# Predator-permanence hypothesis in time: Community dynamics in a seasonally flooded wetland

**Clifton B. Ruehl[1,3], Matthew R. Pintar[2,4], and Joel C. Trexler[1,2,5]**

[1]Department of Biological Sciences, Florida International University, 3000 Northeast 151st Street, North Miami, Florida 33181 USA
[2]Institute of Environment, Florida International University, 11200 Southwest 8th Street OE-148, Miami, Florida 33199 USA

**Abstract:** The predator-permanence hypothesis predicts that as hydroperiod increases in lentic ecosystems, biotic interactions—mainly predation—replace physical factors like drying as the main determinant of community structure and population dynamics. We propose that the same transition occurs over time in seasonally flooded ecosystems that are connected to permanent water bodies. To test for evidence of successional changes that are similar to spatial changes in the relative importance of drying and predation, we used a 12-y time series of snail density, predator density, and water depth at 4 sites arranged along a nutrient gradient in a subtropical, seasonally flooded wetland, the Florida Everglades, USA. The rate of change in snail population size was negatively correlated with their density at all 4 sites, suggesting that density-dependent factors such as resource limitation regulate snail dynamics. The strength of the relationship varied among sites such that when water depth changes were less important, snail population size was more important in predicting changes in snail population size. At the site that consistently had the greatest snail density, crayfish density negatively affected the rate of snail population change, suggesting that crayfish predation may limit snail population growth in areas with more or higher-quality resources that support larger snail populations. Tethering studies were also conducted, which revealed higher snail mortality in the wet season, primarily because crushing predators (e.g., molluscivorous fishes) were more common at that time and added to the chronic mortality by entry-based predators (e.g., crayfish, which access snails through their aperture). In summary, 3 of the sites resembled temporary or permanent fishless ponds where snail populations were primarily structured by abiotic factors, intraspecific competition, and invertebrate predators (e.g., crayfish) during the wet season, whereas 1 site showed evidence that snail populations were also influenced by molluscivorous fish. This temporal change in importance of water permanence factors to fish that affected population dynamics supports the spatial pattern proposed by the predator-permanence hypothesis.
**Key words:** predator permanence, community structure, time series, wetland, Everglades, top down, bottom up, molluscivorous fish, crayfish predation

The predator-permanence hypothesis proposes that aquatic community structure and population dynamics change across space from temporary to permanent aquatic systems because of trade-offs associated with a species' ability to cope with abiotic and biotic factors along the water-permanence gradient (Wellborn et al. 1996). For example, fish do not occur in temporary ponds because they dry, whereas many quickly developing aquatic invertebrates and amphibians are excluded from permanent ponds because they are susceptible to fish predators (Skelly 1997, Wilbur 1997). This spatial framework of community structure can be adapted to better understand effects of temporal variation in water permanence on community structure and population dynamics at a single location (Tonn et al. 2004, Werner et al. 2007). Aquatic communities of seasonally flooded wetlands that are connected to permanent water bodies (e.g., floodplain river systems, ridge and slough wetlands, canals) experience a range of abiotic and biotic

E-mail addresses: [3]Present address: Department of Biology, Columbus State University, 4225 University Avenue, Columbus, Georgia 31907 USA, ruehl_clifton@columbusstate.edu; [4]mpintar@fiu.edu; [5]Present address: Coastal and Marine Laboratory, Florida State University, 3618 US-98, St Teresa, Florida 32358 USA, jtrexler@fsu.edu

Received 28 December 2021; Accepted 1 June 2022; Published online 23 August 2022. Associate Editor, Tadeu Siqueira.

*Freshwater Science*, volume 41, number 4, December 2022. © 2022 The Society for Freshwater Science. This work is licensed under a Creative Commons Attribution-NonCommercial 4.0 International License (CC BY-NC 4.0), which permits non-commercial reuse of the work with attribution. For commercial use, contact journalpermissions@press.uchicago.edu. Published by The University of Chicago Press for the Society for Freshwater Science. https://doi.org/10.1086/721960

factors that change seasonally. These systems may resemble temporary ponds upon reflooding, but transition to mirror permanent water bodies relatively quickly through immigration of fishes and other drying-intolerant animals from hydrological refuges (Whiles and Goldowitz 2005, Dorn 2008). The return time between drying events and immigration rates of community members combine to determine the relative similarity to permanent water bodies that these communities attain during periods of flooding (Trexler et al. 2005).

Disturbance, dispersal, and susceptibility to predation are the central abiotic and biotic drivers of community structure and population dynamics along the predator-permanence gradient. Water permanence is an important disturbance in freshwater ecosystems that affects population size, stability, and growth by removing biomass and affecting community structure by excluding species vulnerable to the drying interval (Grime 1977, Sousa 1984, Grimm and Fisher 1989). Dispersal enables species to move in search of resources and avoid unsuitable habitats (Caceres and Soluk 2002, Abbey-Lee et al. 2013). Predation is an important biotic factor regulating population growth by altering prey traits (e.g., behavior, physiology), removing organisms through consumption, or shifting colonization rates and patterns (Sih et al. 1985, 1998, Lima 2002, Schmitz et al. 2008). For many species along the predator-permanence gradient, trade-offs among traits allow them to persist through drought or fish predation, but usually not both. For example, traits that are successful in habitats that dry frequently include rapid growth and reproduction, aestivation, and desiccation-resistant egg cases (Wellborn et al. 1996). These traits typically trade off with traits that enable coexistence with fish predators like slower growth, maturation at smaller sizes, lower activity, and behavioral changes leading to shifts in habitat use (e.g., avoiding risky habitats) (Wellborn et al. 1996). However, some species can persist across the gradient, whether spatial or temporal, from temporary to permanent habitats and are, therefore, controlled by both abiotic and biotic factors with the relative importance of each depending on the prevailing conditions (Wellborn et al. 1996).

The Florida Everglades in the USA is an expansive subtropical oligotrophic wetland with wet and dry seasons (Davis and Ogden 1994). The Everglades provides a useful ecosystem in which to examine predictions based on the spatially structured predator-permanence hypothesis in a system dominated by temporal changes in water permanence. Although the overall system is nutrient poor, there is a north–south nutrient gradient with more available nutrients (particularly P) in the northern (upstream) Everglades than in the south (Gaiser et al. 2006). Topography changes little across the Everglades landscape, but hydroperiod varies predictably from annual drying near the wetland margins to multi-year inundation in central sloughs. Hydrologic variation is the most important abiotic driver of aquatic communities in the ecosystem (Ruetz et al. 2005, Trexler et al. 2005, Dorn and Trexler 2007, Parkos and Trexler 2011). Periphyton (green algae, cyanobacteria, diatoms, and fungi) forms thick mats in association with bladderworts (*Utricularia* spp.) and grows around submerged stems of emergent aquatic vegetation (e.g., spikerush, *Eleocharis* spp.) that provide habitat complexity, refuge, and resources for macroinvertebrates and snails (Browder et al. 1994, Liston and Trexler 2005, Ruehl and Trexler 2015).

Snails are important primary consumers in the Everglades that exhibit traits enabling them to quickly recolonize marshes that dry frequently, as well as inhabit sloughs that rarely dry (Ruehl and Trexler 2011). Of the many snail species that occur in the Everglades, *Pomacea paludosa* (Say, 1820), *Physella acuta* (Draparnaud, 1805; previously *Haitia cubensis* and *Physella cubensis* [Pfeiffer, 1839]), and *Helisoma* spp. (complex of *Helisoma duryi* [Wetherby, 1879] and *Helisoma scalaris* [Jay, 1839]) are generally thought to be the 3 most common (Thompson 2004, Ruehl and Trexler 2011, Rogers 2016). We focus on *Helisoma* spp. in this study, and reference to snails after this point pertain only to *Helisoma*. A detailed study of *Helisoma* life history in the Everglades is lacking, but *Helisoma* are similar to other planorbids (Dillon 2000). They reach maturity around a month after hatching (~10 mm shell length) and live for about 1 y (Fretter and Peake 1979, Dillon 2000). They lay eggs throughout the wet season and early dry season. In areas where the marsh dries, snails either aestivate or senesce (depending on age) with the survivors emerging as the water returns (Dillon 2000, Ruehl 2010).

