

Abstract

IS PREDATION BY TURTLES SUFFICIENTLY STRONG TO AFFECT
BIODIVERSITY WITHIN FISHLESS PONDS?

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Ecologists have long known that predation can have a strong effect on the diversity and abundance of prey in ecological communities. Much evidence on the importance of predation in aquatic systems has stemmed from studies involving manipulations of abundance or occurrence of predator species thought to play an important role. In freshwater aquatic systems, fish often are considered as the most important predators in permanent ponds; in contrast, salamanders and insects are often considered to be the most important predators in ephemeral ponds. Freshwater turtles are a group that often is overlooked in studies assessing the importance of predation, yet turtles often are locally abundant and can consume a wide array of prey species. I conducted an enclosure experiment in a fishless ephemeral pond to assess whether turtles play an important role in controlling the distribution and abundance of amphibian and invertebrate prey.

The ability of turtles to access and feed in certain experimental plots but not others did not alter the number of prey species present within study plots or the evenness of prey species present within study plots. A comparison of species accumulation curves revealed that turtles tended to reduce the total number of prey species found across all study plots where turtles had

the ability to feed. Areas in which turtles were excluded had higher total number of prey species across all study plots. I found that scale dependent differences in the effect of turtles on species richness are the result of turtles homogenizing the kinds of prey species present in areas where they could graze. My results demonstrate that turtles may have an important effect on the diversity within fishless ponds, possibly by homogenizing species composition of different localities.

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CHAPTER 1: Review of Predation within Ponds

Ecosystem function or “ecosystem services,” includes air and water purification, maintenance of soil fertility, and aesthetic beauty (Daily 1997). Given the importance of functioning ecosystems to life on Earth, it is clear that an understanding of how such complex systems work is essential. Biodiversity, or the collection of life forms within a given ecosystem, has been shown to be an important component in maintaining ecosystem function (Naeem 2002, Srivastava and Vellend 2005). Biodiversity is typically measured in two ways: species richness, the number of species present within a community, or evenness, the relative abundance of each species within a community (Naeem 2002). The composition of ecological communities is the result of a multitude of interacting factors such as competition, predation, and a suite of abiotic factors such as resource availability and climatic patterns. Competition and predation are direct interactions among species. This study focuses on predation, which is known to occur in all natural ecosystems. Predation can alter community structure, or the species occurring within a given geographical area, due to variation in foraging behavior employed by different predators. Therefore, understanding the influence of all predators is important to understanding the complete food web in any ecosystem (Chalcraft and Resetarits 2003).

Prior to the mid 1960’s, little was known of the role of predation in freshwater systems and its impact on community structure. In one of the first studies of predation in freshwater systems, Brooks and Dodson (1965) surveyed lakes in southern New England containing alewives (planktivorous fish) and lakes without alewives, and compared the makeup of cladoceran species found between the lakes. Large cladoceran species were absent in lakes with alewives, but small species of cladocerans were common. Small cladocerans were not eaten by alewives, and the absence of large cladocerans released them from competitive exclusion. This

provided some of the first insights into the effects vertebrate predators could have on community structure within freshwater habitats. Despite these findings, studies of the role of predators affecting freshwater community structure did not really grow in popularity until Paine's marine studies (1966, 1969) on "keystone predators." The interest in freshwater systems grew as ecologists set out to see whether similar "keystone" species were present in freshwater systems.

Continued studies, however, led to a split among freshwater community ecologists. One side argued that predators played a significant role in regulating community structure (Crowder and Cooper 1982, Morin 1984, Cooper 1984); others argued they did not (Thorp and Bergey 1981, Allan 1982). Much of the debate of the 1980's focused on the role of fish as predators in freshwater systems and what effects fish had on community structure. Thorp and Bergey (1981) conducted a study to determine whether vertebrate predation from either a keystone species or a guild was important in regulating the structure of the benthic macroinvertebrate community in the littoral zone of a freshwater reservoir. By excluding natural predators, they found no difference in either density or richness of prey taxa when native predators were present or absent. Potential predators in the reservoir were fish and turtles. All results were attributed to fish; turtles were simply mentioned as a potential predator in the system.

In contrast, Morin (1984) found that excluding fish from feeding in certain plots in a North Carolina farm pond produced dramatic differences in the abundance and dominance of dragonfly species. Intermediate-sized species dominated the odonate assemblage in areas where fish could not forage, but small odonates were dominant where fish could forage. This suggested that fish were selecting the largest odonates available as prey, and fish predation released previously excluded small species from competition, which allowed them to complete metamorphosis and become the dominant species. Morin (1984) addressed downfalls in

previous fish exclusion experiments and attributed the lack of fish predation effects to variation in habitat complexity in various ponds or having low abundances of predators (discussed in detail in Crowder and Cooper 1982). The predators noted in Morin's study were fish and turtles. Again, no assessment of turtle predation was offered, and all results were attributed to predation by fish.

Further works supported the importance of fish predation acting as a strong factor in determining community structure within freshwater systems (Nemjo 1990, Pont et al. 1991, Wellborn and Robinson 1991, Arnott and Vanni 1993, Ryazanova and Mazokhin-Porshnyakov 1993, Binckley and Resetarits 2002). Fish often are absent from ephemeral habitats that endure drying periods; thus, other predators can be potentially important structuring forces. Every time a temporary pond fills with water, it represents a new burst of life with both predators and prey taking advantage of this now open ecosystem (Wilbur 1997). Species-specific tolerances to pond drying, as well as a suite of biotic interactions such as predation and competition, ultimately determine the species composition in the new community (Wellborn et al. 1996).

Predators such as salamanders (Morin 1981, Fauth and Resetarits 1991, Griffiths et al. 1994) and invertebrates (Hall et al. 1970, Lunig 1992, Blinn et al. 1993), especially larval dragonflies (Thorp and Cothran 1984, Chavanec 1992, Skelley and Werner 1990), have been shown to influence aquatic communities. The broken striped newt (*Notophthalmus viridescens dorsalis*) can act as a keystone predator in ponds by playing a role in determining the relative abundance of both zooplankton and anurans (Morin 1981, Morin et al. 1983, Chalcraft and Resetarits 2003). Due to similarity of size to their prey, predatory invertebrates tend to have a disproportionate impact on small-bodied prey (Wellborn 1994), and many prey species may grow too large to be consumed by invertebrate predators (Williamson 1987).

Most predators in temporary freshwater habitats are gape-limited, meaning that they need to capture and swallow their prey whole (Gascon 1992). Gape-limited predation leads to a “morphological arms race” between prey growing large enough to escape predation by such predators and the predators trying to keep up (Hanazato and Yasuno 1989). The presence-absence of fish predators can create a transition of alternative community types. Fish predation on larger-bodied organisms leads to a community of less active, smaller-bodied macroinvertebrates (Lazzaro 1987). Where fish are absent, predatory invertebrates and salamanders assume the role of community regulators, leading to communities consisting of more active, larger bodied taxa (Hanazato and Yasuno 1989, Wellborn et al. 1996).

Turtles are common predators in ponds that lack fish as well as ponds that contain fish. Although noted as potential predators (Morin 1984, Thorp and Bergey 1981), no study has investigated the role turtles may have on biodiversity. Turtles are not limited to permanent ponds; they can migrate from pond to pond and are found in high densities in ponds throughout the United States (Congdon et al. 1986). Gut content analyses also reveal that turtles are known predators of all taxa found in freshwater ponds (Ernst and Lovich 2009).

In this study, I attempt to determine the impact an assemblage of turtles has on spatial variation in biodiversity within a fishless pond in the Croatan National Forest. All turtle species are known predators of prey taxa within the study site. To determine the impact of this turtle assemblage, I deployed short-term predator exclosures in a pond free of fish and measured differences in community structure in areas where turtles could versus could not forage. Given the absence of fish, results can be attributed to predation by turtles and not the combination of the two (Morin 1984). Understanding the role turtles might have in communities can help

further our understanding of freshwater communities and the biotic interactions that structure them.

