



Environmental gradients and the structure of freshwater snail communities

Jason T. Hoverman, Christopher J. Davis, Earl E. Werner, David K. Skelly, Rick A. Relyea and Kerry L. Yurewicz

J. T. Hoverman (jason.hoverman@Colorado.edu), Dept of Ecology and Evolutionary Biology, Univ. of Colorado, Boulder, CO 80309, USA. – C. J. Davis and E. E. Werner, Dept of Ecology and Evolutionary Biology, Univ. of Michigan, Ann Arbor, MI 48109, USA. – D. K. Skelly, Dept of Forestry, Yale Univ., New Haven, CT 06511, USA. – R. A. Relyea, Dept of Biological Sciences, Univ. of Pittsburgh, Pittsburgh, PA 15260, USA. – K. L. Yurewicz, Dept of Biological Sciences, Plymouth State Univ., Plymouth, NH 03264, USA.

A fundamental goal of ecology is to understand the factors that influence community structure and, consequently, generate heterogeneity in species richness across habitats. While niche-assembly (e.g. species-sorting) and dispersal-assembly mechanisms are widely recognized as factors structuring communities, there remains substantial debate concerning the relative importance of each of these mechanisms. Using freshwater snails as a model system, we explore how abiotic and biotic factors interact with dispersal to structure local communities and generate regional patterns in species richness. Our data set consisted of 24 snail species from 43 ponds and lakes surveyed for seven years on the Univ. of Michigan's E. S. George Reserve and Pinckney State Recreation Area near Ann Arbor, Michigan. We found that heterogeneity in habitat conditions mediated species-sorting mechanism to drive patterns in snail species richness across sites. In particular, physical environmental variables (i.e. habitat area, hydroperiod, and canopy cover), pH, and fish presence accounted for the majority of variation in the species richness across sites. We also found evidence of Gleasonian structure (i.e. significant species turnover with stochastic species loss) in the metacommunity. Turnover in snail species distributions was driven by the replacement of several pulmonate species with prosobranch species at the pond permanence transition. Turnover appeared to be driven by physiological constraints associated with differences in respiration mode between the snail orders and shell characteristics that deter molluscivorous fish. In contrast to these niche-assembly mechanisms, there was no evidence that dispersal-assembly mechanisms were structuring the communities. This suggests that niche-assembly mechanisms are more important than dispersal-assembly mechanisms for structuring local snail communities.

Species sorting along environmental gradients has been a major theme in ecological research because, across a landscape, local environments vary in a diversity of environmental factors including disturbance, predation, parasitism, competition, mutualism, moisture, and productivity. Such environmental heterogeneity among sites can constrain species distributions to a subset of available habitats due to physiological constraints or adaptive trade-offs (Leibold et al. 2004, Urban 2004, McCauley et al. 2008). For example, along an abiotic environmental gradient, species that are more tolerant of a wide range of abiotic conditions are expected to have broader distributions than less tolerant species (Wellborn et al. 1996). If such physiological constraints are important for structuring communities, it is expected that communities will be significantly nested when aligned along an environmental gradient (Patterson and Atmar 1986, Wright et al. 1998). In contrast, when species display adaptive trade-offs, high performance at one end of the gradient is often associated with low performance at the opposite end of the gradient. If adaptive trade-offs

structure communities, species turnover would be evident as species replace each other along the gradient (Wellborn et al. 1996, McCauley et al. 2008). Turnover can be further characterized into Gleasonian (i.e. individualistic), Clementsian (i.e. clumped), and evenly spaced patterns depending on how individual species or groups of species respond to the environmental gradient (Presley et al. 2010). Thus, different niche-assembly mechanisms are expected to lead to distinct patterns in species richness across a regional landscape, which can be identified using recently developed metacommunity theory (Leibold and Mikkelsen 2002, Presley et al. 2010).

While niche-assembly mechanisms have been a prominent focus in community ecology, dispersal-assembly models have gained attention particularly in metacommunity theory. Factors including the degree of isolation among communities, dispersal mode of the species, dispersal barriers, and habitat characteristics can determine the dispersal rate of species (Urban 2004, McCauley et al. 2008, Shurin et al. 2009). Within a metacommunity framework, the dispersal

rate of species among local communities can affect our understanding of community structure (Leibold et al. 2004). For example, high dispersal rates among local communities can lead to the regular colonization of species that are poorly adapted to local site conditions (e.g. sinks, mass effects) while low dispersal rates can prevent species from reaching suitable habitats especially following disturbance events (Leibold et al. 2004). While it is widely recognized that regional (dispersal) and local (species-sorting mechanisms) factors are important for structuring communities, there remains substantial debate concerning the relative importance of each of these mechanisms in building and maintaining regional species richness (Leibold et al. 2004, Cottenie 2005). To date, theoretical studies addressing these issues have outweighed empirical studies. Thus, there is a critical need for large-scale observational studies across space and time that address local and regional patterns in species richness to test the predictions of metacommunity theory.