Molluscivores can have strong top-down effects on snail population growth. Crayfish are among the most important snail predators in freshwater ecosystems (Lodge et al. 1994). Two species of crayfish occur in the Everglades: the Everglades Crayfish (*Procambarus alleni* Faxon, 1884), common in frequently drying marshes; and the Slough Crayfish (*Procambarus fallax* Hagen, 1870), common in deeper marshes and sloughs. Both species burrow in response to drying and recolonize quickly after reflooding (Dorn and Trexler 2007, Trexler and Loftus 2016), and both are predators of *Helisoma* snails (Ruehl 2010, Ruehl and Trexler 2013). Large fish are also important snail predators in the Everglades where there is sufficient water for their survival, as well as during the wet season when they disperse (≤20 km) into previously dried marshes (Parkos and Trexler 2011, 2014). The 2 most common molluscivorous fishes in the Everglades are the Redear Sunfish (*Lepomis microlophus* Günther, 1859) and Mayan Cichlid (*Mayaheros urophthalmus* Günther, 1862). Both species consume a wide size range of snails and consume numerous individuals/day (Huckins 1997, Bergmann and Motta 2005, Ruehl 2010).

In this study, we examine the value of applying the predator-permanence hypothesis, originally conceived for understanding spatial variation in community structure, to explain temporal variation in community structure at 4 different locations in the Everglades. We developed a model of marsh drying, habitat complexity, and predation based

on the predator-permanence hypothesis to explain planorbid snail population dynamics over time (Fig. 1). The model predicts that snail populations are limited by water depth during the dry season, habitat complexity facilitates snail population growth, and molluscivorous fishes negatively affect snail populations during the wet season. Crayfish (*Procambarus* spp.) are not as susceptible to drought as fishes (Dorn and Trexler 2007) and should present a persistent, year-round negative influence on snail population growth. Based on these predictions, we developed 3 general research questions: 1) How does hydrologic variation affect snail population dynamics? 2) Does habitat complexity help explain variation in snail population dynamics? and 3) What are the relationships between planorbid snails and both crayfish and fish (known predators of snails)?

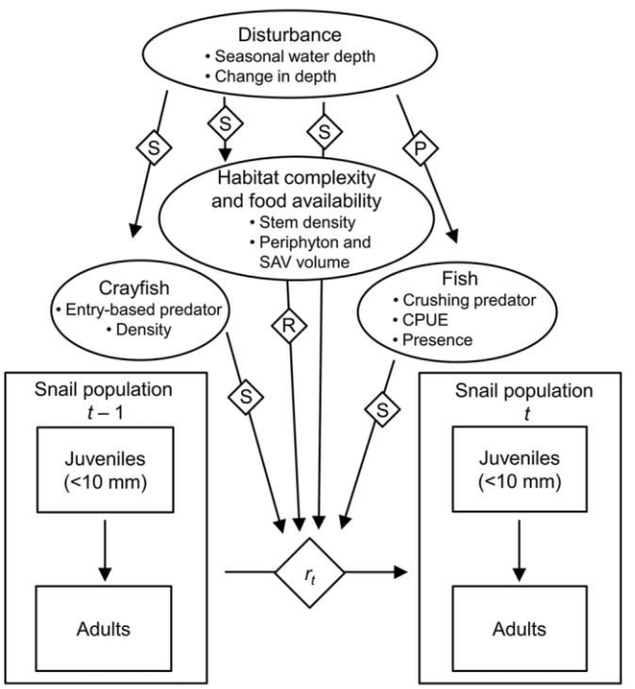


Figure 1. Conceptual diagram of representative ecological drivers that we measured and could affect *Helisoma* spp. populations in the Florida Everglades, USA. Snail populations are shown separately at times $t - 1$ and $t$ and for juveniles and adults because they reproduce continuously with overlapping size structure. Disturbance, such as seasonal change in water depth, affects the survival (S) of emergent stems, periphyton, submerged aquatic vegetation, snails, and crayfish and the presence (P) of large predatory fish in the marsh. Habitat complexity and food availability influence the change in juvenile and adult snail density by affecting resources (R). Fish predators and crayfish predator density affect the change in juvenile and adult snail density through survival. CPUE = catch per unit effort, SAV = submerged aquatic vegetation, $r_t$ = per-capita realized population change.

## METHODS

To evaluate support for our model predictions, we used a 12-y time series of snail density and size, crayfish density, molluscivorous fish catch per unit effort (CPUE), habitat complexity (emergent stem density, periphyton, and submerged aquatic vegetation volume), and water depth at 4 sites with contrasting hydroperiod along a nutrient enrichment gradient. Insight on the effects of predators on snail populations was supplemented with field estimates of snail mortality rates using tethering studies.

### Time series for invertebrates, habitat, and hydrology

***Data collection*** To evaluate abiotic and biotic factors affecting snail population dynamics, we chose sites in spikerush-dominated sloughs with similar water permanence. We chose 2 sites (3, 11) in Water Conservation Area (WCA) 3A and 2 sites (CP, TS) in Taylor Slough (TSL) (for map see Ruetz et al. 2005). Though the sites are oligotrophic, they occur along a P gradient, with sites in WCA relatively enriched with P compared with TSL (Gaiser et al. 2006). At each site, there were 3 plots (100 $m^2$, 0.5–2 km apart) where either 5 (WCA) or 7 (TSL) samples were taken during each sampling event (sampling locations within plots were chosen randomly). Aquatic communities at these 4 sites were sampled during 5 mo each year from July 1996 through December 2007, representing 12 y (June–May). This sampling schedule resulted in a maximum of 58 visits $site^{-1}$ $plot^{-1}$ for all sites (except site 11 in WCA, which had a maximum of 53 visits; regular sampling was discontinued in December 2006 because of vegetation encroachment). The annual sampling regime captured the early (July) and mid (October) wet season, the transition to the dry season (December), and the early (February) and late (April) dry season. Plots within sites were not sampled in periods when water depths were <5 cm and represent missing values in the dataset. In TSL, we sampled the 3 plots at site CP 57/58 (98%) of potential events, and we sampled the 3 plots at site TS 55 (95%), 54 (94%), and 53× (91%). In WCA, at site 3, we sampled 2 plots 56× (97%) and 1 plot 55× (95%). At site 11, we sampled 1 plot 44× (83%), the 2nd plot 43× (81%), and the 3rd plot 35× (66%). Sampling events represent time steps in our models.

We collected samples with 1-$m^2$ throw traps (1.6-mm mesh), following standard procedures (see Jordan et al. 1997 for details). Briefly, trained field technicians identified and counted emergent plants. We quantified periphyton, floating vascular, and submerged aquatic vegetation biovolume with a large graduated cylinder modified with holes to drain water. Trained technicians collected all animals, including snails, with a bar seine (1.6-mm mesh) and 2 nets (1.2- and 4.8-mm mesh) using standardized effort and preserved in 37% formalin, then transferred to 70% ethanol for later analysis. We estimated snail standing stock by measuring the shell length of all collected snails and estimating

individual wet-tissue mass with locally derived length-to-mass relationships (Obaza and Ruehl 2013). The mean snail standing stock among samples at each plot served as the unit of observation, resulting in 3 replicates (3 plots sampled) at each site for each sampling event.

***Data analysis*** To answer our 3 research questions about snail density's relationship with hydrologic variation, habitat complexity, and predator density, we used time-series analysis of the throw-trap dataset. In all time-series models, we used the per-capita realized population change ($r_t$) as the response variable, which was calculated as

$$r_t = \log(N_t/N_{t-1}), \qquad \text{Eq. 1}$$

where $N_t$ is the population density (no./m$^2$) in the current time ($t$) step and $N_{t-1}$ is the population density in the previous time step (i.e., previous sampling event). Using $r_t$ as the dependent variable simplifies model complexity because it accounts for autocorrelation in the time series (Turchin 2003).

