteristics of higher reproductive rates, shorter life cycles, and stronger dispersal abilities. Prosobranchs have gills and are limited to aquatic habitats, with shells that tend to be streamlined, and have life history characteristics that are the opposite of pulmonates. Habitats with increased disturbance, decreased predation pressure, and where food is not a limiting factor are predicted to have higher abundances of pulmonates [21].

We surveyed the aquatic gastropods of Indiana by sampling 137 sites. Our interest was to examine distribution patterns of these species and test for relationships with regional, spatial variables and local environmental variables. We tested if pulmonate and prosobranch species occur in different habitats, as suggested by Brown *et al*. [21]. In addition, we tested if gastropod species co-occurrence patterns are due to species combinations that occur less than expected because of competition.

MATERIALS AND METHODS

Indiana is in the mid-western United States with physiography consisting primarily of glacial till plains and a total area of 94,000 km^2. The majority of the state is in the Central Lowland province with small local topographical relief. The southern limit of glaciation is a boundary line between the Central Lowland and the southern Low Plateau. One fourth of the state along the north is in the Eastern Lake Section, with many moraine lakes formed from glacial drift. Two major watersheds drain the state: the Great Lakes are immediately North, and the remainder of the state is in the Mississippi River basin. The Illinois River watershed includes the Kankakee River to the northwest. The majority of the state is within the Wabash River watershed that drains to the Ohio River [22].

The human footprint has been large in Indiana. About 98 % of land is used for cropland, pasture, or development (GAP Bulletin Number 5, 1996, www.gap.uidaho.edu/ Bulletins/5/Default.htm). The northern 24 % of the state was predominately wetland prior to European settlement, and 85 % of these wetlands have been lost, with drainage for agriculture the primary cause (IDNR, 1996, www.state.in.us/ wetlands/data). Gammon [23] found that the water quality of Indiana streams was severely altered by human impacts. Nearly all Indiana streams that are within the Wabash River watershed (> 70 % of the state) have hydrologic alterations (significant changes to the natural flow regime) that are caused primarily by agriculture and/or reservoir release [24]. The net result is a human-dominated landscape with habitat fragmentation and degradation, widespread pollution, and isolated plant and animal populations.

We visited 100 historical sites during summer months (Jun – Aug) of 2006-8 to collect aquatic gastropods (Fig. **1**). We sampled the historic sites to verify the current presence of museum material and we summarized this information elsewhere [25]. An additional 37 sites were in locations where historic samples were sparse [26]. Methods consisted of sampling all available habitats at each site, primarily by hand collections in shallows, on woody debris, on the undersides of stones, and on aquatic vegetation. Deeper areas and fine substrates were sampled with a net. Collection durations were the equivalent of one individual searching for 60 min. For example, two persons searched for 30 min [17]. Gastropods were preserved in 70 % ethanol and identified in the laboratory to the lowest possible taxonomic level using Burch [26]. Nomenclatural taxonomy was from Turgeon *et al*. [27] or Stewart [28] and all specimens will be deposited at the Illinois Natural History Survey Mollusc Collection (Champaign, IL). Environmental data collected at each site included water quality variables of water hardness using a Hach kit (hach.com), dissolved oxygen, water temperature, conductivity, and pH with a Hydrolab portable unit, GPS coordinates, and a visual estimate of substrate composition. Substrate presence/absence categories (silt, sand, gravel, cobble, boulder/bedrock) were reduced to fewer variables using principal components analysis (PCA). We obtained drainage area for sites from Hoggatt [29] and log-transformed values for analyses.