Freshwater snails are broadly distributed across freshwater habitats and play a significant role in ecological communities as herbivores, prey, and hosts to parasites (Dillon 2000). As such, they are ideally suited to examine the factors that influence local and regional patterns in species richness. Indeed, regional patterns in freshwater snail species richness have been well studied; greater snail species richness is generally associated with harder water (e.g. high calcium concentration, alkalinity, pH), greater habitat area, and longer hydroperiods (Lodge et al. 1987, Dillon 2000). However, to date, few studies have examined how abiotic and biotic factors structure local communities to generate these regional patterns. In temporary ponds, disturbance associated with pond hydroperiod is expected to be the dominant factor limiting species richness; only species with sufficient aestivation abilities can tolerate prolonged dry periods (e.g. pulmonate snails; Lodge et al. 1987). As ponds transition from temporary to permanent hydroperiods, the physiological constraints associated with pond drying are relaxed and species richness is expected to increase. If hydroperiod solely determined species richness within local communities, a nested pattern in community structure would be observed. However, the transition from temporary to permanent hydroperiods is often associated with an increase in the abundance of invertebrate predators and eventually molluscivorous fish in permanent water bodies (e.g. lakes; Turner and Montgomery 2009). Consequently, thin-shelled snail species that are more susceptible to shell-crushing predators are expected to be less common in permanent water bodies (Stein et al. 1984). Thus, substantial species turnover is expected to occur with the transition to permanent water bodies if predation selectively eliminates species with thinner shells (Lodge et al. 1987). While predation may play an important role in structuring snail communities, competition has been hypothesized as a minor factor in snail communities (Lodge et al. 1987). Taken together, this suggests that hydroperiod and predation will play primary roles in structuring freshwater snail communities. In addition to these species-sorting mechanisms, dispersal may play a role in structuring snail communities. Dispersal is predominately a passive process in freshwater snails suggesting that sites in close proximity to each other should have similar species compositions (Rees 1965, Lassen 1975, Boag 1986). For example, Zealand and

Jeffries (2009) documented a positive association between snail community dissimilarity and distance between ponds. While this research suggests that freshwater snails fit a metacommunity framework, few studies have simultaneously examined how local and regional processes structure snail communities (Lodge et al. 1987, Zealand and Jeffries 2009).

In this study, we explored how abiotic and biotic factors interact with dispersal to structure local communities and generate patterns in freshwater snail species richness and composition. Our data set consisted of 24 snail species distributed across 43 ponds and lakes that were surveyed over 7 yr. First, we addressed the relative importance of several environmental factors (hydroperiod, canopy cover, area, pH, competition, and predation) in generating regional patterns in snail species richness. We predicted that species richness would be higher in ponds with higher pH, greater habitat area, and longer hydroperiods. Second, we addressed patterns in species distributions including turnover, nestedness, and clumping (Leibold and Mikkelsen 2002). We used this information to determine whether local snail communities are structured by physiological constraints or adaptive trade-offs associated with environmental gradients. If physiological constraints play a dominant role in structuring snail communities, we predicted a nested pattern in community structure associated with pond hydroperiod. If adaptive trade-offs play a dominant role in structuring snail communities, we predicted turnover in community structure associated with predator abundance. If turnover is evident in the dataset, we assessed whether the metacommunity exhibited Gleasonian, Clementsian, or evenly spaced distributions. We expected Gleasonian structure due to species-specific tolerances of predation risk. Last, we assessed the possible role of dispersal in structuring local communities. We predicted that dissimilarity in species composition would increase with distance between ponds.

Methods

The snail survey

The snail survey was part of a larger research effort initiated in 1996 to sample the abundance and diversity of amphibians and macroinvertebrates in ponds on the E. S. George Reserve near Ann Arbor, Michigan (Werner et al. 2007a, b, 2009, McCauley et al. 2008). As part of this effort, we collected data on snail species from 2001 to 2007 for the 37 ponds on the E. S. George Reserve. Samples were collected the third week of May and July of each year. We collected samples using pipe sampling and dipnetting (for detailed protocols see Werner et al. 2007a). In brief, sampling effort varied depending on the size of the pond (ranging from 20–40 pipe samples and 20–40 person-min of dipnetting; Werner et al. 2007a). During the sampling, all snails and invertebrate predators were collected and preserved in the field. In addition to this sampling effort, we conducted supplemental dipnet samples in June 2003 through 2007. These additional June samples were conducted because all of the snail species except *Helisoma campanulata* and *Gyraulus crista* reach their peak abundance between May and June (Supplementary material Appendix 1). Therefore, we added the June samples to

increase our likelihood of detecting species and our ability to estimate snail abundance. We also expanded the research effort in 2004 and 2005 to include six lakes outside of the reserve in the surrounding Pinckney State Recreation Area. The ponds on the E. S. George Reserve are predominantly non-permanent habitats so we added these lakes to the survey to increase the representation of habitats with permanent hydroperiods and the presence of molluscivorous fish. On average, the lakes were 8 km from the George Reserve and 10 km from each other. For these six lakes, we conducted only dipnet sampling in June at an average effort of 75 person-min (range = 40–90 person-min) using our established protocols (Werner et al. 2007a). We did not continue this additional sampling effort post-2005 due to insufficient resources. Details regarding our sampling efficiency are presented in Supplementary material Appendix 2.