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CHAPTER 2: Testing the Impacts of Turtles on the Spatial Variation in Biodiversity within Fishless Ponds

Introduction

Interactions between predators and prey are among the many processes that influence community biodiversity. The overall impact of a predator or assemblage of predators on the abundance and distribution of prey species can be mediated through either direct consumption or indirect effects (Paine 1966, Connell 1975). Indirect effects are attributed to consequences of behavioral predatory avoidance (Sih 1982), effects on shared resources of both predator and prey (Werner and Gilliam 1984, Sih et al. 1986, Spiller and Schoener 1988), and/or enhancing or reducing effects of other predators or competitors (Schmitt 1987). Community structure of freshwater systems can be greatly influenced by predators. Predatory fish such as bluegill (*Lepomis macrochirus*) have been shown to decrease the biomass of prey species and cause the dragonfly assemblage to be dominated by smaller, less active species than in areas lacking fish (Crowder and Cooper 1982, Morin 1984, Cooper 1984). The broken striped newt (*Notophtalamus viridescens dorsalis*) is an important predator in freshwater pond systems because they selectively consume competitively dominant prey species, which in turn allows competitively inferior prey to increase in relative abundance (Morin 1981, Wilbur et al. 1983). Predatory insects also have been shown to affect community structure in freshwater systems although, not as strongly as fish (Peckarsky 1984).

Although many studies have tested the effects of a diverse array of predators (fish, newts, predatory insects) on the structure of freshwater communities (Morin 1981, Thorp and Bergey 1981, Wilbur et al. 1983, Cooper 1984, Morin 1984, Peckarsky 1984, Chalcraft and Resetarits 2003), no studies have examined the influence of turtles on biodiversity in freshwater

communities. Fish have been shown to have strong impacts on prey density and composition (Morin 1984), yet fish are largely restricted to permanent ponds. Temporary ponds represent islands in time, in which each time a depression fills with water, a new community erupts, and only certain predators that can cope with the drying in these systems can persist. Turtles, which are known predators of a wide array of taxa inhabiting temporary ponds, occur in high densities in temporary habitats (Ernst and Lovich 2009), and could potentially be an important player in structuring freshwater insect communities.

When a temporary pond fills, a new chapter in community ecology begins as species arrive to take advantage of the opportunity to complete the aquatic stage of their life cycle. Dispersal ability of prey and predators often is different; thus the stage is set for either the prey or the predator to arrive first to the pond and gain a size advantage over the other. If the prey gains a size advantage over the predator, then predation pressures by that predator are reduced. Many predation studies have focused on gape-limited predators (Morin 1981, Thorp and Bergey 1981, Wilbur et al. 1983, Cooper 1984, Morin 1984, Peckarsky 1984, Chalcraft and Reserits 2003), which must consume their prey whole (Gascon 1992). Most prey species can be swallowed whole at early stages of their development by most predators. However, if prey species develop at a rate greater than that of the predators in the system, prey may reach a size refuge in later developmental stages (Wilbur 1997). Thus, the risks associated with gape-limited predators change with developmental stage of prey taxa. In contrast, turtles are not gape-limited; they can capture and consume prey larger than their mouth size (Rodel 1999). Thus, prey are not likely to grow to a size refuge that allows them to escape predation from turtles. Consequently, turtles could have strong predatory impacts in certain communities.

Freshwater turtles are extremely abundant in the eastern United States and certain pond-dwelling species have been cited as being potential predators in predatory exclusion experiments (Heyer and Muedeking 1976, Morin 1984). Despite turtles being identified as a predator in previous studies (Heyer and Muedeking 1976, Thorp and Bergey 1981, Morin 1984), impacts on these communities were attributed to fish predation. Potential prey of freshwater turtles inhabiting ponds includes fish, aquatic insects, and frogs (adults, tadpoles and eggs) (Aresco et al. 2006). The common snapping turtle (*Chelydra serpentina*) is an omnivore, consuming both fresh prey and carrion (Schneider 1998). The chicken turtle (*Deirochelys reticularia*) is almost exclusively carnivorous, with some accidental ingestion of plant material (Demuth and Buhlmann 1997). The pond slider (*Trachemys scripta*) is an opportunistic omnivore that undergoes ontogenetic diet shifts from carnivory as juveniles to consuming significantly more plant material as adults (Bouchard 2005). Although their diets may shift, adult sliders prefer animal food when it is available (Clark and Gibbons 1969, Parmenter and Avery 1990). Both the eastern mud turtle (*Kinosternon subrubrum*) and striped mud turtle (*Kinosternon baurii*) are omnivorous but have been reported to have diets consisting of insects accounting up to 98.3% of their total diet (Mahmoud 1968). Given that turtles consume a wide array of taxa found in both temporary and permanent ponds, it is surprising that their role as predators within these systems has not been investigated.

The aim of this project was to examine the potential impact turtles have on spatial variation of prey biodiversity within a fishless pond. I hypothesized that turtles play a significant role in controlling the distribution and abundance of prey within a fishless pond. To test this hypothesis, I conducted an experiment in which I manipulated the ability of turtles to forage in different areas within a fishless pond.

Methods

“Boat Ramp Pond” is a roughly 2000 m² (0.5 ha) pond in the Croatan National Forest (CNF) (34.720998,-76.962962). The CNF is located in the eastern part of North Carolina between New Bern and Emerald Isle. The pond is dominated by the fragrant water lily (*Nymphaea odorata*), with little other vegetation, and has an open canopy with no shading or overhanging trees. Maximum depth of the pond is approximately 1.5 m, with a soft muddy bottom. Dominant trees in surrounding forest are longleaf pines (*Pinus palustris*). This particular pond was chosen because it was known to have turtles but no fish (David Chalcraft, personal communication). The absence of fish is vital to this study, ensuring that effects of treatment manipulations (exclosure devices) can be attributed to the exclusion of turtles (not to the exclusion of fish).

To assess the turtle assemblage in Boat Ramp Pond, I conducted a mark-release-recapture study. I used six hoop net traps baited with sardines to capture turtles with no bias towards size or sex. Traps were dispersed in a manner to cover the entire pond with the available traps (Figure 1). Sardine bait was placed in a tube sock to attract turtles. This method prevents turtles from becoming “trap happy,” which refers to individual turtles returning to traps because they know they will be rewarded. Placing sardines in a sock also prevented captured turtles from consuming the bait and making the trap less enticing to other turtles. Trapping was carried out over a 2 wk period (July 6-20, 2009) and traps were checked daily. Upon capture, I identified the species and sex of each turtle, and marked each turtle with a unique two letter code using a nail file to notch their marginal scutes (Gibbons 1983). Notching the marginal scutes is a harmless and effective way to mark and identify turtles; the notch is permanent and poses no

risks to the turtle. The longest time in which any turtle spent in a trap was 24 hours; traps were checked daily and the trapped turtles were released.

The Lincoln–Petersen method was used to estimate population size of the turtle species present in Boat Ramp Pond. This method assumes that the study population is “closed.” In other words, the time between the marking phase and the recapturing phase is sufficiently short so that the number of individuals who die, move into the study site (immigrate), or move out of the study area (emigrate) is greatly diminished over the short time frame between visits. The model also assumes that no marks on animals are lost between visits to the field site by the researcher and that the researcher correctly records all marks (Jolly 1965, 1979). The Lincoln-Peterson method is as follows: $P_t = (P_m * S_t) / S_m$. All animals captured and marked in week one were counted as (P_m). Recaptures during the same sampling week were noted but were not included in the count of number marked during week one. The second week, I recorded the total number of individuals caught regardless of whether they were marked or unmarked (S_t). Any marked animal recaptured in week two that was not caught any other day that week was considered as a marked recapture (S_m). Population estimates were derived for each species (P_t).

I experimentally examined the short term impact of turtles on the aquatic biodiversity of Boat Ramp pond by the use of screen pens, which prevented turtles from foraging in certain portions of the pond. I constructed open-topped pens (1 m long x 1 m wide x 1.5 m high) of bamboo stakes wrapped in one inch (2.54 cm) rigid plastic mesh around the sides with no bottom (to utilize the natural pond bottom). I made ten pens impenetrable to turtles by staking the mesh into the detritus layer using six-12 inch (30.48 cm) garden stakes per side. Hereafter these ten pens are referred to as enclosures. Turtles were free to forage in any area in the pond except for

the ten locations where they were excluded. The enclosure treatment provided an estimate of prey abundance in locations where turtles could not access them.

To obtain an estimate of prey abundances in areas where turtles had access, I made ten open plots by using four bamboo stakes with no fencing. The use of the term “open” refers to this particular treatment being absent of any fencing. Any difference between enclosure treatments and open treatments could be the result of the presence/absence of turtles or a fence (which could affect prey independently of the presence of turtles); thus, I also employed a fence control (hereafter termed “sham plot”) that provided the fence structure but allowed turtle access (by lifting the fence off of pond bottom). This is a standard procedure in ecology to decouple the confounding effects of “fence” and “excluded organism” (Lively 1986, Royo and Carson 2008).