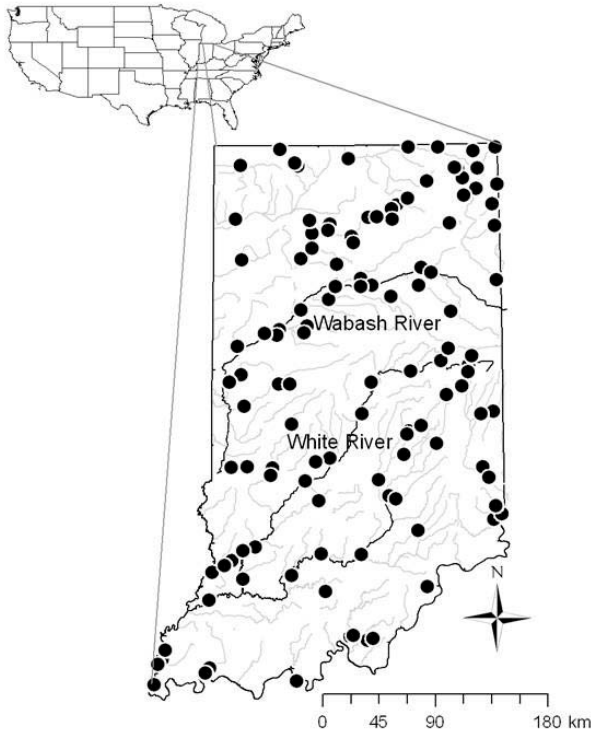

Fig. (1). Sites where aquatic gastropods were collected in Indiana, USA.

We calculated abundance as number of snails per min per person and tested for relationships with water hardness, dissolved oxygen, water temperature, conductivity, pH, and substrate variation using nonmetric multidimensional scaling (NMS) in PC-ORD (McCune and Grace, 2002). NMS is a multivariate analysis procedure that uses an iterative approach to produce an ordination that does not assume linear relationships [30]. We eliminated species that occurred at

fewer than three sites, transformed abundance by log (x+1) and used the following options for NMS: Bray-Curtis distance measure, a random starting configuration, and 40 runs with real data. We compared the ordination of pulmonate and coenogastropod taxa, and lake vs. stream sites with t-tests of resulting NMS axes. Water quality variables, subsequent substrate PCA axes, and Cartesian coordinates for northing and easting were examined for correlations with NMS axes.

We used EcoSim [31] to test for structure of gastropod assemblages from competition. We asked if species co-occur significantly more than expected based on a presence/absence matrix of species occurrences at sites. We calculated the C-score, the average number of checkerboard units between all possible pairs of species. The observed C-value was compared to expected values generated by 5000 randomizations using EcoSim default parameters.

Table 1. Ranked Abundances of Gastropod Taxa Collected in Indiana in 2006-8. Abbreviations are for Taxa in Figures

Taxa	Abundance	Abbreviation
Elimia livescens Menke, 1830	10,068	ElLi
Pleurocera acuta Rafinesque, 1831	3,262	PlAc
Physa acuta Draparnaud, 1805	2,069	PhAc
Stagnicola elodes Say, 1821	544	StEl
Fossaria spp. Say, 1822	544	Foss
Pleurocera canaliculata Say, 1821	279	PlCa
Planorbella trivolvis Say, 1817	218	PlTr
Pseudosuccinea columella Say, 1817	116	PsCo
Pomatiopsis cincinnatiensis I. Lea, 1850	75	PoCi
Birgella subglobosus Say, 1825	74	BiSu
Campeloma decisum Say, 1817	71	CaDe
Ferrissia rivularis Say, 1817	69	FeRi
Gyraulus parvus Say, 1817	34	GyPa
Gyraulus deflectus Say, 1824	34	GyDe
Amnicola limosus Say, 1817	25	AmLi
Physa gyrina Say, 1821	24	PhGy
Leptoxis praerosa Say, 1821	22	
Helisoma anceps Say, 1867	19	HeAn
Bellamya japonica von Martens, 1861	17	BeJa
Valvata lewisi Currier, 1868	13	
Bellamya chinensis Reeve, 1863	9	BeCh
Lithasia obovata Say, 1829	9	
Pyrgulopsis lustrica Pilsbry, 1890	9	PyLu
Viviparus georgianus Lea, 1834	7	
Cincinnatia integra Say, 1821	3	
Ferrissia fragilis Tryon, 1863	3	FeFr
Promenetus exacuous Say, 1821	2	
Stagnicola exilis I. Lea, 1838	2	
Laevapex fuscus C. B. Adams, 1841	1	
Planorbella campanulata Say, 1821	1	
Stagnicola catascopium Say, 1867	1	
Lymnaea stagnalis Linnaeus, 1758	1	