We identified all snails (except *Physa* and *Ferrissia*) to species using Burch (1982) and measured their shell length. *Physa* and *Ferrissia* were identified to genus due to our inability to reliably differentiate between congeners based on shell morphology (i.e. *Physa gyrina* and *Physa acuta*; *Ferrissia fragilis* and *Ferrissia parallela*). To assess the role of competition in structuring snail communities, we estimated the biomass of snails collected per unit effort of sampling. We used biomass as a surrogate for competition rather than density to account for differences in snail size among species, which would not be possible with density estimates alone. We have used a similar approach to assess the importance of competition in larval anuran communities on the E. S. George Reserve (Werner et al. 2007a). Given that snail abundance peaks between May and June, we focused on the June samples to estimate snail biomass. We used the June dipnet sampling data for the analysis because no pipe samples were taken. To estimate snail biomass at our study sites, length-weight regressions were calculated for each species. We used the regressions to calculate total snail biomass in each field sample based on the length of each individual snail in the sample and we standardized for sampling effort by dividing biomass by the number of dipnet minutes conducted at each site. Then, we averaged the June estimate across years (2003–2007) at each site for use in the analyses. For sites in the Pinckney State Recreation Area, we averaged the June 2004 and 2005 samples given that these were the only two years we collected at these sites.

Invertebrates were identified using Pennak (1991) and Merritt and Cummins (1996). The invertebrate predator taxa in our survey included larval and adult Dytiscidae, larval and adult Hydrophilidae, Belostomatidae, larval Anisoptera and crayfish. While many of these predators consume a diversity of prey items, they all are known to consume snails (Dillon 2000). The predators were identified to species or genus depending on the reliability of available keys. We used predator biomass in the analyses to correct for the presence of larger predator species that likely feed on a wider range of snail species and consume more prey biomass (Werner et al. 2007a). Biomass estimates were obtained by drying representative samples of each invertebrate species at 60°C for 24 h and obtaining length-weight regressions. The regression was then used to calculate predator biomass in each field sample based on length of each predator species in the sample. Biomass was standardized by the dipnet effort

employed at each site. Similar to above, we employed the mean June invertebrate predator biomass (2003–2007) in our analyses for each site to determine their impact on snail species richness. Only the dipnet samples were used in the analysis because pipe samples were not conducted in June. Also, we averaged the 2004 and 2005 samples for sites in the Pinckney State Recreation Area.

Habitat characteristics

We have previously described our methods for obtaining estimates of habitat area, canopy cover, and hydroperiod for sites on the E. S. George Reserve and Pinckney State Recreation Area (Werner et al. 2007a, b, McCauley et al. 2008). A summary is provided here. Pond hydroperiod (% of days the wetland held water averaged across years) ranged from 28% in temporary ponds to 100% in the lakes. We broadly categorized the ponds into permanent (100% of days wet) and non-permanent hydroperiods (<100% of days wet). Canopy cover ranged from 0% in lakes to 93% in ephemeral ponds surrounded by forest. We categorized the ponds into open canopy (<75% canopy cover) and closed canopy ($\geq 75\%$ canopy cover). Habitat area varied substantially across our survey sites (74–15 000 m²). The pH of each site was measured in 2003 and 2004 using a handheld pH meter (WTW, Gold River, CA). The average of the values for the two years was used as our estimate of pH at each site and ranged from 5 to 9. We were unable to quantitatively sample fish biomass at our sites in the Pinckney State Recreation Area. Therefore, we simply classified each habitat as fish or fishless for analyses based on our previous experience at the sites. Only eight of the ponds contained molluscivorous fish (e.g. mudminnows *Umbra limi*; pumpkinseed sunfish *Lepomis gibbosus*) including all six lakes in the Pinckney State Recreation Area and two ponds on the E. S. George Reserve.

Statistical analyses

We used Pearson correlation analysis to examine the relationship between each measured variable and cumulative species richness across our sites. We also used stepwise multiple regression analysis to examine the relative importance of our variables in explaining species richness. Canopy cover, hydroperiod, and area are intimately linked through biological processes and highly correlated (Williams 2001). To eliminate issues associated with variance inflation, we used principal component analysis (PCA) to reduce these three variables into one. In the PCA, the first principal component (PC1) explained 85% of the environmental variation between sites (eigenvalue = 2.55). All three original variables loaded strongly on PC1 (canopy cover = -0.928, ln (area) = 0.971, hydroperiod = 0.867). The remaining principal components had eigenvalues less than one (0.071 and 0.373) and were not retained using broken-stick criteria (Jackson 1993). PC1 was used as our estimate of the physical environment in the regression analysis. The remaining four variables in the stepwise regression included the occurrence of fish, mean snail biomass, mean invertebrate predator biomass, and site pH; the variance inflation factors for these

variables were <2.6 suggesting that severity of multicollinearity was relatively low. We used cumulative species richness in each pond as our dependent variable.