We used multiple regression to model the data in 3 hierarchical steps driven by the linkages among the response variables and the 3 types of independent variables in our conceptual model (Fig. 1). We used a model selection approach that compared Akaike's Information Criterion (AIC) among multiple regression models to choose the best model at each step. Models with the lowest AIC were considered preferred (i.e., best) because they captured greater amounts of information in the data than those with larger AIC values (Anderson 2008). Models differing by ≤2 AIC were considered equivalent models in the amount of information they explained, whereas models differing by >2 AIC were considered to capture less information and were not retained in subsequent steps.

In step 1, we examined the effects of hydrologic variation on changes in snail population size by contrasting 8 models that contained different combinations of water depth, change in water depth ($\Delta D = D_t / D_{t-1}$), lag water depth ($LD = D_{t-1}$), days since a site was last dry (DSD), and DSD$^2$. We used the change in water depth between sampling events to model recession or flooding of the marsh. Lag water depth modeled the effect of water depth in the prior sampling event on the change in snail density. The DSD variable modeled drying of the site, and we included the squared term (DSD$^2$) because past work demonstrated that the effects of days since dry diminishes with time (Ruetz et al. 2005).

In step 2, we took the best model from step 1 and added the different variables that described habitat complexity. Predictor variables in this step included 1) stem density; 2) the combined biovolume of periphyton, floating vascular, and submerged plants; and 3) the prior 2 combined. Variables in all 3 datasets were log transformed to correct for overdispersion.

In step 3, we took the best model from step 2 and added combinations of lag ($t - 1$) snail density, lag snail size, and lag crayfish density to examine biotic interactions. Lag snail density tested for negative density dependence, and lag snail size tested for the effect of body size on the change in snail density. Together, these variables tested for intraspecific effects on snail populations. For crayfish density, we combined both crayfish species into a single variable because laboratory trials (Ruehl 2010) indicated they had similar effects on snails, smaller individuals were not identifiable to species, and we were interested in the net effect of crayfish on snails. We modeled the effects of crayfish on the change in snail density using crayfish density in the prior sampling event (lag crayfish density) because if crayfish predation affects snail population size, past crayfish density should predict current snail population size. We log transformed crayfish density to correct for overdispersion.

We report the parameter estimates and SE ($\beta \pm$ SE), the standardized $\beta$ weights, the squared semi-partial correlation, and the adjusted $R^2$ for the final model at each site (Table 1). The standardized $\beta$ weights are parameter estimates that are adjusted by their SD and provide a weighted effect size for each parameter (Tabachnick and Fidell 2007). The squared semi-partial correlation relates the amount of variation explained by the whole model to each parameter. The adjusted $R^2$ reports the amount of variation in the dependent variable that is explained by the total model and adjusted for model complexity.

### Large molluscivorous fish

***Data collection*** Large fish (>8 cm standard length [SL]) are present at low density in the Everglades (Chick et al. 2004) but could influence snail population dynamics because they can consume large numbers of snails in short periods of time (Lodge et al. 1987, Huckins 1997). We addressed the potential for large Redear Sunfish and Mayan Cichlids (>8 cm SL) to affect snail density with time series data from airboat-mounted electrofishing (Chick et al. 1999). CPUE of large fishes was collected from 1997 to 2007 at 3/4 sites (site 11 in WCA was not sampled because vegetation was too thick to be effective) with three 5-min electrofishing transects (pulsed DC current at 1500 W; Smith-Root, Vancouver, Washington) near the 3 throw-trap plots around the same time as throw-trap samples were collected (for detailed methods see Chick et al. 1999, 2004, Parkos and Trexler 2011). We report catches of these fishes at sites but model their presence for each region because they travel among sites within regions (Parkos and Trexler 2011).

***Data analysis*** Because large fish are rare in the Everglades, we created a presence–absence variable and used logistic regression to model the probability of large fish occurrence within each region (i.e., TSL, WCA). We tested

Table 1. Summary statistics for the final models predicting per-capita rate of change in snail density from the model selection procedure for each site in the Florida Everglades, USA. Sites 3 and 11 are in Water Conservation Area (WCA) 3A, and sites CP and TS are in Taylor Slough (TSL). Model selection steps and Akaike's Information Criterion selection are in Tables S1–S4. – = no data, β = standardized regression coefficient, β weights = β adjusted by standard deviation.

| Region | Site | $n$ | Independent variables | β ± SE | β weights | Squared semi-partial correction | Adjusted $R^2$ | Rank |
|---|---|---|---|---|---|---|---|---|
| WCA | 3 | 87 | Lag water depth (cm) | −0.004 ± 0.008 | −0.082 | 0.002 | 0.4 | 7 |
| | | | Δ water depth (cm) | −0.2 ± 0.1 | −0.2 | 0.03 | – | 3 |
| | | | Log periphyton volume (mL) | 0.09 ± 0.07 | 0.1 | 0.01 | – | 5 |
| | | | Log lag crayfish density (no./m$^2$) | −0.3 ± 0.2 | −0.2 | 0.03 | – | 2 |
| | | | Log lag snail size (mm) | −0.13 ± 0.19 | −0.13 | 0.004 | – | 4 |
| | | | Log Δ snail size (mm) | −0.005 ± 0.1 | −0.006 | 0.00 | – | 6 |
| | | | Log lag snail density (no./m$^2$) | −0.6 ± 0.1 | −0.6 | 0.3 | – | 1 |
| WCA | 11 | 35 | Δ water depth (cm) | −0.2 ± 0.01 | −0.3 | 0.07 | 0.35 | 2 |
| | | | Log stem density (no./m$^2$) | −0.032 ± 0.16 | −0.036 | 0.001 | – | 4 |
| | | | Log lag snail density (no./m$^2$) | −0.46 ± 0.19 | −0.39 | 0.13 | – | 1 |
| | | | Log Δ snail size (mm) | 0.064 ± 0.069 | 0.15 | 0.018 | – | 3 |
| TSL | CP | 66 | Δ water depth (cm) | −0.2 ± 0.06 | −0.3 | 0.07 | 0.36 | 2 |
| | | | Log stem density (no./m$^2$) | −0.1 ± 0.07 | −0.2 | 0.03 | – | 3 |
| | | | Log lag snail density (no./m$^2$) | −0.5 ± 0.1 | −0.5 | 0.2 | – | 1 |
| | | | Log Δ snail size (mm) | 0.058 ± 0.048 | 0.13 | 0.016 | – | 4 |
| TSL | TS | 55 | Δ water depth (cm) | −0.07 ± 0.07 | −0.1 | 0.01 | 0.46 | 3 |
| | | | Log periphyton volume (mL) | −0.1 ± 0.04 | −0.3 | 0.08 | – | 2 |
| | | | Log lag snail density (no./m$^2$) | −0.784 ± 0.125 | −0.656 | 0.4 | – | 1 |
| | | | Log Δ snail size (mm) | 0.003 ± 0.046 | 0.006 | 0.00 | – | 4 |

for effects of year, sampling period (month), year-by-sampling period, water depth, DSD, and DSD$^2$, and we used model selection to determine the best model from the set for each region as described above. Effects of large fishes were investigated independently of the throw-trap dataset because we conducted electrofishing during only 4 sampling periods/y and sampling was often limited during the dry season, resulting in different sample sizes between datasets.