RESULTS

We collected 15,227 individuals, in 27 taxa at 137 sites (Fig. **1**). We did not find gastropods at 14 of these sites. The taxa with the highest abundances were *Elimia livescens, Physa acuta, Pleurocera acuta, Stagnicola elodes* and *Fossaria* spp. (Table **1**). The majority of taxa occurred at few sites – the average number of sites that individual taxa occurred was 11 (range, 1 - 75). The mean abundance of individuals at sites was 144 (range, 0 – 1463) and the mean number of species per site was 2.8 (range, 1 – 9). Twenty-seven of the sites were lakes or ponds and the other 110 sites were streams. The Principal Components Analysis of substrate categories resulted in a first axis that explained 23.3 % of total variation and contrasted sites with silt substrates negative, compared with positive sites that contained gravel and/or cobble substrates. Additional axes did not provide strong explanation of gastropod abundance patterns and are not further reported.

Mean water hardness was 302 mg $CaCO_3$ / l, and several species occurred at sites with higher mean hardness values (Fig. **2a**; *Amnicola limosus, Helisoma anceps, Physella gyrina, Campeloma decisum*). Mean conductivity was 558 µmhos, and variation among sites resulted in a similar pattern as mean water hardness (Fig. **2b**). Mean pH was 8.2 and only one species occurred at sites with low mean pH values (Fig. **2c**; *Ferrissia fragilis*). Gastropod species predominately occurred at sites with mean pH values between 7.8 - 8. Mean water temperature was 23 ℃ (range, 9 – 32) and mean dissolved oxygen was 8 mg/l (range, 4 – 13).

The NMS analysis resulted in three dimensions for the final solution with stress of 16.3, that was significantly lower than stress generated in 40 Monte Carlo randomizations ($P < 0.05$). The proportion of variance represented by each axis (R^2 between distance in ordination space and distance in original space) was reasonable for each axis (Table **2**). Gastropod assemblages in lakes were not significantly different from assemblages in streams for any of the NMS axes (2-sample t-tests, $P > 0.05$). The NMS ordination of the first two axes resulted in sites on the right (Fig. **3a**) with higher abundances of *Bellamya chinensis, Pleurocera acuta, Elimia livescens, Helisoma anceps,* and *Campeloma decisum* (Fig. **3b**). These sites had gravel and/or cobble substrates, lower conductivity, and were larger watersheds than sites on the left of the ordination (Fig. **3c**). Sites on the left of the NMS ordination had higher abundances of *Pyrgulopsis lustrica* and *Gyraulus deflectus*. The second NMS axis contrasted sites with increased abundances of *Stagnicola elodes, Physa gyrina, Ferrissia rivularis,* and *Planorbella trivolvis* (Fig. **3b**) and higher concentrations of dissolved oxygen (Fig. **3c**), with sites lower on the NMS ordination that had increased abundances of *Gyraulus parvus* and *Bellamya japonica* (Fig. **3b**). The third NMS axis contrasted sites on the top of the figure (Fig. **4a**) with increased abundances of *Pleurocera acuta* to lower sites that had higher abundances of *Planorbella campanulata, Ferrissia rivularis,* and *Fossaria* spp.