We employed the methods of Leibold and Mikkelsen (2002) to explore patterns of turnover, nestedness, and clumping in our data set and identify the best-fit structure (Presley et al. 2010). We used reciprocal averaging on our incidence matrix to arrange sites with the most similar species compositions and species with the most similar distributions close together. The resulting ordinated matrix was then tested for coherence, turnover or nestedness, and boundary clumping. The degree to which a pattern in species presences can be collapsed into a single dimension is called coherence. To test for coherence, the presences and absences in the matrix were arranged using a null model that fixed row totals (species richness at sites) to equal empirical values but assigned equiprobable chance of occurrence of each species (Presley et al. 2009). We considered a matrix coherent if it had significantly fewer embedded absences than the mean of the randomized null model matrices (Leibold and Mikkelsen 2002). If the matrix was coherent, it was tested for nestedness or turnover and boundary clumping. To test for turnover or nestedness, the number of replacements in the matrix after filling in the ranges of species was examined (Leibold and Mikkelsen 2002). We considered species ranges to be dominated by nestedness if there were fewer replacements than expected under the null model and dominated by turnover if there were more replacements. Finally, boundary clumping, defined as the degree to which species ranges are grouped or clumped along the dominant axis of variation, was evaluated using Morisita's index (Morisita 1971, Hoagland and Collins 1997, Leibold and Mikkelsen 2002). Index values significantly >1 indicated that boundaries were clumped while values significantly <1 indicated that boundaries were over-dispersed. A Chi-square test was used to test if Morisita's index differed from 1. For all tests, we compared our observed matrix to 1000 iterations of the randomized matrix. Tests were conducted in Matlab, release 2010b with script files downloaded at www.tarleton.edu/~higgins/EMS.htm (Presley et al. 2009). We employed these methods for three different analyses. The first analysis used the entire site-by-species incidence matrix. Inspection of the ordinated matrix demonstrated that communities changed markedly at the transition from non-permanent to permanent hydroperiods. Based on this observation, we split the original data matrix into non-permanent sites versus permanent sites to assess additional metacommunity patterns within each category (i.e. compartments; Presley et al. 2010).

We conducted partial Mantel tests to assess the relative importance of pond spatial distribution (distance between ponds) and habitat characteristics in structuring snail communities (Fortin and Dale 2007, McCauley et al. 2008, Zealand and Jeffries 2009). We constructed pond community dissimilarity, pond distance, and habitat dissimilarity matrices for the analyses. We calculated pond community dissimilarity as 1-Jaccard's index of similarity using EstimateS, ver. 8.2 (Colwell 2005). The distance between ponds was log transformed for the analyses. We calculated habitat dissimilarity as the absolute value of the difference in PC1 scores between ponds. We focused on PC1 because

it explained the majority of the variation in species richness among sites according to the stepwise multiple regression. One partial Mantel test examined the correlation between pond community dissimilarity and pond distance while controlling for habitat dissimilarity. A second partial Mantel test examined the correlation between pond habitat dissimilarity and community dissimilarity while controlling for pond distance. A concern in our dataset was that our six lakes were located outside of the reserve, which would confound spatial arrangement and environmental factors. To address this issue, we conducted the same partial Mantel tests on just the sites on the George Reserve and qualitatively compared the results to the original analysis. For the analyses, the observed correlation was compared to correlations obtained from 10 000 random permutations using XLSTAT, ver. 2009.

Results

Snails were detected in 40 of the 43 surveyed sites. A total of 24 snail species representing seven families were collected during the survey: Ancyliidae (two species), Hydrobiidae (three species), Lymnaeidae (four species), Physidae (two species), Planorbidae (10 species), Valvatidae (one species), and Viviparidae (two species). The seven families can be divided into two major groups; four of the families were pulmonates (Ancyliidae, Lymnaeidae, Physidae, and Planorbidae), which possess a pallial lung that enables air breathing, while the remaining three families were prosobranchs, which possess opercula and gills. Species richness is similar to or exceeds other gastropod surveys conducted in Michigan and similar lentic systems in temperate regions (Dillon 2000).

We found that cumulative species richness was positively correlated to area, hydroperiod and pH, but negatively related to canopy cover (Fig. 1). Thus, habitats with high snail species richness tended to be large, permanent water bodies with minimal canopy cover and alkaline conditions. There were no significant correlations between cumulative species richness and either mean invertebrate predator biomass ($r = -0.230$, $p = 0.142$) or mean snail biomass ($r = 0.207$, $p = 0.189$).

The most likely factors driving species richness were physical environmental variables (i.e. area, canopy cover, and hydroperiod), pH, and fish presence. Stepwise multiple regression analysis revealed that these three variables accounted for 81% of the variation in species richness (Table 1). The environmental PC explained the majority of the variation in species richness (66%), while habitat pH and fish presence explained an additional 11 and 5%, respectively (Table 1). Parameter estimates demonstrated a positive relationship between the predictor variables and species richness with the environmental PC as the strongest predictor (Table 2). Invertebrate predator biomass and snail biomass were not significant predictors in the final model ($p \geq 0.180$).

In the analysis of the entire site-by-species incidence matrix, it was clear that snail species were not randomly distributed across sites (Fig. 2). We found strong coherence in the ordinated matrix with 174 observed embedded absences (expected mean $+1$ SD; $418+27$, $p < 0.001$).