### Tethering experiment

***Data collection*** We conducted a tethering experiment to estimate the relative rate of predation at the 4 sites for each sampling event during 2007. Tethering was done in conjunction with throw-trap sampling. We tethered 20 snails (9–14 mm shell length, sourced from captive populations; see Ruehl and Trexler 2013, 2015 for details) to separate PVC stakes that were spaced 3 m apart in 2 blocks at each site. Stakes were driven into the marsh floor and a 1-m length of 6-lb (2.7-kg) monofilament was tied to the stake. We attached the snails to the tether with cyanoacrylate adhesive (superglue) applied to the shells. Tethers allowed snails to move freely and feed on periphyton and offered the opportunity to hide. We retrieved tethers after 4 d. We controlled for effects of handling, abiotic factors (e.g., low dissolved oxygen), and the potential for escape from tethers by tethering 4 snails in a 1-m$^2$ cage in each block. There was no mortality for snails tethered inside cages. A strong windstorm flipped 1 cage during 1 event, and all but 1 snail remained attached to their tether in the flipped cage. The mode of predation was determined based on the remains at the end of the tether. Crushing predators, like fish, turtles, or small alligators, left shell fragments. Entry-based or shell-chipping predators, like crayfish or belostomatid bugs, left empty shells (Fig. 2). Tethers with no snail or remains were removed from all analyses because we were specifically interested in quantifying the relative effects of crushing and entry-based predators.

***Data analysis*** Sites 11 and 3 were too shallow to sample in April, and site 11 remained too dry in July to sample. Because this analysis was based on only 1 y of data, idiosyncrasies among sites were more easily interpreted than in the time-series study; therefore, spatial and seasonal variation were included in a single statistical model. We used logistic regression to separately model the probability that snails were consumed in each region, sites nested within regions, sampling period (month), water depth, tethered snail size, and the associated interactions (Table S1). Similar to the time series, model selection was used to find the

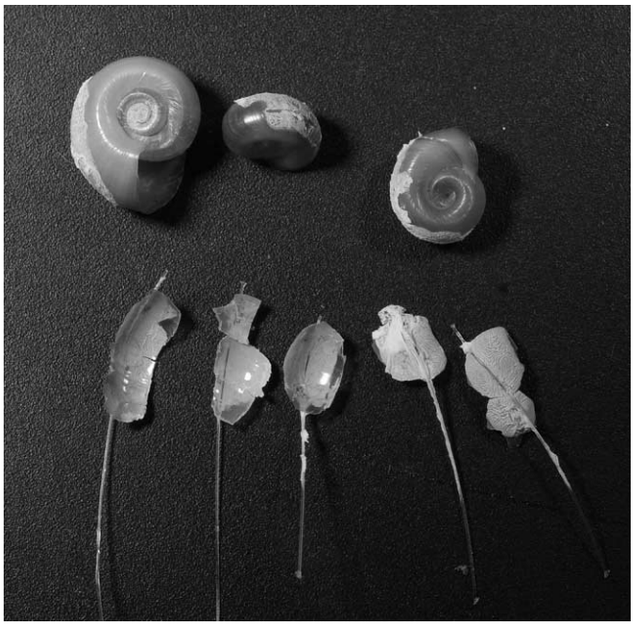

Figure 2. Representative snail shell remains found at the end of tethers in the Florida Everglades, USA. Intact empty shells (tethers removed) were left by entry-based predators like crayfish or belostomatids (top), whereas crushing predators, like fish, left shell fragments (bottom; interpretations supported by laboratory feeding trials). The glue we used to attach tethers left the white residue on the shells. Photo credit: CBR.

best model out of the set. We used SAS® (version 9.4; SAS Institute, Cary, North Carolina) PROC GLM, PROC REG, and PROC MIXED for time series analyses and PROC LOGISTIC for logistic models for all analyses and dataset management.

## RESULTS

### Time series for invertebrates, habitat, and hydrology

We found considerable spatial and temporal variation in snail density (no./m$^2$), crayfish density, and water depth at all 4 sites during the 12-y study but relatively small annual variation in snail and crayfish density within each site (Fig. 3A–D). At all sites, both snails and crayfish recovered quickly (<1 sampling period) after sites reflooded. Snail density tended to be higher and more variable at site 3 in WCA (Fig. 3A) compared with the other 3 sites (Fig. 3B–D). Site 11 in WCA had many gaps in the time series and experienced large fluctuations in snail and crayfish densities because water residence times were shorter than at all other sites (Fig. 3B). Site CP in TSL tended to have fewer variable populations of crayfish and snails throughout the time series, along with lower crayfish densities, compared with other sites (Fig. 3C). At site TS in TSL, populations of snails and crayfish fluctuated considerably, and crayfish tended to be more numerous than at other sites (Fig. 3D).

Seasonal trends in crayfish density, snail density, and snail body size were more apparent after averaging across years (Fig. 4A–D). During the early wet season (July), snail densities were low (Figs 4B, S1A–D) and average body sizes were large (Fig. 4C). Large snails were replaced with numerous small individuals by December, and populations again consisted of many large individuals by April (Fig. S2A–D). These changes in density and snail body size corresponded with fluctuations in water depth among sampling periods over the 12-y time series at all 4 sites (Fig. 4D). Water depth was greatest (50–60 cm) in the wet season (July–December) and gradually declined during the dry season (February–April; Fig. 4D). Comparatively, there was much less seasonal variation in stem density and periphyton volume (Fig. S3A, B).

The 1$^{st}$ set of regression models assessed the importance of water permanence and depth on the change in snail density. At site 3, water depth during the prior sampling event (i.e., lag water depth) and change in water depth between sampling events (i.e., ΔD) were the best

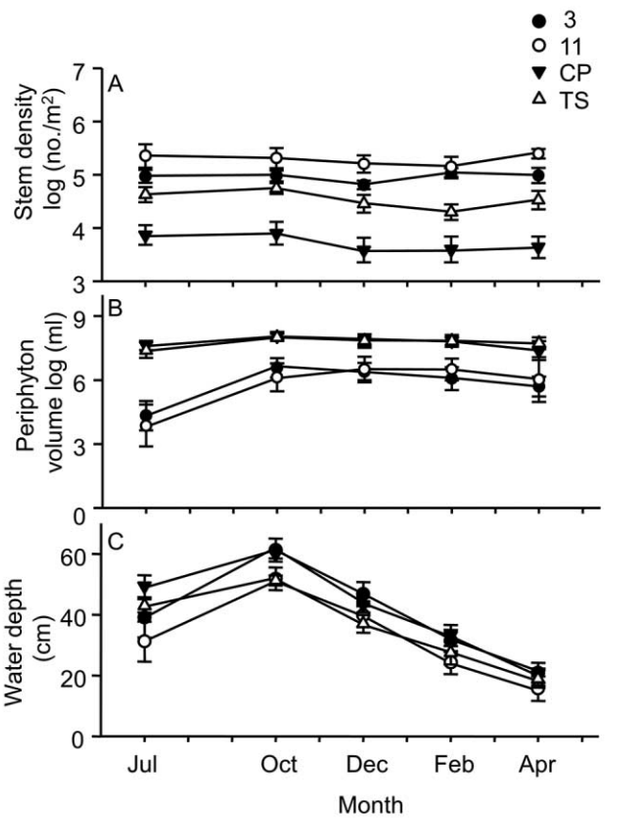


Figure 3. Snail density (mean, $n$ = 3 plots, closed circles) and crayfish density (mean, $n$ = 3 plots, squares) compared with water depth (mean, $n$ = 3 plots, open circles) for a 12-y period at 4 sites in the Florida Everglades, USA. The year is marked on the $x$-axis every July. Sites 3 (A) and 11 (B) are in Water Conservation Area 3A, and sites CP (C) and TS (D) are in Taylor Slough. Note the log scale on the left $y$-axis for density and the linear scale on the right $y$-axis for water depth. Gaps in the plot indicate when the sites were dry (<5 cm deep).