The experiment began with the final staking and placement of pens into the water on 6 July 2009. Altogether I employed ten spatial blocks of the three treatments; blocks are a collection of the treatments in close spatial proximity that account for differences in any unwanted variables that could influence response variables within the study site (i.e., productivity gradient across pond resulting in higher localized productivity in one block). Plots were checked every two days to ensure that no animals had become lodged in fencing and enclosures remained intact (i.e., exclusion pens remained securely staked into the ground ensuring that turtles could still access sham pens).

The experiment was terminated after ~1 month, when the pond began to dry. On August 9 and 10, 2009 all plots were destructively sampled. The plots were sampled by dropping a 0.5 m x 0.5 m x 0.5 m steel box (with no top or bottom) into the water in each plot to trap all animals within the box location. One box was used in each plot. Once the box was in place, we took a complete sweep of the bottom removing the top layer of mud from the bottom of the pond and all

organisms within the detritus layer. This detritus sample was placed into a bottle containing 70% ethanol, preserving organisms in the substrate. Nets were then used to sweep inside the box, and any vertebrate captured in the sweep was identified, counted, and released. Sweeps were continued within a box until five successive sweeps resulted in no macroinvertebrates or amphibian caught. All invertebrates captured within the box were preserved in 70% ethanol to be identified and counted at a later time. Any sampling biases were assumed to be similar between treatments.

Preserved insects were separated by size classes using three different sieve sizes (>2 mm, >1 mm and >500 μm). I subsampled 30% of the sieve of the >500 μm . To select 30% of the sample, the mass of the >500 μm subsample was divided equally into 20 sections. I randomly selected six of the 20 sections (i.e., 30% of the original subsample) to sample for insects. The insects in 30% of the >500 μm sample are sufficient and accurately represent the diversity within the sample (Lamberti et al. 1991). Insects were identified to genus or species (Brigham et al. 1982, Merritt and Cummins 1996, Ciegler 2003).

Statistics

I calculated species richness (S), total abundance, and species evenness, $E = (1/\sum p_i^2)/S$, where p_i is the proportional abundance of species i of the insects and amphibians collected from each sample plot. Species richness (S) was estimated in each experimental unit (plot) by counting the number of distinct species present in the sample. Individuals identified only to genus were excluded from species richness estimates, unless they were the sole representative of the genus. In this case, a sole representative of the genus would increase species richness by one species although individuals of the genus may actually represent several species. The few instances the sole representative of a genus was used in the calculation of species richness were

dispersed evenly among treatments and should not bias treatment effects in this study. Species evenness was assessed using genera because it was the lowest taxonomic level ascertainable for all insects collected.

I also estimated species richness and abundances for particular taxonomic groupings of species present in each sample plot. I first looked at the possible impact turtles had on both the abundance and species richness of invertebrates present in an enclosure; invertebrates make up much of the diet of the turtle species represented in Boat Ramp Pond (Ernst and Lovich 2009). A second taxonomic grouping of interest was the odonates. Odonates are known prey items of the turtles in the study site (Ernst and Lovich 2009) and represented 75% of all taxa sampled in my study.

To determine whether treatment manipulations affected metrics of biodiversity and abundance measured at the scale of a study plot, I conducted separate ANOVAs for each response variable. Each ANOVA model specified the effects of blocks and treatment. I tested two hypotheses within each of these ANOVAs using orthogonal planned contrasts. The first contrast compared responses in open and sham plots to those in enclosure plots to evaluate differences among areas in which turtles could forage versus those turtles were excluded. This approach assumes that both the sham and open plots are effectively the same treatment, i.e., areas where turtles could forage. The second contrast compared responses in open plots to sham plots. This contrast tested the assumption that the sham plots do not exert an unusual influence on aquatic insects compared to open plots (Marquis and Whelan 1994, Sabo and Power 2002). The significance value for all tests was set at $p = 0.05$. All analyses were performed in SAS (SAS Institute 2008).

Species richness, although easy to ascertain and understand, is a relatively difficult measure to compare. This is due mainly to the fact that as one increases sampling effort or increases the number of individuals sampled, species richness also tends to increase (Gotelli 2001). Also, comparing species richness in ANOVA assumes that the residuals are normally distributed. Richness data, however, can assume values of zero; thus comparisons of richness data using ANOVA require transformation. Transformation, in this case, is used to help correct the lack of normality in the distribution of the residuals. In my study, I also had equal sampling effort across all samples taken among treatments and assumed all changes in abundance and richness were an effect of turtle predation or an effect of exclosure. I used a Kolmogorov-Smirnov test to test if the residuals deviated from a normal distribution. I found the residuals did not statistically differ in their distribution from normality. Total abundance data were log-transformed to homogenize variances among treatments.

I also estimated the total number of species present in all study plots of a particular treatment to determine whether turtles affect biodiversity at a spatial scale that is larger than a single study plot. I refer to this metric of species richness as “regional species richness.” This metric of species richness is not equivalent to that estimated for an average study plot. Instead, regional richness incorporates information on the extent of variation in the identities of different species present in different study plots within the same treatment. To derive this metric and its associated 95% confidence interval, I created a sample-based species accumulation curve for each treatment using EstimateS (Colwell 2006). Species accumulation curves are used to compare richness values at similar abundances given that locations with more individuals will likely have more species. Regional species richness was derived for each treatment as the

richness value from the species accumulation curve observed when abundance was scaled to the fewest number of individuals sampled.

To examine whether species composition varied among treatments, I performed a PERMANOVA (permutational multivariate analysis of variance) on a Bray-Curtis distance matrix that was based on square root-transformed abundance data. This approach compares compositional differences that may arise as the result of differences in the relative abundances of taxa among treatments, but lessens the importance of numerically dominant taxa. To give equal representation to all taxa, I also performed the same analysis on a matrix derived from a presence/absence transformation of species data. NMDS (non-metric multidimensional scaling) plots were derived for both square root-transformed data and presence/absence data. The purpose of these plots is to represent samples as points in low dimensional space such that the relative distances apart of all points are in the same rank order as the relative dissimilarities of the samples as determined by the Bray-Curtis matrix. Therefore, the interpretation of these plots is straightforward. Points that are close together represent samples that are more similar in community composition, and points that are far apart correspond to plots that differ more in their species composition. PERMDISP (permutational analysis of multivariate dispersions) was conducted on the matrix derived from presence/absence data to determine if the amount of spatial variation in the presence/absence of species among replicates within a treatment (i.e., beta diversity) is different among treatments. If PERMANOVA or PERMDISP revealed significant treatment effects, I controlled the experiment-wise error rate associated with pairwise comparisons among the different treatments with a Bonferroni adjustment to account for three possible pairwise comparisons (critical alpha = 0.0167). All analyses were performed in PRIMER-E (Clarke 1993).

Results

A total of 94 individual turtles were captured in Boat Ramp Pond: *Trachemys scripta scripta* (yellow pond slider; n = 35), *Deirochelys reticularia* (chicken turtle; n = 28), *Kinosternon subrubrum*/*K. baurii* (eastern mud turtle/striped mud turtle; n = 28), and *Chelydra serpentina* (common snapping turtle; n = 3, Figure 2). Striped mud turtles in North Carolina often are hard to distinguish from eastern mud turtles because their striping on their carapace fades (Lamb and Lovich 1990). *K. subrubrum* and *K. baurii* are assumed to have similar diets (Ernst et al. 1994), so they are lumped in together in population estimates.

Biodiversity

A total of 32 species consisting of nearly 3000 individuals belonging to different taxonomic groups was observed during this study. Total community abundance of prey items did not differ between open and sham plots ($F_{1,27} = 0.06$, $p = 0.8132$), but there was a strong trend for more prey to be found in enclosure plots ($F_{1,27} = 4.31$, $p = 0.0533$, Figure 3). Mean species richness of all prey taxa did not differ between open and sham treatments ($F_{1,27} = 0.56$, $p = 0.4651$) or between enclosure vs. open and sham ($F_{1,27} = 1.77$, $p = 0.2014$, Figure 4). Evenness also did not differ between the open and sham treatments ($F_{1,27} = 2.05$, $p = 0.1703$) or between enclosure and control plots ($F_{1,27} = 0.11$, $p = 0.7495$, Figure 5).