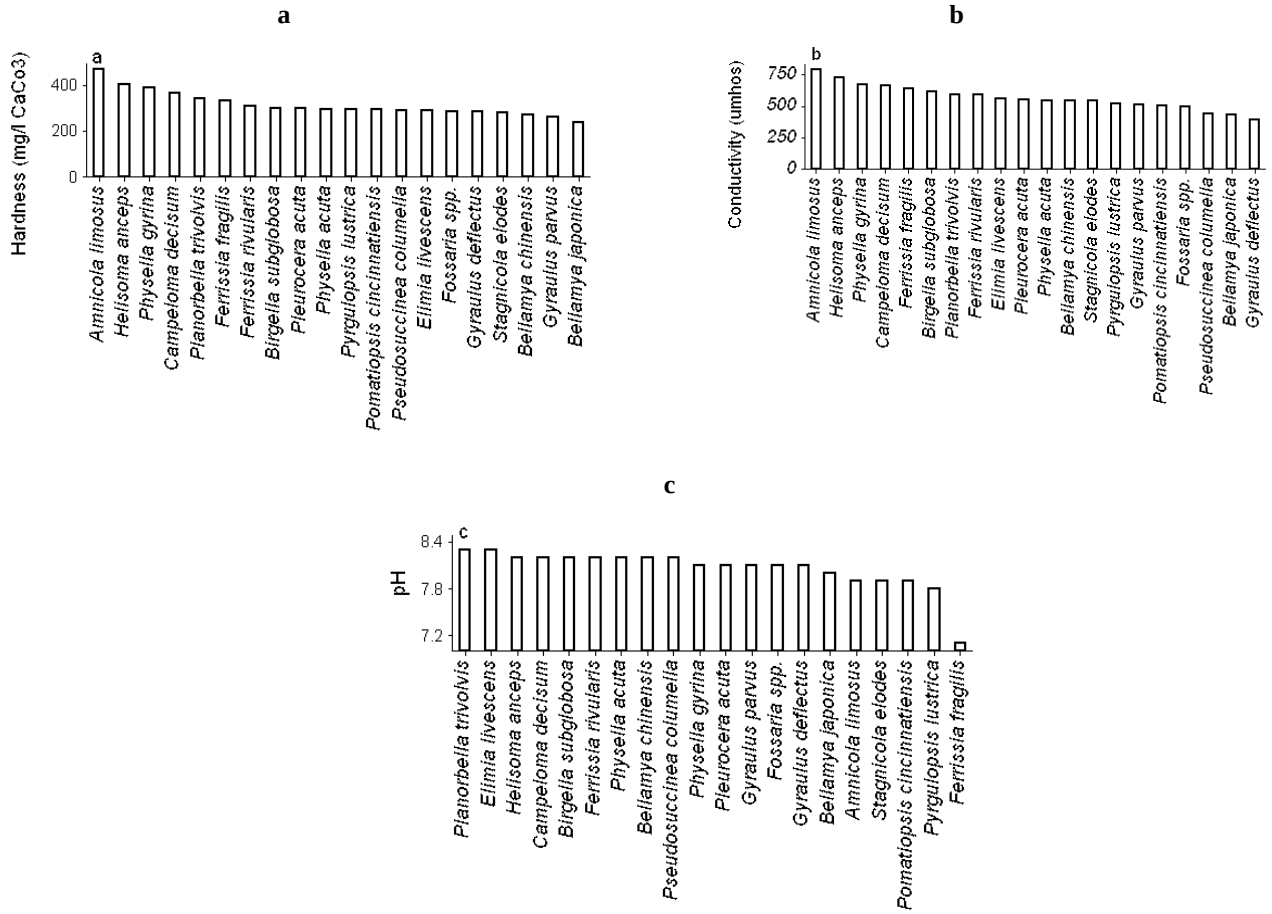

Fig. (2). Mean site hardness (**a**), conductivity (**b**), and pH (**c**) for gastropod species with the highest abundances.

Table 2. Pearson Correlations (and *P*-values) for Nonmetric Multidimensional Scaling Axes and Significant Environmental Variables (Bold), and the Proportion of Variance Represented by Each Axis (R^2 Between Distance in Ordination Space and Distance in Original Space) for Each Axis

Variable	NMS1	NMS2	NMS3
Conductivity	- 0.20 (0.05)	- 0.01 (0.94)	- 0.11 (0.25)
Dissolved oxygen	- 0.07 (0.46)	**0.20 (0.04)**	0.01 (0.98)
Log drainage area	0.12 (0.20)	0.11 (0.24)	**0.40 (0.01)**
Substrate PC1	**0.21 (0.03)**	- 0.04 (0.65)	**0.24 (0.01)**
% variance	33.2	25.4	25.2