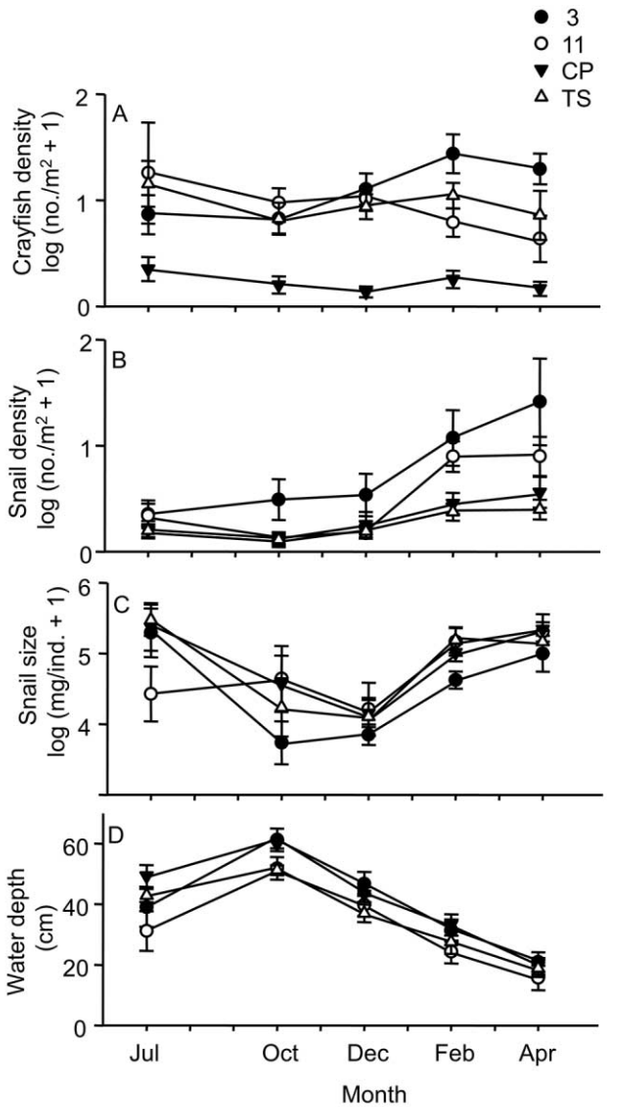


Figure 4. Seasonal (sampling period) variation (mean ±1 SE, 12 y) in crayfish density (A), snail density (B), individual snail size (C), and water depth (D) at 2 sites in Water Conservation Area 3A (3, 11) and Taylor Slough (CP, TS) in the Florida Everglades, USA. We took samples during months labeled on the *x*-axis. Jul = July, Oct = October, Dec = December, Feb = February, Apr = April.

predictors of snail density change and were included in the final model (Table S2). For the other 3 sites (11, CP, and TS), change in water depth was the single best predictor of snail density change and was included in the final models (Tables S3–S5). Therefore, variables associated with water depth fluctuation improved model fit more than variables associated with water permanence, such as DSD and $DSD^2$.

Adding habitat complexity variables to the best models for water depth improved model fit. Periphyton volume predicted snail density change better than stem density at sites 3 and TS and was included in the final model for those sites, whereas stem density predicted snail density change at sites 11 and CP better than periphyton volume and was included in the final model for those sites (Tables S2–S5). Interestingly, stem density was highest at site 11 and lowest at CP (Fig. S3A). Sites 3 and TS had the highest periphyton volume among the 4 sites (Fig. S3B).

Adding biotic variables to the best abiotic models improved model fit considerably. Snail density in the previous sampling event (lag snail density) was the best predictor of snail density change between sampling events for all sites and was included in the final models (Tables S2–S5). Snail body size in the previous sampling event (lag snail size) was included in the final model at site 3, and change in snail size between sampling events was included in the final model at all 4 sites. Crayfish density in the prior sampling event (lag crayfish density) improved model fit at site 3. None of the other biotic variables were retained in the final models of the other sites.

Parameter estimates from the final models for each site revealed the magnitude and direction of relationships between the different independent variables and the dependent variable change in snail density. The rate of snail density change was negatively related with the change in water depth at all sites (β weights: 3 = −0.231, 11 = −0.297, CP = −0.286, TS = −0.116), indicating that changes in snail density slowed as changes in water depth increased (Table 1, Fig. 5A–D). None of the relationships between snail density change and habitat complexity were very strong (Table 1). However, stem density was negatively related to the change in snail density at sites 11 (β weight: −0.036) and CP (−0.191), and periphyton volume was negatively associated with snail density change at TS (−0.289). Conversely, the relationship between periphyton volume and change in snail density was positive at site 3 (β weight: 0.132).

Snail density change was negatively related to snail density in the previous time step at all sites, indicating negative density dependence (β weights: 3 = −0.551, 11 = −0.391, CP = −0.447, TS = −0.656). The effects of prior snail density on the change in snail density were much stronger than changes in water depth and habitat complexity variables (Table 1). Crayfish density in the prior sampling event (lag crayfish density) was negatively correlated with the change in snail density at site 3 (β weight: −0.216) and ranked $2^{nd}$ in importance among the variables behind prior snail density. Lag crayfish density was not included in the final models for the other sites (Table 1, Fig. 5A–D).

### Large molluscivorous fishes

Large molluscivorous fishes were sparsely distributed in the marshes of the Everglades. Over the 11-y period in TSL, 60 Mayan Cichlids and 60 Redear Sunfish were caught at CP, and 46 Mayans and 24 Redear were caught at TS. In

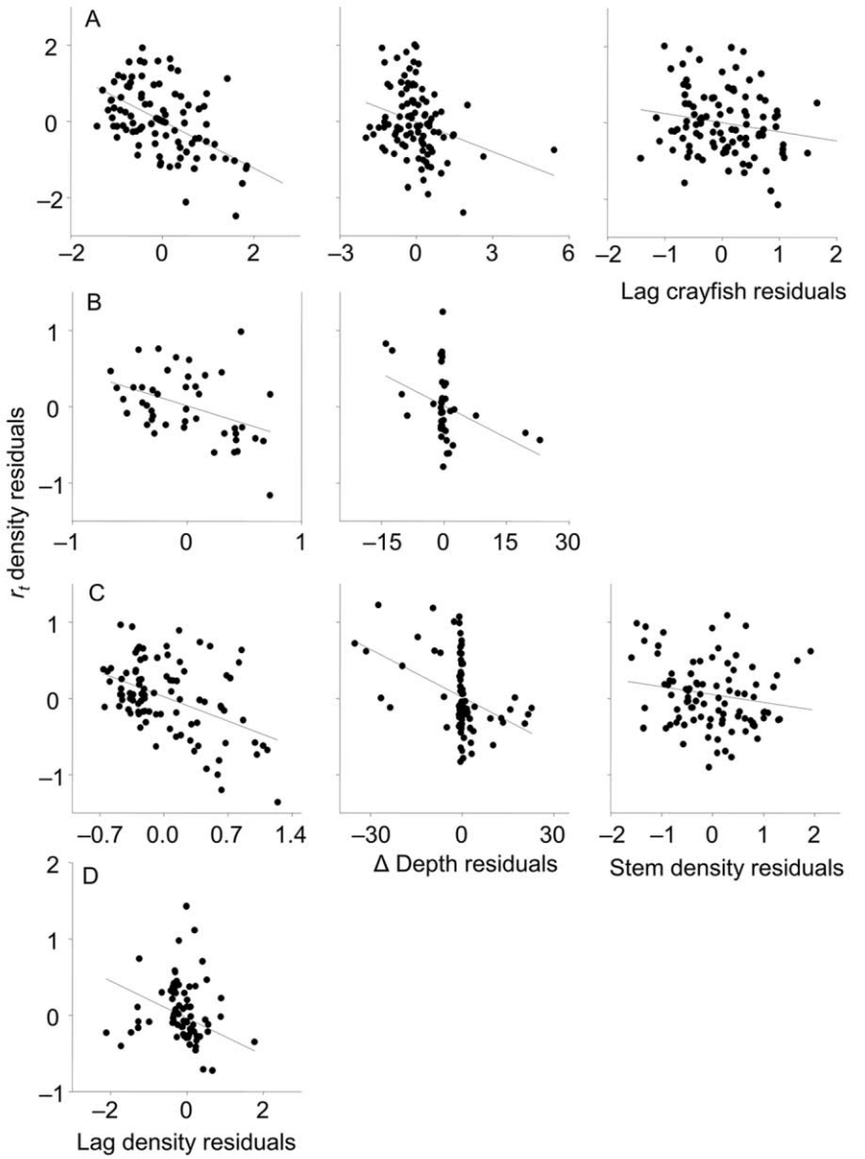


Figure 5. Partial regression plots for the log lag snail density (no./m$^2$), change in water depth (cm), and log stem density (no./m$^2$) or log lag crayfish density (no./m$^2$) at 4 sites in the Florida Everglades, USA. Sites 3 (A) and 11 (B) are in Water Conservation Area 3A, and sites TS (C) and CP (D) are in Taylor Slough. Plots show residuals for the dependent and independent variables after each was regressed separately on the other independent variables. Note that the *x*- and *y*-axes scales are different. Not all independent variables retained in the final model exhibited strong correlations (>|0.2|) with the change in snail density and are therefore not shown.