Invertebrate abundance did not differ between either open or sham treatments ($F_{1,27} = 0.05$, $p = 0.8178$), but there was a strong trend towards lower invertebrate abundance in enclosure plots compared to open and sham plots ($F_{1,27} = 4.25$, $p = 0.0548$, Figure 6). Mean invertebrate richness did not differ between open and sham plots ($F_{1,27} = 1.44$, $p = 0.2463$) or between enclosure and the combination of open and sham ($F_{1,27} = 1.10$, $p = 0.3090$, Figure 7). Odonates, which made up 75% of all taxa observed in the study, did not differ in abundance between open

and sham treatments ($F_{1,27} = 0.21$, $p = 0.6555$), but there was a strong trend towards lower abundance of odonates in enclosures versus open and sham treatments ($F_{1,27} = 3.79$, $p = 0.0683$, Figure 8).

Results from species accumulation curves suggest that regional species richness is greatest in enclosure treatments and lower in open and sham treatments (Table 1, Figure 9). Some species were present in all treatments; however, seven species not found within open plots occurred within enclosures (Table 1). There does not appear to be a difference in regional species richness between open and sham treatments. Results from PERMANOVA on square root transformed abundance data revealed no statistical difference in species composition among treatments ($F_{2,28}$, $p = 0.104$, Figure 11). When the same test was performed on presence/absence data, I found that there was a trend for treatments to vary in their species composition ($F_{2,28} = 1.8371$, $p = 0.053$), but this trend was primarily driven by the fact that enclosure treatments were more variable in their species composition than were sham and open treatments (Figure 12). PERMDISP revealed a significant difference among the treatments in the heterogeneity in species composition ($F_{2,26} = 7.659$, $p = 0.003$, Figure 12). When controlling the experiment-wise error rate with a Bonferroni adjustment, I found that enclosures were more heterogeneous in their species composition than were open plots ($t_{26} = 3.334$, $p = 0.003$); however, enclosure plots were not statistically more heterogeneous than sham plots ($t_{26} = 2.282$, $p = 0.058$). Open treatments and sham treatments did not differ significantly in their heterogeneity of species composition ($t_{26} = 1.885$, $p = 0.082$).

Discussion

This study demonstrated that freshwater turtles may affect the biodiversity of prey species in a way that differs from that reported for other aquatic predators. Turtles appear to have reduced the number of species present within the study site, possibly by homogenizing the species composition among different localities within the pond. Other predators, such as fish (Morin 1984) and predatory insects (Hall et al. 1970), appear to reduce the number of species present in a pond by reducing the number of individuals present in different localities. The broken striped newt (*Notophthalmus v. dorsalis*) and the marbled salamander (*Ambystoma opacum*) act as keystone predators, and actually cause an increase in the number of species present by reducing the abundance of competitive dominants (Morin 1981, Wilbur et al. 1983). In contrast to other predators, we did not find that turtles significantly altered prey abundance.

Turtles are often locally abundant in ponds across the eastern United States and are known to consume a multitude of taxa within them (Ernst and Lovich 2009). The species of turtles found at the study site were all known predators (Ernst and Lovich 2009). The particular species of turtles residing in Boat Ramp Pond represent a natural population; no stocking or removal of turtles occurred during the experiment. Population densities for three turtle species found in Boat Ramp Pond have been evaluated in other ponds (*Trachemys scripta scripta*, 17-80/ha; *Deirochelys reticularia*, 17.7/ha; *Chelydra serpentina*, 5/ha; [Congdon et al. 1986, Dreslik et al. 2005]. These reported densities are lower than those I found in Boat Ramp Pond (Figure 2). It is worth noting, however, that none of these other studies were done in North Carolina and sampling was carried out for multiple field seasons. My estimates came from one field season and it is possible that surveys through time at Boat Ramp Pond could cause estimates to better match what has been found in other studies.

Predation by turtles does not appear to have an effect on prey community structure between small study plots where turtles could forage and where they could not. Contrary to freshwater predators in other studies (Morin 1981, Wilbur et al. 1983, Cooper 1984, Morin 1984, Peckarsky 1984), the presence of turtles did not cause shifts in prey species abundance (Figure 3, Figure 6, Figure 8) or diversity (Figure 4, Figure 7) within study plots. Mittelbach (1981) found that bluegill sunfish had profound impacts on the invertebrate abundance but not diversity. Odonates have been shown to undergo major shifts in abundance and dominance in the presence of predation by fish, with small competitively inferior species dominating in the presence of fish (Morin 1984). Some salamanders (broken striped newt, marbled salamander) have been shown to increase the diversity of prey species by selectively consuming competitively dominant prey that otherwise competitively exclude competitively inferior prey species (Morin 1981, Wilbur et al. 1983, Chalcraft and Resetarits 2003).

Although I found no differences in diversity within a plot (small scale), other works suggest examining impacts of predators at greater spatial scales. Chase et al. (2009) were the first to report the influence of aquatic predators on species diversity at multiple spatial scales. They found that fish reduced prey richness at both local (average diversity within a pond within a three pond array) and regional (compositional divergence between ponds within treatment group) levels. These effects were markedly greater at regional scales (total diversity within ponds in an array), due to the fact that predation by fish made localities within metacommunities more similar in their prey species composition. No other studies with predators within pond systems have been assessed in such a manner. My study was the first to explore the effects of turtles on biodiversity at multiple scales (localities within a pond versus the entire pond). Within this study, I derived estimates of gamma diversity (across the pond within a treatment) by creating

accumulation curves, which take into account the diversity at local scales but also incorporates community divergence across plots within the same treatment. When I derived this metric using species accumulation curves, the presence of turtles influenced diversity across the pond at a scale larger than alpha diversity. Areas in which turtles foraged had much lower diversity than areas in which they were excluded (Table 1, Figure 10). Species accumulation curves show that areas in which turtles were excluded had greater diversity after standardizing differences in the number of individuals sampled. These observations suggest that turtles homogenized species composition in comparison with areas in which turtles were excluded (Figure 9 and 10).

Species composition, as reflected by the relative abundances of taxa present, did not differ among treatments (Figure 11). There was, however, a strong trend for treatments to differ when species composition is viewed as presence or absence of species (Figure 12). This suggests that turtles do not influence the relative abundances of species present, but rather the identity of species found among treatments (Table 1). Other studies have found that predators within lentic freshwater systems may have less of an impact on prey species composition yet profoundly impact the abundance and dominance of prey items (Morin 1981, Wilbur et al. 1983, Morin 1984).

I found that a natural assemblage of turtles had a substantial but not traditionally viewed impact on biodiversity within a fishless pond. Unlike other predators, turtles did not cause shifts in dominance or reductions in abundance of prey items. Instead, turtles appeared to influence biodiversity by homogenizing the species composition of areas in which they foraged. Other predators within the system have been shown to influence abundance more than diversity of prey taxa. My work suggests that the loss of turtles from ponds could cause a change in prey biodiversity that could not be compensated for by other predators. Given no studies have

examined turtles as predators in this particular framework, this study provides novel information on a potentially important group of predators within freshwater lentic systems. Lentic freshwater systems support a wide array of taxa and provide habitat for many species of reptiles and amphibians. Amphibians, in particular, are undergoing widespread declines worldwide (Stuart et al. 2004). To better conserve these systems, it is important to understand how all species within the food web contribute to diversity. Also, I show the importance of looking at responses to predation at a scale greater than local (alpha diversity). At small local scales, turtles appeared to have no impact on the communities in which they were present; however, when I examined at a scale larger than within a plot, I found that turtles did influence the diversity within the pond. When making efforts to conserve certain regions, it is important to consider diversity at more than one scale. This study identifies the importance for future studies assessing the impacts of predators to examine responses in diversity at multiple scales.

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Table 1. Species found within each treatment group. Shared species among treatments can be found on the same line. Any unique species found in one treatment but missing from another is indicated by an empty space.