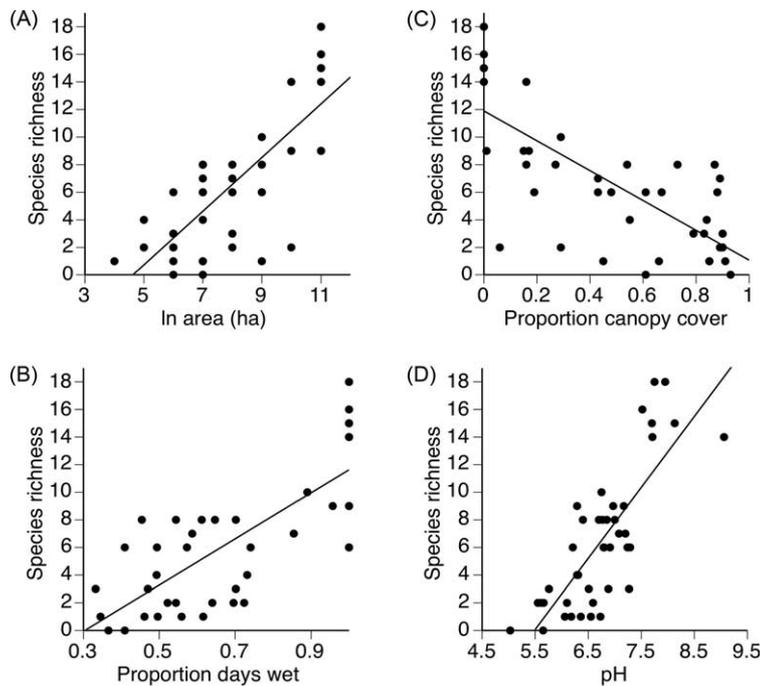


Figure 1. Cumulative species richness of the E. S. George Reserve and Pinckney State Recreation Area sites as a function of (A) pond area, (B) hydroperiod, (C) canopy cover, and (D) pH. Cumulative species richness was positively correlated to area ($r = 0.779$, $p < 0.001$), hydroperiod ($r = 0.755$, $p < 0.001$), and pH ($r = 0.782$, $p < 0.001$) but negatively related to canopy cover ($r = -0.738$, $p < 0.001$).

Thus, there was support for a dominant axis of variation in the overall data set. Species' ranges displayed significant turnover with 13 684 replacements (expected mean +1 SD; $8515 + 1874$, $p = 0.006$). However, species' range boundaries were not significantly clumped or dispersed (Morisita's index = 1.5, $p = 0.075$). Thus, the metacommunity displayed Gleasonian structure. Based on visual examination of the ordinated matrix, species turnover generally occurred at the transition from non-permanent to permanent hydroperiods. For example, four species (i.e. *Aplexa elongata*, *Fossaria parva*, *Gyraulus circumstriatus*, and *Stagnicola elodes*) were generally present at non-permanent sites but absent from all permanent sites except one (i.e. Southwest Swamp). In contrast, eight species across four families were found solely at permanent sites (Supplementary material Appendix 3). However, there were a number of species, predominately planorbids, found across the hydroperiod gradient (Supplementary material Appendix 3).

When we split our data set by pond hydroperiod, the non-permanent hydroperiod matrix consisted of 29 sites and 14 species (Supplementary material Appendix 4). The incidence matrix was significantly coherent with 86 embedded absences (expected mean +1 SD; $143 + 14$, $p < 0.001$) providing support for a dominant axis of variation in the data set. Species' ranges were significantly

nested with 560 replacements (expected mean +1 SD; $1464 + 466$, $p = 0.052$). However, species' ranges were not significantly clumped or dispersed (Morisita's index = 1.2, $p = 0.334$). Thus, the non-permanent pond metacommunity displayed nestedness with random species loss. Ponds with low ordination scores were generally highly ephemeral ponds that dry every year and contain species that possess adaptations to cope with frequent drying such as aestivation behaviors (e.g. *Aplexa elongata*, *Gyraulus circumstriatus*, *Stagnicola elodes*). Ponds with high ordination scores were semi-permanent sites that dry intermittently (e.g. every few years) but contain similar species as ephemeral ponds in addition to several larger bodied planorbid snail species.

The permanent hydroperiod matrix consisted of 11 sites and 22 species. The incidence matrix was significantly coherent with 21 embedded absences (expected mean +1 SD; $61 + 6$, $p < 0.001$) providing support for a dominant axis of variation in the data set. Species' ranges did not show nestedness or turnover (175 observed replacements, expected mean +1 SD; $334 + 88$, $p = 0.070$). However, species' ranges were significantly clumped (Morisita's index = 1.7, $p = 0.032$). Thus, the permanent pond metacommunity displayed quasi-Clementsian structure.

There was no significant correlation between community dissimilarity and distance between ponds while

Table 1. Stepwise multiple regression analysis of habitat variables (environmental PC, pH, fish presence, snail biomass, and invertebrate predator biomass) and pond ordination scores from habitats on the E. S. George Reserve and Pinckney State Recreation Area.