WCA, 60 Mayans and 40 Redear were caught at site 3 (no samples were taken at site 11). Selection of potential logistic regression models revealed that water depth and sampling event were the best predictors of large fishes in the marshes surrounding site 3 (df = 2, Wald's $\chi^2 = 9.87$, $p = 0.007$, adjusted $R^2 = 0.27$; Table S6). Sampling event explained more variation in large fish presence (β ± SE = 1.26 ± 0.56) than depth (0.06 ± 0.02), indicating that molluscivorous fishes were more numerous in the marshes during the wet season regardless of water depth. Another reason sampling event accounted for more variation than water depth was that, in some years, water remained relatively deep at some sites in WCA even in the dry season, so sampling period and depth were imperfectly correlated. Water depth (β ± SE = 0.03 ± 0.01) was the single best predictor of encountering large molluscivores in TSL compared with the other candidate models (df = 1, Wald's $\chi^2 = 8.24$, $p = 0.004$, adjusted $R^2 = 0.06$; Table S6). Therefore, in both regions, the probability of encountering large molluscivores increased with increasing water depth.

### Tethering experiment

Of 389 tethered snails, 115 were consumed during the year, and mortality ranged from 1 to 20%/d among the 4 sites across the 5 sampling periods. Logistic regression models that included season or season and water depth were the best predictors of snail mortality (Table S1). In the season-only model, snails had a higher probability of being consumed during the wet season (July, October) than in the dry season (df = 1, Wald's $\chi^2 = 13.26$, $p = 0.0003$, $\beta = -0.367$). Adding water depth to the season-only model did not qualitatively change the probability of snail consumption due to season (df = 1, Wald's $\chi^2 = 15.34$, $p < 0.0001$, $\beta = -0.449$), and water depth was not strongly related to the probability of snail consumption (df = 1, Wald's $\chi^2 = 2.34$, $p = 0.126$, $\beta = -0.0145$). Among the 115 snails that were eaten, 75 were consumed by entry-based predators (Fig. 2, top) and 40 were consumed by crushing predators (Fig. 2, bottom). Water depth was the only independent variable in the final model from the set used to predict the mode of predation (Table S1). The probability of being consumed by a crushing predator increased with increasing water depth (df = 1, Wald's $\chi^2 = 7.89$, $p = 0.005$, $\beta = 0.043$).

## DISCUSSION

Snail populations in the Everglades are controlled by a combination of biotic and abiotic factors that vary with the seasonal hydrologic cycles in the ecosystem (Trexler et al. 2005, Dorn 2013, Ruehl and Trexler 2013, 2015, Knorp and Dorn 2014, Dorn and Cook 2015). We took advantage of this variation to explore the application of the spatially explicit predator-permanence hypothesis to better understand community structure in a single location over time. At all 4 study sites, snail populations experienced strong negative feedback on population size with a ~3-mo time lag, consistent with density-dependent regulation during the 12-y study period. Among the 4 sites, prior snail density (biotic) and changes in water depth (abiotic) were the strongest predictors of changes in snail population size. We found that prior crayfish density was negatively correlated with the change in snail density at site 3, where snails were most common throughout the time series, suggesting a role for crayfish in regulating snail populations at that site. These results generally support our conceptual model that in addition to the expected abiotic factors, both competition and predation affect population dynamics (Fig. 1). Moreover, the seasonal changes in the relative importance of abiotic and biotic factors we observed at site 3 align with those predicted by the predator-permanence hypothesis across space (Wellborn et al. 1996). We discuss the importance of disturbance on planorbid snail population dynamics, how resources may limit snail population growth, despite resources being common, and examine the role of crayfish and fish in controlling snail populations. We then use our conceptual model to relate seasonal variation at a site to the spatial gradient proposed by the predator-permanence hypothesis.

Wetland drying is a disturbance that affects populations of aquatic species at different spatial and temporal scales. Time since the last disturbance, a measure of water permanence, is widely used to quantify population or community responses to disturbances (Noble and Slatyer 1980, Grimm and Fisher 1989). DSD generally accounts for development of small-bodied fish assemblages after a drying event in the Everglades (Ruetz et al. 2005, Trexler et al. 2005). However, DSD did not explain changes in snail density in this study. Rather, change in water depth and lag water depth were the best abiotic predictors of snail density change (Table 1). Changes in snail density were negatively correlated with changes in water depth and lag water depth (site 3), indicating that increasing water depths corresponded to decreasing snail densities (no./$m^2$). This pattern was most evident at the onset of the wet season when the marsh refilled (Figs 3A–D, 4A–D). Changes in water depth and lag water depth are more sensitive to processes occurring before and after a drying event (e.g., rainfall) rather than being representative of the drying event itself (DSD).

Snail life-history characteristics enable populations to be more resilient to drying events than fishes and some crayfishes. Many aquatic snails aestivate during dry periods, and large individuals are more likely to survive drying periods. At the onset of the wet season, survivors reproduce and then senesce (Richards 1963, Heeg 1977, Fretter and Peake 1979, Dillon 2000). Body-size variation, which was also included in the final models for all sites (Figs S2A–D, S3A–C), exhibited a relatively weak effect on changes in snail population size. This weak correlation may be explained by the relatively small size (10-mm shell length; Dillon 2000, Ruehl 2010) at which snails begin laying eggs, indicating that snails of many sizes contribute to snail population growth. Our data on seasonal variation in snail densities strongly support this mechanism. Snail populations emerged from the driest months (May, June) with much lower densities of large individuals that likely laid eggs before senescing. Hence, water-depth variables (e.g., change in water depth) explain changes in snail density better than water-permanence variables (e.g., DSD).

Competition for resources may account for much of the variation in snail density change during the wet season and early dry season. Periphyton mats are ubiquitous in the Everglades and range in quantity and quality as both food and shelter for grazers (Browder et al. 1994, Turner et al. 1999, Gaiser et al. 2005, Liston and Trexler 2005, Ruehl and Trexler 2011, Trexler et al. 2015). Northern areas of the system are relatively enriched with P, leading to different periphyton composition and higher chlorophyll *a* content compared with southern areas (Gaiser et al. 2006, 2011). Field studies and experiments indicate that moderate P enrichment increases periphyton resource quality and higher consumer density and biomass of Everglades' grazers (Turner

et al. 1999, Gaiser et al. 2005, Sargeant et al. 2011, Trexler et al. 2015). A similar pattern of increased biomass with P enrichment emerges specifically from studies on *Helisoma* snails (Ruehl and Trexler 2013, 2015). In this study, snail density peaked and was, on average, higher in the relatively P-enriched northern region (WCA) compared with the P-poor southern region (TSL). At all sites regardless of region, prior snail density was the strongest predictor of snail density change. This result suggests that P enrichment may have a positive effect on snail population growth across the study landscape and that resource limitation from poor-quality food may account for a large proportion of the factors regulating snail populations in the Everglades. The relationship between P enrichment and resource availability for snail populations may also explain the general pattern of lower snail density and biomass in karst wetlands compared with other freshwater ecosystems (Ruehl and Trexler 2011). However, we could not directly address the relationship between P levels and snail populations using the time series because nutrient analysis was not included in the sampling protocol.