Open Plot	Sham Plot	Exclosure
<i>Notophthalmus viridescens</i>	<i>Notophthalmus viridescens</i>	<i>Notophthalmus viridescens</i>
<i>dorsalis</i>	<i>dorsalis</i>	<i>dorsalis</i>
<i>Hyla gratiosa</i>	<i>Hyla gratiosa</i>	<i>Hyla gratiosa</i>
<i>Ladona</i> spp.	<i>Ladona</i> spp.	<i>Ladona</i> spp.
<i>Erythemis simplicicollis</i>	<i>Erythemis simplicicollis</i>	<i>Erythemis simplicicollis</i>
<i>Tramea carolina</i>	<i>Tramea carolina</i>	<i>Tramea carolina</i>
<i>Erythrodiplax conata</i>	<i>Erythrodiplax conata</i>	<i>Erythrodiplax conata</i>
<i>Caenis</i> spp.	<i>Caenis</i> spp.	<i>Caenis</i> spp.
<i>Berosus larvae</i>	<i>Berosus larvae</i>	<i>Berosus larvae</i>
<i>Berosus aculeatus</i>	<i>Berosus aculeatus</i>	<i>Berosus aculeatus</i>
<i>Buenoa macrotibialis</i>	<i>Buenoa macrotibialis</i>	<i>Buenoa macrotibialis</i>
<i>Notonecta indica</i>	<i>Notonecta indica</i>	<i>Notonecta indica</i>
<i>Neogerris hesione</i>	<i>Neogerris hesione</i>	<i>Neogerris hesione</i>
<i>Pelocoris carolinensis</i>		<i>Pelocoris carolinensis</i>
<i>Procamburus acutus</i>		<i>Procamburus acutus</i>
<i>Hesperocorixa brimleyi</i>		<i>Hesperocorixa brimleyi</i>
<i>Acris gryllus</i>		<i>Acris gryllus</i>
<i>Neoporus dilatatus</i>		<i>Neoporus dilatatus</i>
	<i>Tropisternus larvae</i>	<i>Tropisternus larvae</i>
	<i>Tropisternus collaris</i>	<i>Tropisternus collaris</i>
	<i>Physa acuta</i>	<i>Physa acuta</i>
	<i>Thermonectus basillaris</i>	<i>Thermonectus basillaris</i>
	<i>Cybister fembriolatis</i>	
	<i>Gerris argenticollis</i>	
	<i>Hesperocorixa vulgaris</i>	
	<i>Enallagma geminatum</i>	
		<i>Copelatus caelatipennis</i>
		<i>Enochrus consors</i>
		<i>Mesovelgia mulsanti</i>
		<i>Orthotricha</i>
n = 17	n = 20	n = 25

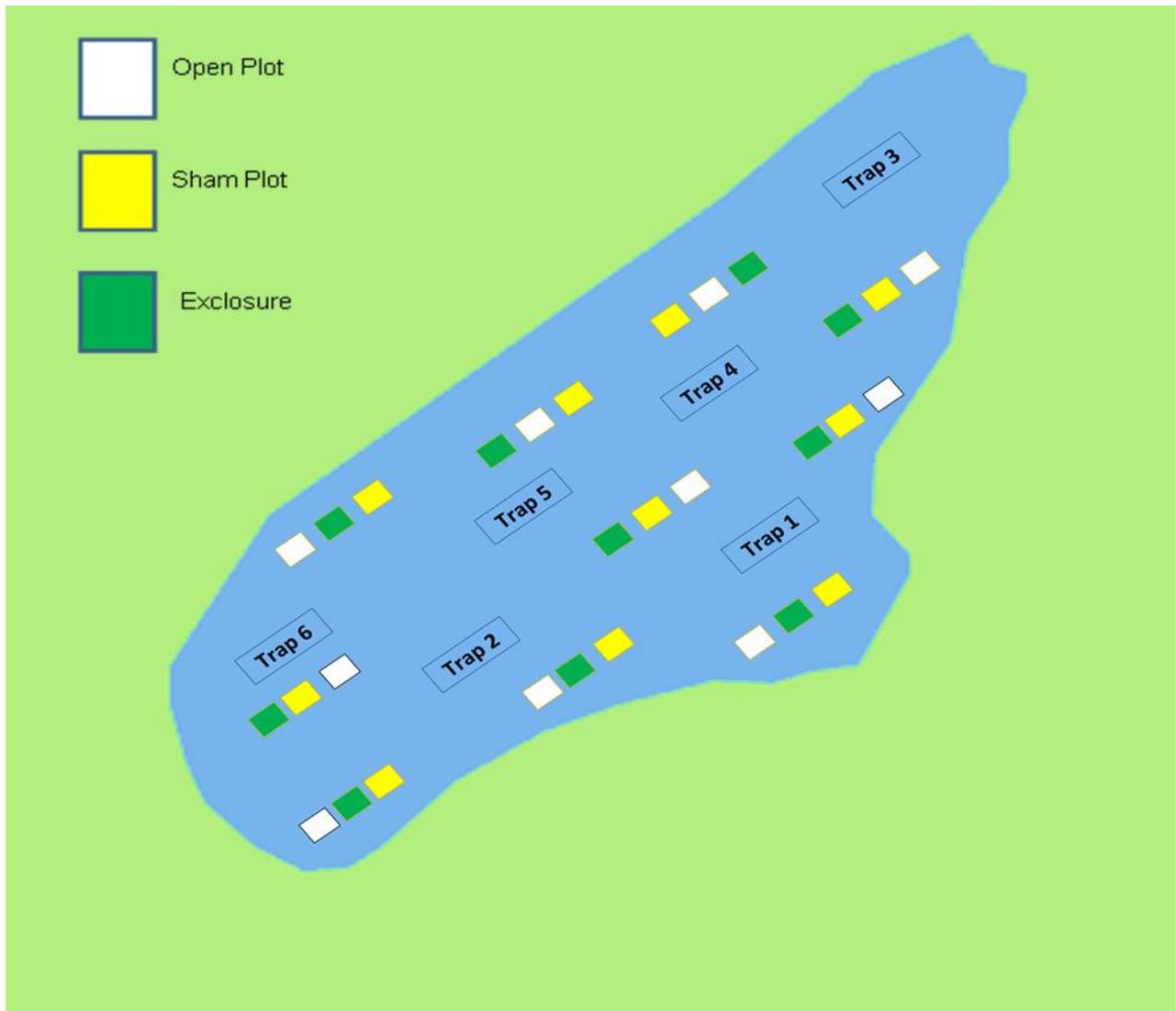


Figure 1. Graphical representation of “Boat Ramp Pond,” located in the Croatan National Forest. “Traps” indicate locales utilized for mark recapture study. Also shown is randomized block design consisting of treatments and their relative locations within the study site.

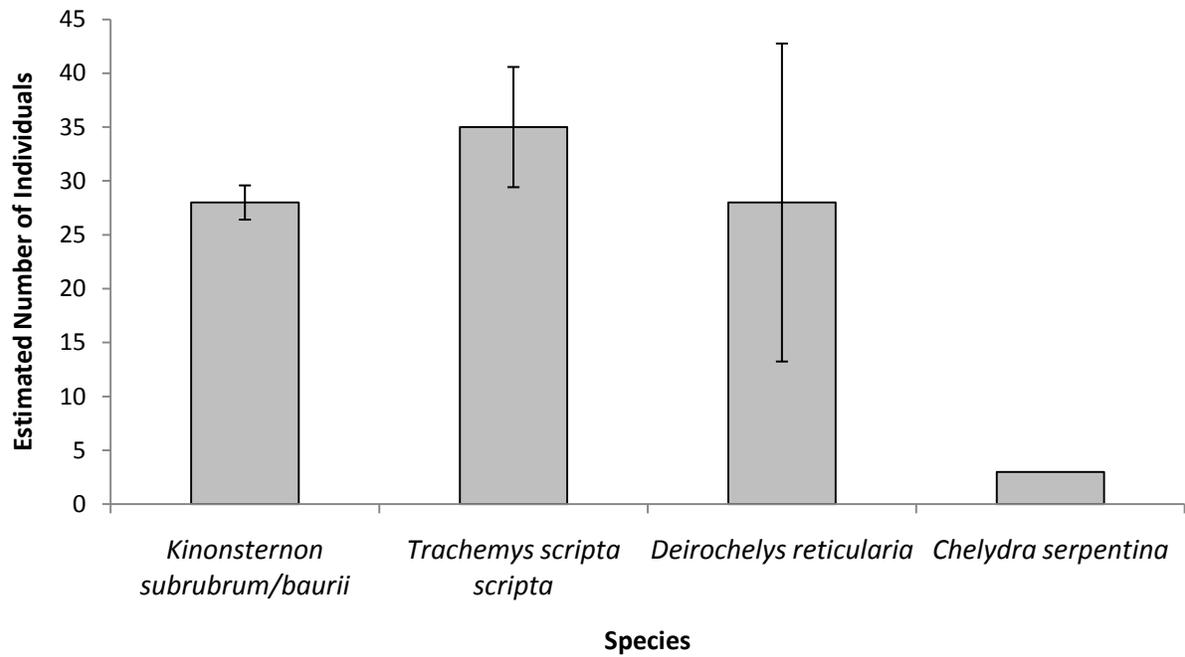


Figure 2. Estimated population size of turtles (± 1 SE) within study site by species. Estimates were derived from Lincoln Peterson Method. SE was not calculated for *Chelydra serpentina* due to no recaptures.