Model	Adjusted R ²	DF	F	p	FΔ	p
Physical environmental PC	0.658	1,40	80.0	<0.001		
Physical environmental PC and pH	0.767	2,39	68.4	<0.001	19.6	<0.001
Physical environmental PC, pH, and fish presence	0.813	3,38	60.3	<0.001	10.6	0.002

Table 2. Parameter estimates for the final model from the stepwise multiple regression analysis. Invertebrate predator biomass (Beta = 0.100, $p=0.170$) and snail biomass (Beta = 0.137, $p=0.095$) were not significant predictors in the final model.

Parameter	B	SE	Beta	p
Constant	-10.5	4.2		0.018
Physical environmental PC	1.7	0.5	0.337	0.003
pH	2.4	0.6	0.347	0.001
Fish presence	4.4	1.3	0.344	0.002

accounting for habitat dissimilarity ($r = -0.018$, $p = 0.474$). However, there was a significant positive correlation between habitat dissimilarity and community dissimilarity while controlling for distance between ponds ($r = 0.477$, $p < 0.001$). Similar results were found when the analysis was restricted to ponds on the E. S. George Reserve ($r = 0.049$, $p = 0.354$ and $r = 0.150$, $p < 0.003$ for the two analyses, respectively).

Discussion

We found evidence that heterogeneity in habitat conditions mediates species-sorting mechanisms and structures local freshwater snail communities. Physical environmental variables were most strongly associated with freshwater snail species richness followed by pH and molluscivorous fish presence. Metacommunity analyses revealed Gleasonian structure to snail distributions (i.e. significant species turnover with stochastic species loss). Turnover was driven by the replacement of several pulmonate species with prosobranch species at the pond permanence transition. These results combined with a positive correlation between habitat dissimilarity and community dissimilarity while controlling for distances between ponds strongly suggest that species-sorting mechanisms were structuring local communities. However, there was no evidence that distance between ponds was associated with community composition. Below, we address the role of environmental factors in influencing local community structure and generating regional patterns in snail species richness.

Physical environmental factors

Species–area relationships have a long history in ecological research (Rosenzweig 1995, Drakare et al. 2006) and work on freshwater snails has widely supported an increase in snail species richness with increasing habitat area (Lassen 1975, Aho 1978, Browne 1981, Brönmark 1985, Lodge et al. 1987). We found that species richness increased as habitat area increased. While species–area relationships are evident in many data sets, there are a multitude of variables that are correlated with increases in habitat area that hinder the identification of the dominant factor(s) influencing species richness. Thus, the challenge in any study conducted across a gradient in habitat area is determining the relative contribution of other variables to species richness.

We found a negative correlation between canopy cover and snail species richness. Canopy cover is often used as a surrogate for pond productivity because as canopy cover increases the amount of available light for autotrophs

(e.g. macrophytes, algae) decreases. Moreover, the nutritional quality of algal resources in closed-canopy ponds is lower than open-canopy ponds (Schiesari 2006). For freshwater snails, the greater productivity of open-canopy ponds should provide greater resource availability as well as increased cover from predators due to the greater abundance of macrophytes. Brönmark (1985) demonstrated that snail species richness increased as macrophyte species richness increased, which was associated with an increase in habitat area. While the specific effects of canopy cover on snail species richness have rarely been addressed, there have been examinations of the effects of pond productivity on snail species richness. Lassen (1975) demonstrated that eutrophic habitats had greater snail species richness compared to oligotrophic habitats across a gradient in habitat area. Together, this research suggests that heterogeneity in canopy cover and associated changes in system productivity contribute to the structure of freshwater snail metacommunities.

Habitat pH was a significant factor influencing snail species richness. Malacologists have routinely shown the positive effects of water chemistry variables such as calcium concentration, alkalinity, conductivity, and pH on snail distributions (Dillon 2000). These field patterns support laboratory studies demonstrating reduced growth and reproduction of snails reared at low calcium concentrations (i.e. $< 5 \text{ mg L}^{-1}$; Thomas et al. 1974, Madsen 1987). However, Lodge et al. (1987) point out that there is a weak direct relationship between environmental calcium concentration and shell calcification. They also suggest that extremely soft waters (e.g. calcium concentration $< 4.5 \text{ mg L}^{-1}$) can limit successful snail establishment in a pond but other factors probably drive community level patterns in hard waters. Others have suggested that the relationship between water chemistry and snail richness is indirect (Boycott 1936, Dillon 2000). Harder waters are often associated with greater abundance and diversity of plant species and greater detrital decomposition, which would provide a greater resource base for snails compared to softer waters (Dillon 2000). This underscores the challenges faced in identifying the most important factors driving patterns in diversity.

Pond hydroperiod was positively correlated with snail species richness and associated with turnover in species' distributions. These results appear to be associated with physiological differences in the mode of respiration between the two main groups of snails in our study (pulmonates and prosobranchs); prosobranchs use internal gills that require water for respiration, while pulmonates possess an internal 'lung' that can either be filled with air at the surface or filled with water and oxygen extracted across the lung's surface (Russell-Hunter 1978). Given the requirement for water movement across their gills (i.e. a physiological constraint), all three prosobranch families were restricted to permanent water bodies in our survey (Fig. 2, Supplementary material Appendix 3). In contrast, the ability of pulmonates to use atmospheric air for respiration enables them to aestivate (Russell-Hunter 1961, 1978, Richards 1963, Brown 1979). Species such as *A. elongata*, *F. parva*, *G. circumstriatus*, and *S. elodes* are well known for their aestivation ability (Dillon 2000) and were strongly associated with our small ephemeral ponds.