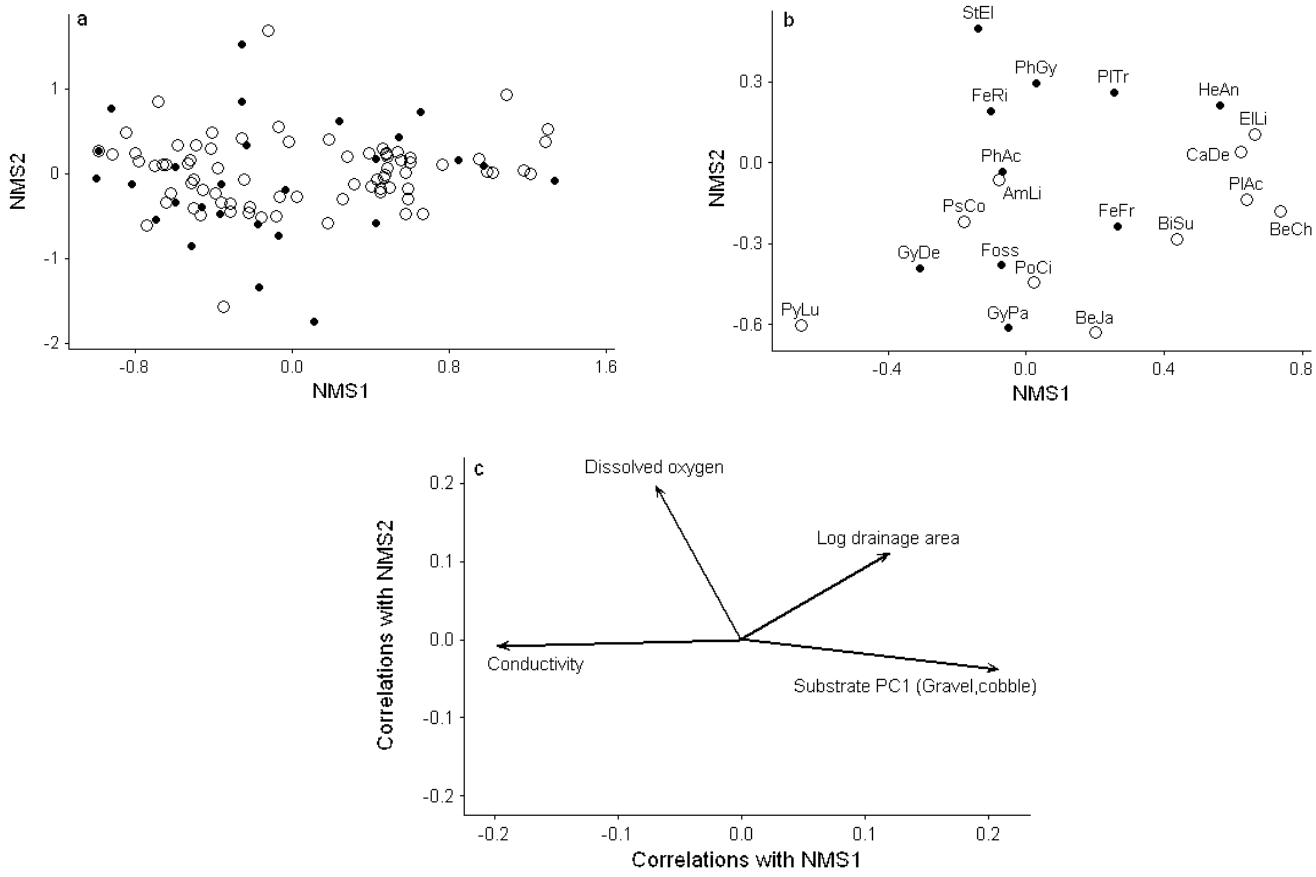

Fig. (3). Ordinations of sites on the first and second NMS axes (**a**). Closed circles are lakes, open circles are streams. Species (**b**) and vectors (**c**) represent correlation coefficients of environmental variables with the first and second axes. Open circles are prosobranch taxa and closed circles are pulmonate taxa. See Table **1** for abbreviations.