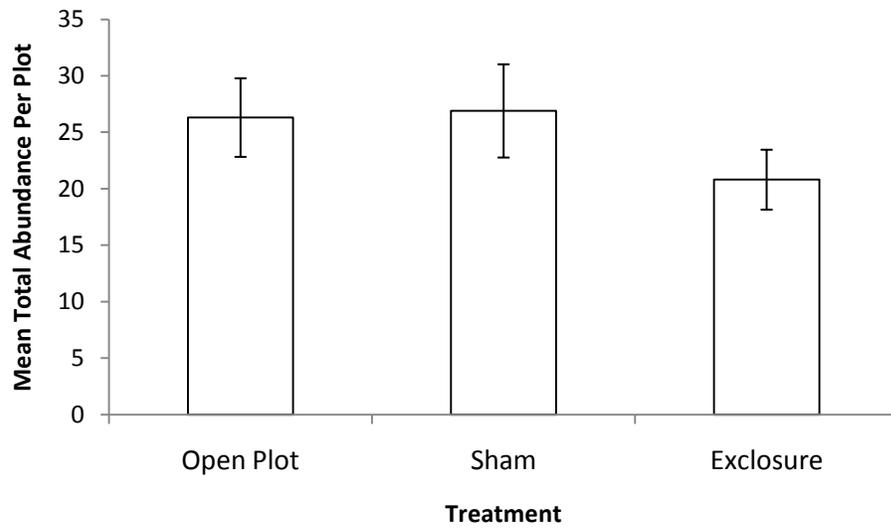


Figure 3. Mean total abundance of all prey taxa (± 1 SE) by treatment.

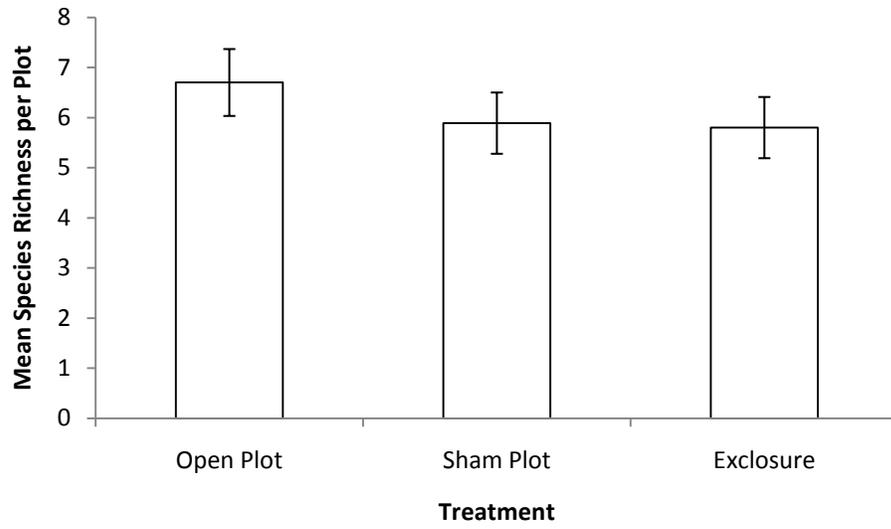


Figure 4. Mean species richness (± 1 SE) for all taxa by treatment.

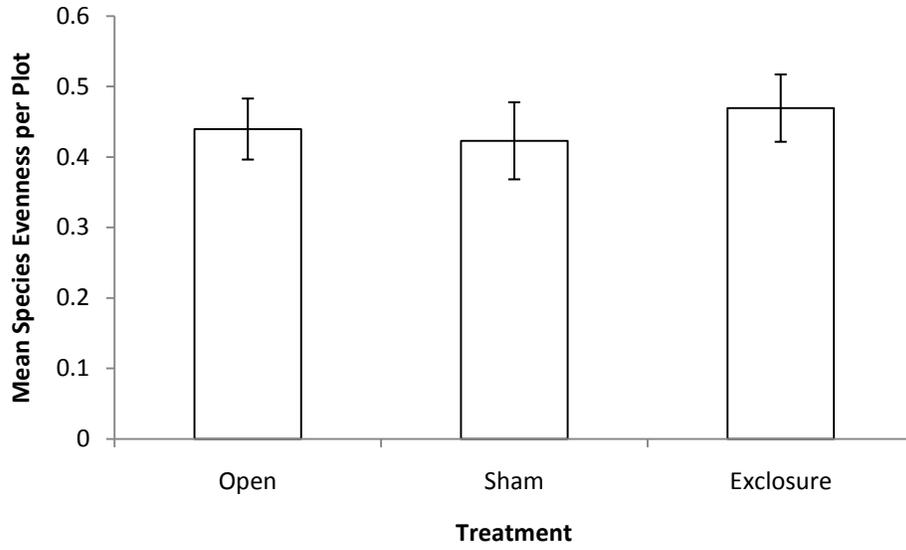


Figure 5. Mean species evenness (± 1 SE) by treatment.

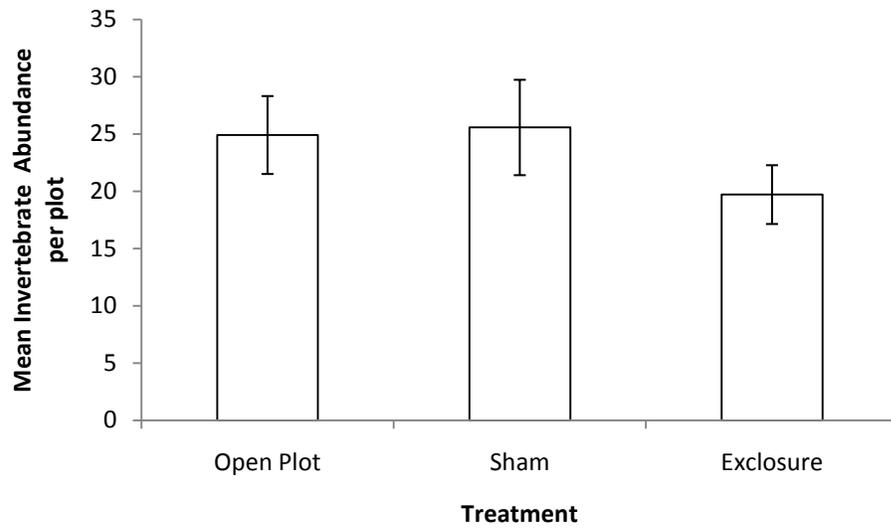


Figure 6. Mean invertebrate abundance (± 1 SE) by treatment.

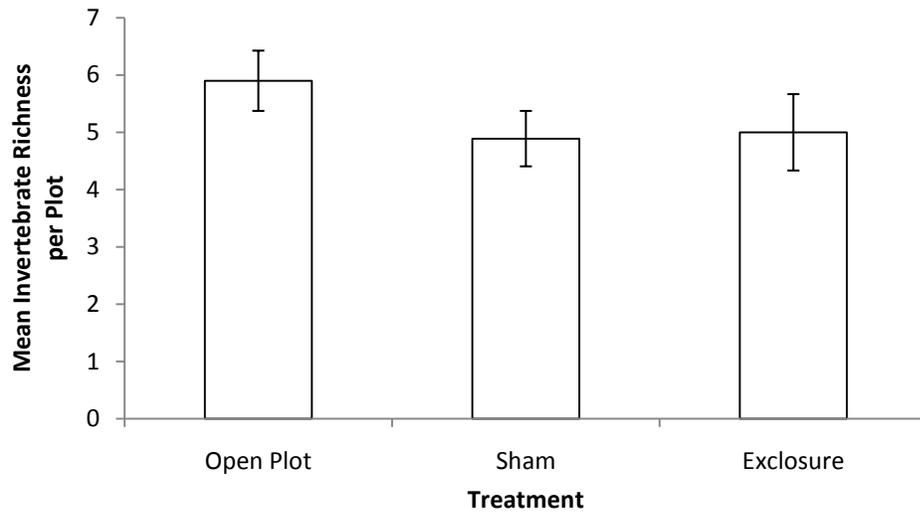


Figure 7. Mean invertebrate richness (± 1 SE) by treatment.