Hydroperiod category	Fish presence	Canopy cover	Pond	Species																							
				<i>Fossaria parva</i>	<i>Aplexa elongata</i>	<i>Stagnicola elodes</i>	<i>Gyraulus circumstriatus</i>	<i>Promenetus exacuius</i>	<i>Promenetus umbilicatellus</i>	<i>Planorbula armigera</i>	<i>Physa</i> sp.	<i>Planorbella trivolvis</i>	<i>Fossaria obrussa</i>	<i>Gyraulus parvus</i>	<i>Planorbella campanulata</i>	<i>Pseudosuccinea columella</i>	<i>Ferrissia</i> sp.	<i>Amnicola limosus</i>	<i>Helisoma anceps</i>	<i>Viviparus georgianus</i>	<i>Gyraulus deflectus</i>	<i>Valvata tricarinata</i>	<i>Pyrgulopsis leisoni</i>	<i>Gyraulus crista</i>	<i>Amnicola walkeri</i>	<i>Laevapex fuscus</i>	<i>Cipangopaludina chinensis</i>
NP	N	C	North Fence Pond																								
NP	N	C	North Fence Swamp																								
NP	N	C	Willow Pond																								
NP	N	C	Spring Pond South																								
NP	N	C	Red Maple Swamp																								
NP	N	O	Gravel Pit Pond																								
NP	N	O	Cattail Marsh																								
NP	N	C	West Woods Little																								
NP	N	O	Cassandra Bog West																								
NP	N	C	Dreadful Hollow																								
NP	N	C	West Woods Big																								
NP	N	O	Aspen Grove Pond																								
NP	N	O	Ilex Pond																								
NP	N	O	Buffer Zone Marsh																								
NP	N	O	Gravel Pit Marsh																								
NP	N	C	Spring Pond North																								
NP	N	C	Uzzell's #1																								
NP	N	O	West Marsh # 06																								
NP	N	O	West Marsh # 10																								
NP	N	C	West Marsh # 11																								
NP	N	C	Buck Hollow																								
NP	N	O	Cassandra Pond East																								
NP	N	O	Star Pond																								
NP	N	C	Uzzell's #4																								
NP	N	O	Dreadful Swamp																								
NP	N	C	Southwest Woods																								
NP	N	O	Crescent Pond																								
NP	N	O	West Marsh Dam																								
NP	N	O	Fishhook Marsh																								
P	N	O	Southwest Swamp																								
P	N	O	Burt Pond																								
P	F	O	East Marsh																								
P	N	O	George Pond																								
P	F	O	Doyle Lake																								
P	F	O	Sullivan Lake																								
P	F	O	Sayles Lake																								
P	F	O	Walsh Lake																								
P	F	O	Duck Lake																								
P	F	O	Crane Pond																								
P	F	O	Gosling Lake																								

Figure 2. Incidence matrix for the E. S. George Reserve and Pinckney State Recreation Area sites. The incidence matrix was ordinated using reciprocal averaging implemented by the ordination program of Leibold and Mikkelsen (2002). Solid areas indicate that a species was present in that habitat at least once over the survey duration. Hydroperiod category (NP = non-permanent, P = permanent), fish presence (N = no fish present, F = fish present), and canopy cover (O < 75% canopy cover [open canopy], C ≥ 75% canopy cover [closed canopy]) are listed for each site. Sites characterized as either permanent, fish present, or open canopy are shaded. Prosobranch species also are shaded.

Moreover, differences in aestivation ability among our species may function to limit snail distributions leading to the observed pattern of nestedness in the semi-permanent ponds. As pond hydroperiod increased, large bodied pulmonates such as *Planorbella trivolvis*, *P. campanulata*, and *Physa* sp. were increasingly present in communities alongside species from more ephemeral ponds. Importantly,

the four species associated with temporary ponds (*A. elongata*, *F. parva*, *G. circumstriatus*, and *S. elodes*) were absent from all but one permanent hydroperiod site. Combined with the appearance of prosobranch species in permanent ponds, this explains the observed turnover in the metacommunity analysis. However, the absence of the four pulmonate species from sites that appear to fulfill the

physiological requirements of the species suggests that other factors may be contributing to the exclusion of these species.