(Fig. **4b**). The sites that were lower on the third NMS axis had smaller drainage areas and decreased frequencies of gravel and/or cobble substrates (Fig. **4c**). Pulmonate taxa were separate in the lower region of the third NMS axis, while prosobranch taxa tended to occur higher (2-sample t-test, $t_{12} = 2.5$, $P < 0.03$; Fig. **4b**). No strong patterns were detected for Cartesian coordinates or water temperature with NMS axes.

The observed mean C-score, number of checkerboard units between all pairs of species, was 44.4 and was not significantly larger than the mean from simulations ($P = 0.19$).

DISCUSSION

Freshwater gastropod assemblages are structured by a multitude of variables at regional and local scales. Lodge *et al.* [1] concluded that at large biogeographic scales the important variables were colonization ability and water chemistry, and at local scales disturbance regimes, competition, and predation were stronger explanatory variables. Our study included regional scales of latitude and longitude. Regional location at the scale of multiple watersheds was not a significant explanatory variable of assemblage variation. At local scales, substrate type, water conductivity, and drainage

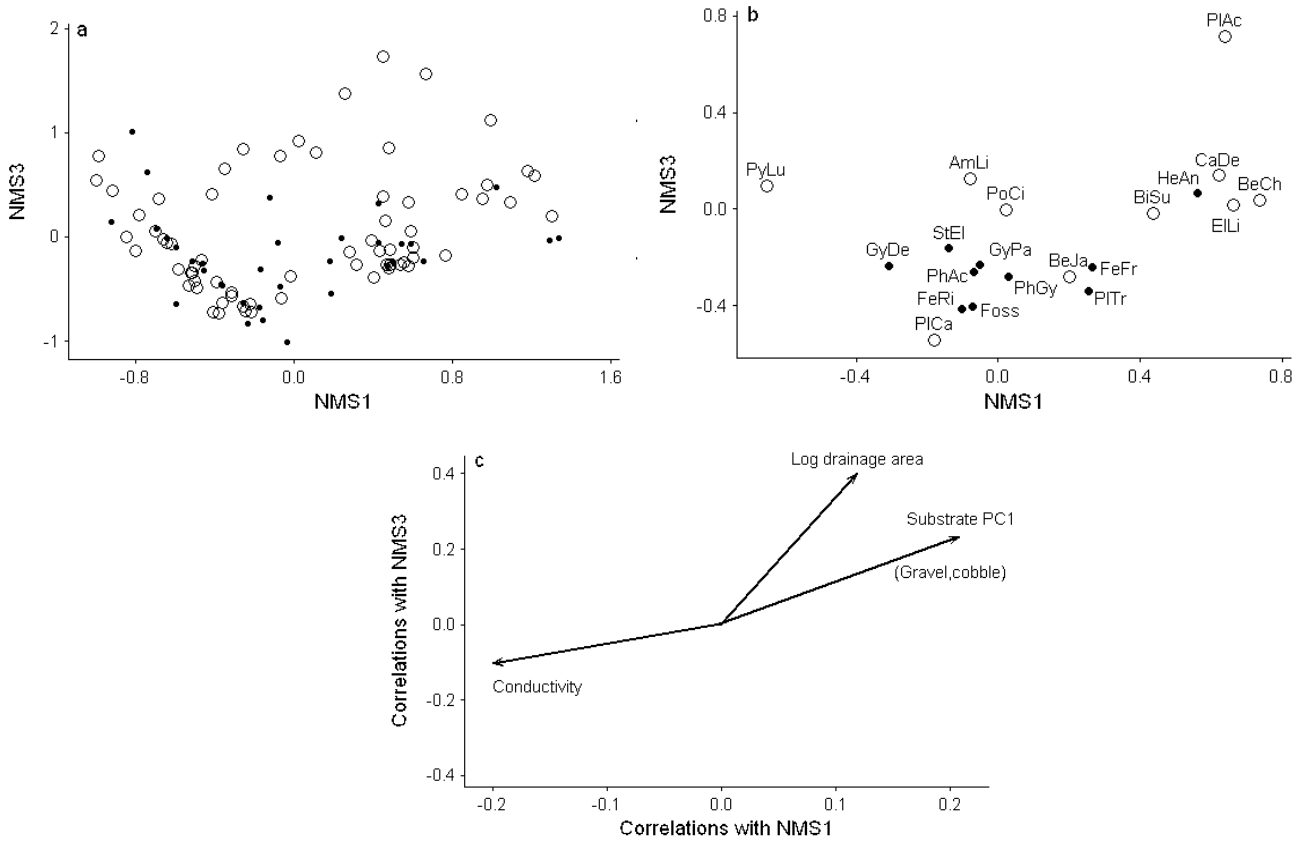

Fig. (4). Ordinations of sites on the first and third NMS axes (**a**). Closed circles are lakes, open circles are streams. Species (**b**) and vectors (**c**) represent correlation coefficients of environmental variables with the first and second axes. Open circles are prosobranch taxa and closed circles are pulmonate taxa. See Table **1** for abbreviations.

area were significant influences on assemblage variation. In addition, our results showed that smaller drainage area water bodies had higher abundances of pulmonates than prosobranchs. Brown *et al.* [21] found similar patterns for a pulmonate and prosobranch in a tributary of the Ohio River and attributed it to physiological adaptations of pulmonates. Prosobranchs were suggested to occur in larger rivers because of their ability to withstand competition, and inability to withstand harsh physicochemical variation in smaller streams. At the scale of a single small stream, Johnson and Brown [32] found highest densities of a prosobranch in slow-flow, sunny locations. Our study provides additional evidence that pulmonate taxa occur in higher abundance in smaller systems with higher water conductivity and silt substrates. Our interpretation is that these small-order streams likely have increased disturbance, lower predation