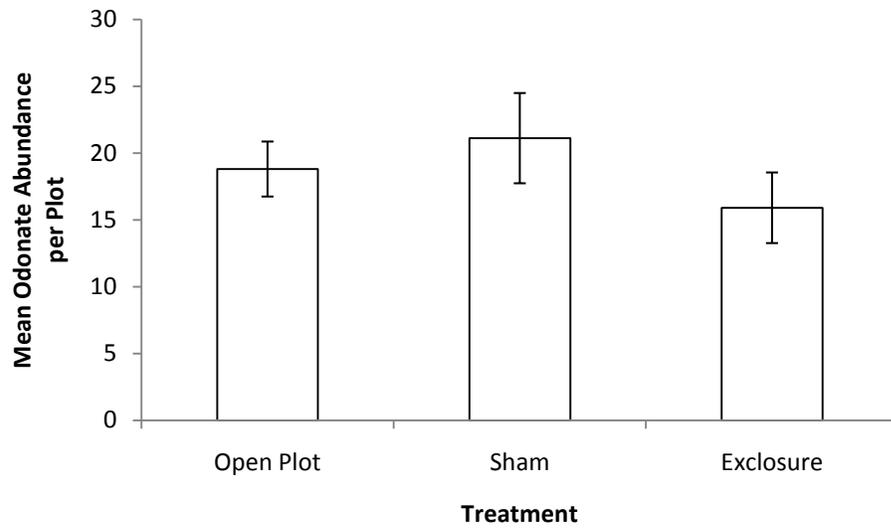


Figure 8. Mean odonate abundance (± 1 SE) by treatment.

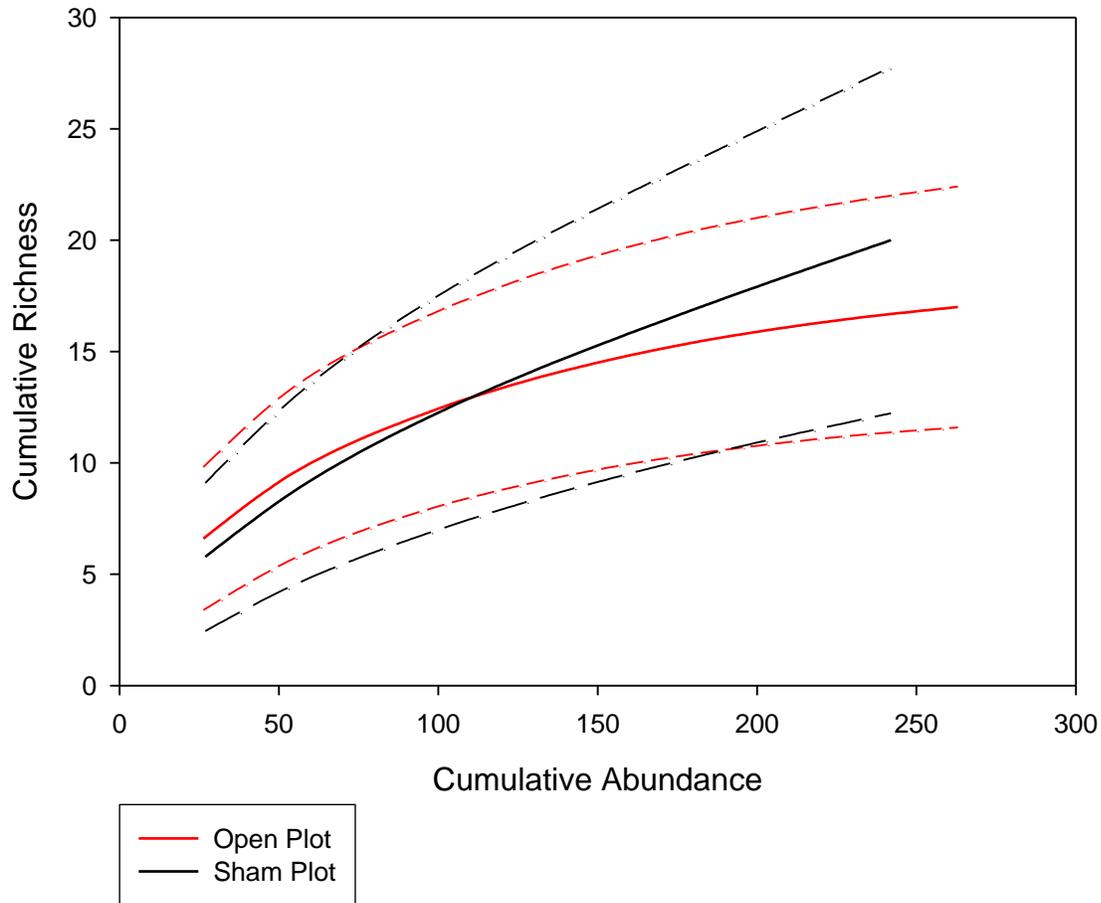


Figure 9. Sample-based species accumulation curves following planned contrast groupings of treatments. Cumulative richness is plotted across cumulative abundance for all sample plots within a treatment. Estimates of average richness for a particular contrast group are represented by solid lines and their associated 95% confidence intervals (dashed lines).

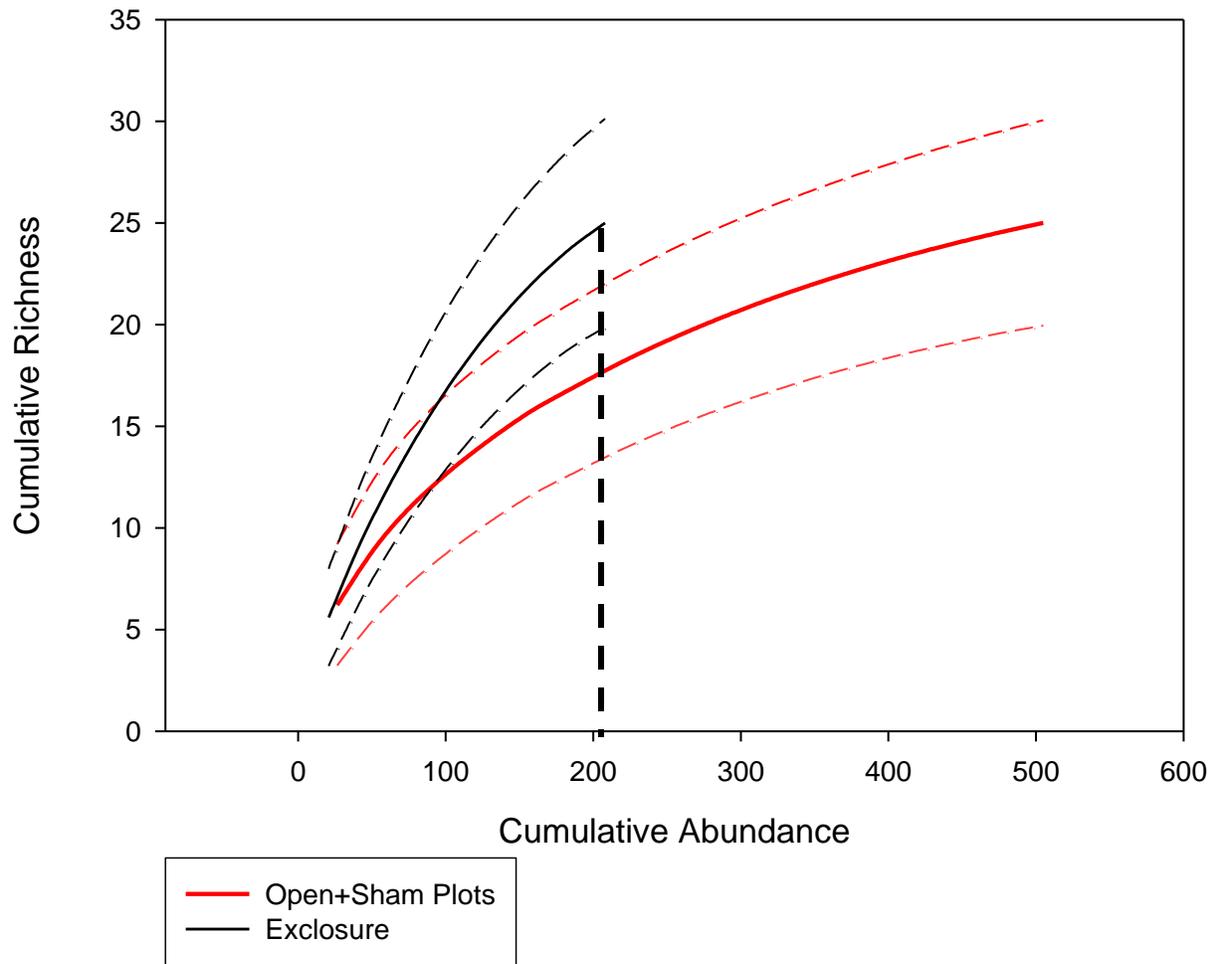


Figure 10. Sample-based species accumulation curves following planned contrast groupings of treatments. Cumulative richness is plotted across cumulative abundance for all sample plots within a treatment. Estimates of average richness for a particular contrast group are represented by solid lines and their associated 95% confidence intervals (dashed lines). The dashed vertical line shows the comparison between the two accumulation curves after accounting for the least number of individuals sampled within a treatment.