Biotic environmental factors

Biotic factors have frequently been proposed as important factors in structuring snail communities. We found no support that snail biomass negatively affected snail species richness. While laboratory and mesocosm studies have demonstrated that competition can negatively affect snail growth and fecundity (Eisenberg 1970, Chase 1999, Hoverman et al. 2005), both Lodge et al. (1987) and Dillon (2000) suggest that habitat disturbances and predation reduce snail densities to levels that prevent competitive interactions from negatively affecting species richness. Alternatively, competition could be minimal in highly productivity sites despite high snail biomass. Although predators can reduce snail densities, we found no evidence that invertebrate predator biomass or fish presence negatively affected snail species richness. However, the presence of molluscivorous fish may have contributed to species turnover. Molluscivorous fish including pumpkinseed sunfish and mudminnows were only found at eight of our sites (all permanent hydroperiod sites). Molluscivorous fish pose the greatest threat to thin-shelled snail species and have significant effects on snail abundance (Mittelbach 1984, Brown and Devries 1985, Lodge et al. 1987, Osenberg and Mittelbach 1989). Interestingly, the only snail species in our study that were never found coexisting with fish were the thin-shelled, temporary pond species (e.g. *A. elongata*, *F. parva*, *G. circumstriatus*, and *S. elodes*) suggesting that fish could be eliminating these species from the community and contributing to turnover in species distributions. While molluscivorous fish are capable of reducing snail population sizes, habitat characteristics such as macrophyte density can provide refuges that alleviate the negative impacts of fish (Lodge et al. 1987). Moreover, many snail species are capable of altering their behavior and morphology to reduce predation rates with predatory fish (DeWitt et al. 2000, DeWitt and Langerhans 2003, Hoverman and Relyea 2007, 2008). The transition to permanent hydroperiods was also associated with the presence of prosobranch species. Compared to pulmonates, prosobranch snails are generally resistant to predation by molluscivorous fish due to their relatively thick shells and resistant to shell-invading invertebrate predators due to the presence of an operculum (Lodge et al. 1987). Thus, the presence of prosobranch species in permanent water bodies may not only be a consequence of physiology but traits that aid in predator defense.

Inter-pond distance

There was no evidence supporting the role of inter-pond distance in influencing snail community similarity while controlling for habitat similarity at the scale we were investigating. In a study of freshwater snails in the United Kingdom, Zealand and Jeffries (2009) reported a weak correlation ($r = -0.18$) between community similarity and inter-pond distance. However, they concluded that

the distance effect may not have been due to distance per se, but greater differences in land use as distance between ponds increased. To date, few studies have examined the dispersal abilities of freshwater snails. Despite the limited vagility of adult snails, there is evidence that water birds can passively disperse hatchling snails (Rees 1965, Lassen 1975, Boag 1986). Additionally, snails can disperse to new habitats during periods of substantial rainfall that cause flooding and facilitate snail movement (Brönmark 1985). Some freshwater snails are hermaphroditic or parthenogenetic, which can increase their likelihood of successful colonization assuming the appropriate environmental conditions are present at the new habitat (Dillon 2000). However, given the limited dispersal abilities of snails, species-sorting mechanisms played the dominant role in snail metacommunity dynamics.

Local vs regional processes

Determining the relative importance of regional and local processes in structuring communities has been a challenge for community ecologists due to the diversity of systems used to explore metacommunity dynamics. Indeed, in a recent meta-analysis, Cottenie (2005) demonstrated that both regional (spatial) and local (environmental) processes accounted for 48% of variation in community composition. However, species-sorting dynamics were structuring the majority of the data sets followed by the combination of species-sorting dynamics and dispersal. Importantly, Cottenie (2005) demonstrated that system characteristics such as dispersal type, habitat type, and spatial scale were useful for classifying metacommunity types and determining the relative importance of regional and local processes. For example, species-sorting mechanisms were the dominant factors structuring communities characterized by passive dispersal. While species-sorting mechanisms remained significant for taxa with active dispersal, mass effects increased in importance contingent on habitat type and spatial scale. As more data sets become available, ecologists can gain insights into the characteristics of systems that determine the relative importance of local and regional processes in structuring communities.

Our work on snail, amphibian, and dragonfly metacommunities on the ESGR largely supports the work of Cottenie (2005). For freshwater snails (i.e. passive dispersers), heterogeneity in local conditions accounts for the majority of the variation in snail species richness with no contribution from spatial factors. Amphibian and dragonfly communities also are strongly structured by local environmental conditions (Werner et al. 2007a, McCauley et al. 2008). Larval amphibian communities exhibit significant turnover along the freshwater habitat gradient, which is largely driven by adaptive trade-offs in traits that allow rapid development to metamorphosis in temporary ponds versus lower predation rates in permanent ponds (Wellborn et al. 1996, Werner et al. 2007a). Adaptive trade-offs also occur in larval dragonfly communities; distinct suites of species are found along the freshwater habitat gradient, which is strongly associated with the presence of large-bodied fish (McCauley et al. 2008). However, given that amphibians and dragonflies have complex life cycles, dispersal across

the landscape plays an important role in structuring these communities (Werner et al. 2007a, 2009, McCauley et al. 2008). For these species, mean annual species richness within a pond averages between 32 and 50% of the cumulative species richness demonstrating significant interannual turnover in species composition. Such interannual turnover appears to be a function of spatial factors such as pond connectivity and mass effects that maintain species in marginal habitats (i.e. source-sink dynamics) combined with environmental factors such as pond hydroperiod. For example, dispersal-assembly mechanisms are particularly important in temporary ponds that are colonized each year following pond drying. Together, our work demonstrates that vagility largely determines the relative importance of species-sorting and dispersal-assembly mechanisms in structuring communities.

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Supplementary material (Appendix E6856 at <www.oikosoffice.lu.se/appendix>). Appendix 1–4.