pressure, and may have increased abundance of algae/detritus food sources, as suggested by Brown *et al*. [21]. Variation in water chemistry variables such as conductivity, are not typically strong explanatory variables of aquatic gastropods at local scales [1]. Our results may be influenced by our site selection. A majority of our sites were small streams that lack high groundwater input, and/or have increased anthropogenic influence including sewage effluent that increases salinity.

Competition does not appear to be a strong influence on gastropod assemblages at our sites. We did not find species co-occurrence patterns different from simulations. Brown *et al*. [21] predicted increased competitive ability for pulmonate taxa and decreased competitive ability for prosobranch taxa at sites where food is a limiting factor. We did not quantify primary productivity or other measures of food availability. However, lower abundance of prosobranchs at small-order stream sites suggests they may not disperse well to, or survive in these locations. Increased predation by invertebrate predators at small-order stream sites may contribute to the patterns we observed [11].

Our collection effort was not exhaustive at all sites and we could not survey every potential site in the region. For example, our lake surveys were not thorough because we collected at only one location in each lake. Many of these lakes have additional habitats that we did not sample due to lack of access or time using our 60-min search protocol. Our prediction is that additional sites and further sampling of these habitats would demonstrate that gastropod assemblages in lakes differ from streams.

The current gastropod assemblages of Indiana are likely extremely different than prior to human alteration of habitats [25]. Impacts on aquatic ecosystems include point and non-point pollution, hydrologic alteration from a variety of sources, primarily dams and agriculture [24], and exotic and invasive species. Successful conservation of aquatic gastropods will require consideration of the details of gastropod distributions. Aquatic gastropods in North America are threatened with an increasingly bleak future without further conservation efforts [33]. Detailed habitat information for these aquatic organisms can provide information for conservation potential.

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ABBREVIATIONS

mg = Milligram

Ca = Calcium

km = Kilometer

min = Minutes

log = Logarithm

μmhos = Micromhos

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