Predation contributes to prey population regulation in many freshwater ecosystems, including wetlands (Sih et al. 1998, Batzer et al. 2000, Lima 2002, Dorn et al. 2006, Chick et al. 2008). Our time-series data revealed a negative correlation between predator density and the change in snail density at 1 (site 3) of the 2 relatively P-enriched sites in the northern region, suggesting that predation contributed to population regulation there. Three lines of evidence from other studies in the Everglades support the role of fish and crayfish in limiting snail populations at that site and other similar sites. First, non-consumptive effects of predators negatively affect snail populations, and those effects tend to be larger in P-enriched areas. A mesocosm experiment found that nonlethal crayfish in P-enriched conditions reduced snail reproductive output by 60% compared with no-crayfish conditions (Ruehl and Trexler 2013). A field experiment found that snails grew 21% slower on P-enriched periphyton in areas (near canals) with more predators (mostly fish) compared with the same periphyton in areas with fewer predators (far from canals) (Ruehl and Trexler 2015).

Second, crayfish have strong consumptive effects on snail populations in the Everglades (Dorn 2013), their populations rebound quickly after dry-down events (Dorn and Trexler 2007, Dorn and Volin 2009), and they are common in marshes (Dorn et al. 2005), enabling crayfish (and other invertebrate predators) to be a persistent source of snail mortality year round. Our tethering experiment supported these other studies, with snail mortality averaging around 10%/d and entry-based predators accounting for 65% of consumption events. Further, lab-based performance trials demonstrated that crayfish consumed as many as 2 (0.2 g wet-tissue mass) snails/d, although only smaller snails were consumed by crayfish because snails reached a size refuge from crayfish around 8 mm in shell length (Ruehl 2010).

Third, fish predators consume numerous snails during the wet season, thereby negatively affecting snail populations during this period. Mayan Cichlids and Redear Sunfish were present in both marshes during the wet season based on electrofishing data (water depth >60 cm). The tethering experiment revealed that 35% of all mortality was from crushing predators (e.g., fish), which was more likely with increasing water depth. Handling-time and consumption-rate trials revealed that the largest Mayan Cichlids (21-cm SL) ate the largest snails (~22-mm shell length) and consumed almost 60 (6.8 g wet-tissue mass) snails/d (Ruehl 2010). Smaller (10–14-cm SL) Mayan Cichlids could only eat snails with shell lengths <14 mm and consumed as many as 7 (0.6 g wet-tissue mass) snails/d. Therefore, the combination of P enrichment (which supports higher snail and crayfish abundance) and greater water permanence (which increases the probability of encountering molluscivorous fishes during the wet season) results in stronger bottom-up and top-down processes controlling snail populations at site 3.

The predator-permanence model predicts that aquatic communities change along a spatial gradient from temporary to permanent systems because life-history tradeoffs enable prey to cope with the dominant abiotic and biotic processes along the gradient (Wellborn et al. 1996, Skelly 1997, Wilbur 1997). We propose a conceptual model that substitutes the spatial gradient for a seasonal gradient in water permanence to account for structural changes in communities at a single location (Fig. 1). Across seasons, or drying–reflooding cycles, a wetland could resemble a temporary pond dominated by abiotic processes, a pond regulated by a combination of abiotic and primarily invertebrate predators, and ultimately a pond with large fish primarily regulated by biotic factors.

We found evidence supporting this temporal predator-permanence gradient at site 3 in the WCA. This site exhibited characteristics of a temporary pond with few crayfish toward the end of the dry season in April. In the middle of the dry season, site 3 resembled a permanent pond when crayfish reached their peak densities before large fish became numerous. The site was then similar to a permanent pond with large fish in the wet season based on the presence of molluscivorous fish in the marsh and a higher number of mortality events by crushing predators. Site 11 was dominated by emergent aquatic vegetation and resembled a relatively nutrient-rich, temporary pond dominated by abiotic factors because this site dried frequently and had low average depths (Fig. 3B). Invertebrate predators and, potentially, small fishes influence snail populations in the wet season (Loftus 2000; CBR personal observation that Eastern Mosquitofish [*Gambusia holbrooki* Girard, 1859] readily eat *Helisoma* eggs in aquaria), but large fish do not appear to, likely because of the ephemeral nature of this site. Further south in the TSL, sites CP and TS had characteristics of a permanent pond dominated by invertebrate predators during the dry season and a permanent pond with large fish during the wet season

because these sites rarely dried and the presence of large fish increased during the wet season. However, we did not see a relationship between crayfish and snail populations at sites CP and TS as we did at site 3 in the more northern part of the system. P enrichment may be partially responsible for this difference given the north–south P gradient in the Everglades (Gaiser et al. 2004, 2006, 2011) and because higher P levels lead to higher consumer biomass, structural changes in aquatic communities, stronger species interactions, and greater snail predation (Turner et al. 1999, Sargeant et al. 2010, Ruehl and Trexler 2013, 2015).

Use of the conceptual model developed here will facilitate identification of relevant abiotic and biotic processes that contribute to population dynamics and community structure in time-series data from similar marshes as well as other systems. For example, wetlands and temporary ponds that lie in floodplains are irregularly or seasonally flooded and, therefore, likely experience a range of predator-permanence conditions over time. Designing sampling protocols that capture the temporal variation in abiotic processes that modify biotic processes will aid in identifying the relative importance of each process to population dynamics and community structure. Likewise, experimental designs might benefit from using this conceptual model to choose treatments that will yield greater insights into the factors controlling populations and communities.

## ACKNOWLEDGEMENTS

Author contributions: CBR and JCT developed the conceptual model and designed the study. CBR analyzed the data, conducted the tethering trials, and wrote the 1st draft of the manuscript. JCT obtained funding for the work, provided the time series data and resources for lab and fieldwork, and assisted throughout the study. MRP developed figures on snail size and density among seasons. CBR, JCT, and MRP revised the manuscript for publication.

We thank all those who collected data for the time series. Casey Smith and Lisa Jiang measured snails. Financial support was provided by an Everglades Foundation fellowship to CBR. JCT received field data from Everglades National Park-Florida International University Cooperative Agreement H5000060104, Task numbers J5284060023 and J5297070024. This material is also based upon work supported by the National Science Foundation through the Florida Coastal Everglades Long Term Ecological Research (grant No. DBI-0620409).

## LITERATURE CITED

Abbey-Lee, R. N., E. E. Gaiser, and J. C. Trexler. 2013. Relative roles of dispersal dynamics and competition in determining the isotopic niche breadth of a wetland fish. Freshwater Biology 58:780–792.

Anderson, D. R. 2008. Model based inference in the life sciences: A primer on evidence. Springer, Berlin, Germany.

Batzer, D. P., C. R. Pusateri, and R. Vetter. 2000. Impacts of predation on marsh invertebrates: Direct and indirect effects. Wetlands 20:307–312.

Bergmann, G. T., and P. J. Motta. 2005. Diet and morphology through ontogeny of the nonindigenous Mayan cichlid *Cichlasoma* (*Nandopsis*) *urophthalmus* (Gunther 1862) in southern Florida. Environmental Biology of Fishes 72:205–211.

Browder, J. A., P. J. Gleason, and D. R. Swift. 1994. Periphyton in the Everglades: Spatial variation, environmental correlates, and ecological implications. Pages 379–418 *in* S. M. Davis and J. C. Ogden (editors). Everglades: The ecosystem and its restoration. St Lucie Press, Del Ray Beach, Florida.

Caceres, C. E., and D. A. Soluk. 2002. Blowing in the wind: A field test of overland dispersal and colonization by aquatic invertebrates. Oecologia 131:402–408.

Chick, J. H., S. Coyne, and J. C. Trexler. 1999. Effectiveness of airboat electrofishing for sampling fishes in shallow vegetated habitats. North American Journal of Fisheries Management 19:957–967.

Chick, J. H., P. Geddes, and J. C. Trexler. 2008. Periphyton mat structure mediates trophic interactions in a subtropical marsh. Wetlands 28:378–389.

Chick, J. H., C. R. Ruetz, and J. C. Trexler. 2004. Spatial scale and abundance patterns of large fish communities in freshwater marshes of the Florida Everglades. Wetlands 24:652–664.