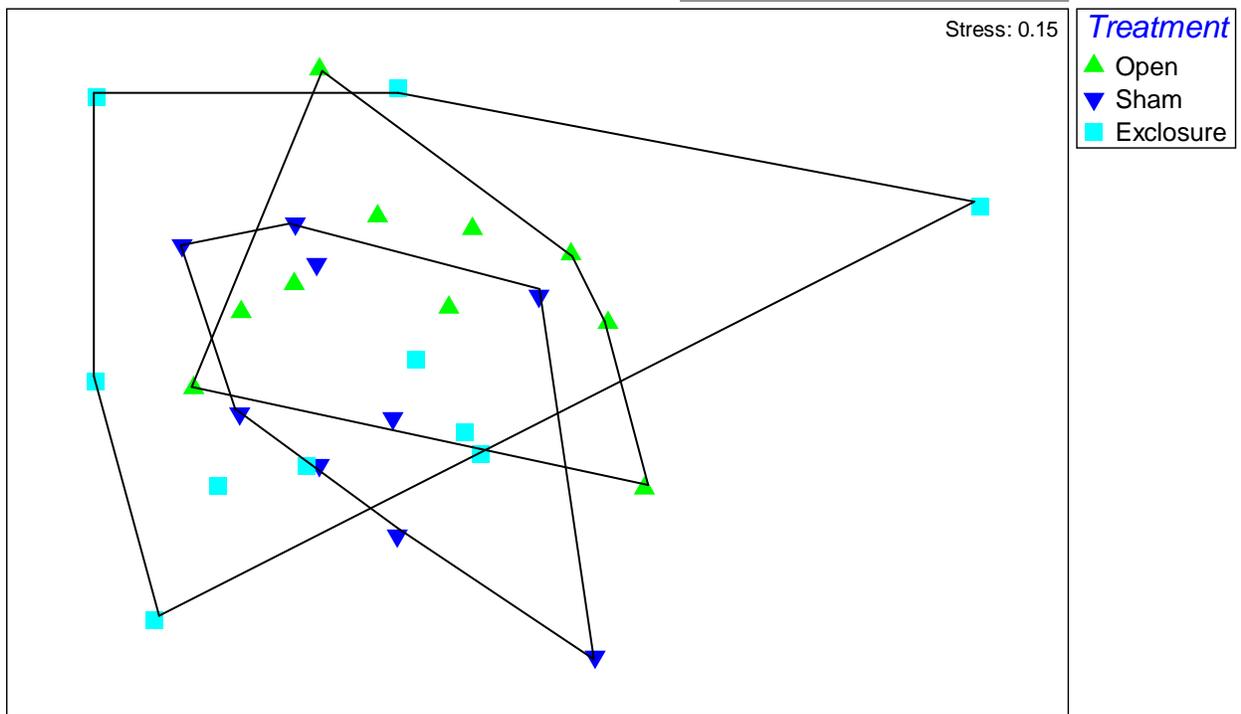


Figure 11. Non-metric multidimensional scaling (NMDS) plot of square root transformed abundance data (first two of three dimensions are shown). The distance between any two points represents how dissimilar the two study plots are in their species composition as measured by Bray-Curtis dissimilarity metric.

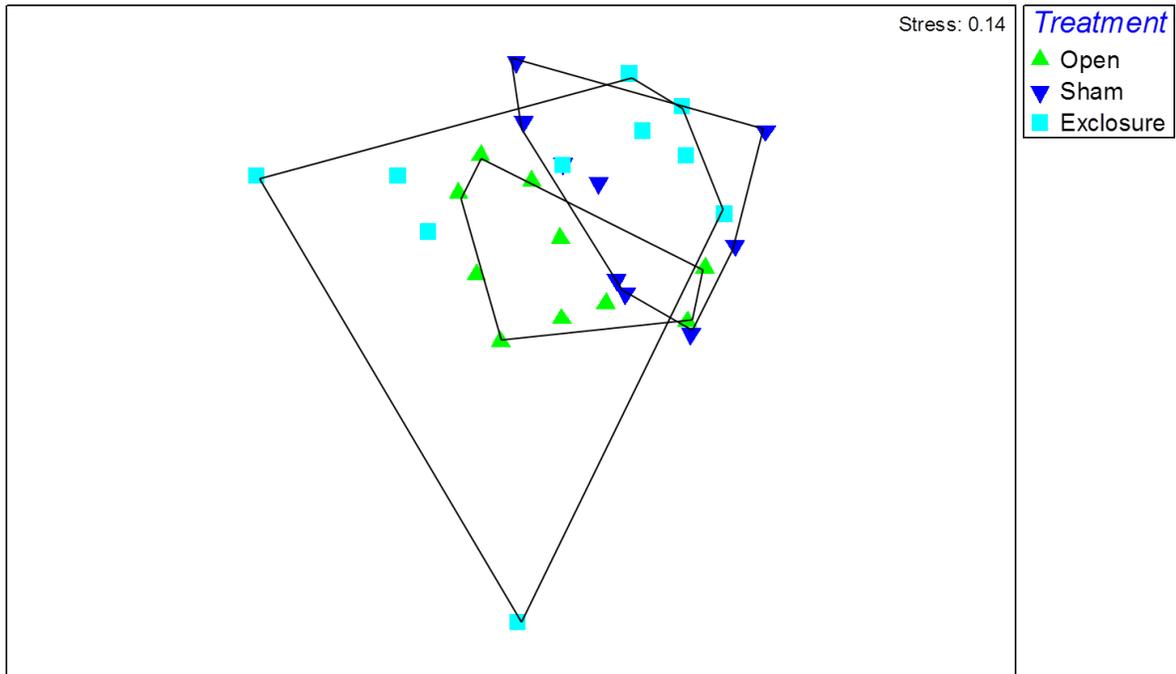


Figure 12. Non-metric multidimensional scaling plot of presence/absence transformed abundance data (first two of three dimensions are shown). The distance between any two points represents how dissimilar the two study plots are in their species composition as measured by Bray-Curtis dissimilarity metric.

APPENDIX A: Animal Use Protocol Approval



**Animal Care and
Use Committee**

212 Ed Warren Life
Sciences Building
East Carolina University
Greenville, NC 27834

June 21, 2010

252-744-2436 office
252-744-2355 fax

David Chalcraft, Ph.D.
Department of Biology
Howell Science Complex
East Carolina University

Dear Dr. Chalcraft:

Your Animal Use Protocol entitled, "The Effects of Turtle Exclusion on Temporary Pond Biodiversity," (AUP #D245) was reviewed by this institution's Animal Care and Use Committee on 6/21/10. The following action was taken by the Committee:

"Approved as submitted"

A copy is enclosed for your laboratory files. Please be reminded that all animal procedures must be conducted as described in the approved Animal Use Protocol. Modifications of these procedures cannot be performed without prior approval of the ACUC. The Animal Welfare Act and Public Health Service Guidelines require the ACUC to suspend activities not in accordance with approved procedures and report such activities to the responsible University Official (Vice Chancellor for Health Sciences or Vice Chancellor for Academic Affairs) and appropriate federal Agencies.

Sincerely yours,

A handwritten signature in cursive script that reads 'Robert G. Carroll, Ph.D.'.

Robert G. Carroll, Ph.D.
Chairman, Animal Care and Use Committee

RGC/jd

enclosure