Davis, S. M., and J. C. Ogden. 1994. Everglades: The ecosystem and its restoration. St Lucie Press, Delray Beach, Florida.

Dillon, R. T. 2000. The ecology of freshwater molluscs. Cambridge University Press, Cambridge, United Kingdom.

Dorn, N. J. 2008. Colonization and reproduction of large macroinvertebrates are enhanced by drought-related fish reductions. Hydrobiologia 605:209–218.

Dorn, N. J. 2013. Consumptive effects of crayfish limit snail populations. Freshwater Science 32:1298–1308.

Dorn, N. J., and M. I. Cook. 2015. Hydrological disturbance diminishes predator control in wetlands. Ecology 96:2984–2993.

Dorn, N. J., and J. C. Trexler. 2007. Crayfish assemblage shifts in a large drought-prone wetland: The roles of hydrology and competition. Freshwater Biology 52:2399–2411.

Dorn, N. J., J. C. Trexler, and E. E. Gaiser. 2006. Exploring the role of large predators in marsh food webs: Evidence for a behaviorally-mediated trophic cascade. Hydrobiologia 569:375–386.

Dorn, N. J., R. Urgelles, and J. C. Trexler. 2005. Evaluating active and passive sampling methods to quantify crayfish density in a freshwater wetland. Journal of the North American Benthological Society 24:346–356.

Dorn, N. J., and J. C. Volin. 2009. Resistance of crayfish (*Procambarus* spp.) populations to wetland drying depends on species and substrate. Journal of the North American Benthological Society 28:766–777.

Fretter, V., and J. Peake. 1979. Pulmonates. Academic Pres, San Diego, California.

Gaiser, E. E., P. V. McCormick, and S. E. Hagerthey. 2011. Landscape patterns of periphyton in the Florida Everglades. Critical Reviews in Environmental Science and Technology 41:92–120.

Gaiser, E. E., J. H. Richards, J. C. Trexler, R. D. Jones, and D. L. Childers. 2006. Periphyton responses to eutrophication in the Florida Everglades: Cross-system patterns of structural and compositional change. Limnology and Oceanography 51:617–630.

Gaiser, E. E., L. J. Scinto, J. H. Richards, K. Jayachandran, D. L. Childers, J. C. Trexler, and R. D. Jones. 2004. Phosphorus in periphyton mats provides the best metric for detecting low-level P enrichment in an oligotrophic wetland. Water Research 38:507–516.

Gaiser, E. E., J. C. Trexler, J. H. Richards, D. L. Childers, D. Lee, A. L. Edwards, L. J. Scinto, K. Jayachandran, G. B. Noe, and R. D. Jones. 2005. Cascading ecological effects of low-level phosphorus enrichment in the Florida Everglades. Journal of Environmental Quality 34:717–723.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111:1169–1194.

Grimm, N. B., and S. G. Fisher. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. Journal of the North American Benthological Society 8:293–307.

Heeg, J. 1977. Oxygen consumption and the use of metabolic reserves during starvation and aestivation in *Bulinus* (*Physopisis*) *africanus* (Pulmonata: Planorbidae). Malacologia 16:549–560.

Huckins, C. J. F. 1997. Functional linkages among morphology, feeding performance, diet, and competitive ability in molluscivorous sunfish. Ecology 78:2401–2414.

Jordan, F., S. Coyne, and J. C. Trexler. 1997. Sampling fishes in vegetated habitats: Effects of habitat structure on sampling characteristics of the 1-$m^2$ throw trap. Transactions of the American Fisheries Society 126:1012–1020.

Knorp, N. E., and N. J. Dorn. 2014. Dissimilar numerical responses of macroinvertebrates to disturbance from drying and predatory sunfish. Freshwater Biology 59:1378–1388.

Lima, S. L. 2002. Putting predators back into behavioral predator-prey interactions. Trends in Ecology & Evolution 17:70–75.

Liston, S. E., and J. C. Trexler. 2005. Spatiotemporal patterns in community structure of macroinvertebrates inhabiting calcareous periphyton mats. Journal of the North American Benthological Society 24:832–844.

Lodge, D. M., K. M. Brown, S. P. Klosiewski, R. A. Stein, A. P. Covich, B. K. Leathers, and C. Brönmark. 1987. Distribution of freshwater snails: Spatial scale and the relative importance of physicochemical and biotic factors. American Malacological Bulletin 5:73–84.

Lodge, D. M., M. W. Kershner, J. E. Aloi, and A. P. Covich. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. Ecology 75:1265–1281.

Loftus, W. F. 2000. Accumulation and fate of mercury in an Everglades aquatic food web. PhD Dissertation. Florida International University, Miami, Florida.

Noble, I. R., and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant-communities subject to recurrent disturbances. Vegetatio 43:5–21.

Obaza, A. O., and C. B. Ruehl. 2013. Regressions for estimating gastropod biomass with multiple shell metrics. Malacologia 56:343–349.

Parkos III, J. J., and J. C. Trexler. 2011. Disturbance regime and limits on benefits of refuge use for fishes in a fluctuating hydroscape. Oikos 120:1519–1530.

Parkos III, J. J., and J. C. Trexler. 2014. Origins of functional connectivity in a human-modified wetland landscape. Canadian Journal of Fisheries and Aquatic Sciences 71:1418–1429.

Richards, C. S. 1963. Apertural lamellae, epiphragms, and aestivation of planorbid mollusks. American Journal of Tropical Medicine and Hygiene 12:254–263.

Rogers, D. C. 2016. Class Gastropoda. Pages 190–209 in J. H. Thorp and D. C. Rogers (editors). Keys to Nearctic fauna: Thorp and Covich's freshwater invertebrates. Volume 2. Academic Press, San Diego, California.

Ruehl, C. B. 2010. The interactive effects of predators, resources, and disturbance on freshwater snail populations from the Everglades. PhD Dissertation. Florida International University, Miami, Florida.

Ruehl, C. B., and J. C. Trexler. 2011. Comparison of snail density, standing stock, and body size between Caribbean karst wetlands and other freshwater ecosystems. Hydrobiologia 665:1–13.

Ruehl, C. B., and J. C. Trexler. 2013. A suite of prey traits determine predator and nutrient enrichment effects in a tri-trophic food chain. Ecosphere 4:art75.

Ruehl, C. B., and J. C. Trexler. 2015. Reciprocal transplant reveals trade-off of resource quality and predation risk in the field. Oecologia 179:117–127.

Ruetz III, C. R., J. C. Trexler, F. Jordan, W. F. Loftus, and S. A. Perry. 2005. Population dynamics of wetland fishes: Spatiotemporal patterns shaped by hydrological disturbance? Journal of Animal Ecology 74:322–332.

Sargeant, B. L., E. E. Gaiser, and J. C. Trexler. 2010. Biotic and abiotic determinants of intermediate consumer trophic diversity in the Florida Everglades. Marine and Freshwater Research 61:11–22.

Sargeant, B. L., E. E. Gaiser, and J. C. Trexler. 2011. Indirect and direct controls of macroinvertebrates and small fish by abiotic factors and trophic interactions in the Florida Everglades. Freshwater Biology 56:2334–2346.

Schmitz, O. J., J. H. Grabowski, B. L. Peckarsky, E. L. Preisser, G. C. Trussell, and J. R. Vonesh. 2008. From individuals to ecosystem function: Toward an integration of evolutionary and ecosystem ecology. Ecology 89:2436–2445.

Sih, A., P. Crowley, M. McPeek, J. W. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities – A review of field experiments. Annual Review of Ecology and Systematics 16:269–311.

Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology & Evolution 13:350–355.

Skelly, D. K. 1997. Tadpole communities: Pond permanence and predation are powerful forces shaping the structure of tadpole communities. American Scientist 85:36–45.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353–391.

Tabachnick, B. G., and L. S. Fidell. 2007. Using multivariate statistics. 5th edition. Pearson Education, Boston, Massachusetts.

Thompson, F. G. 2004. Freshwater snails of Florida ID guide. Florida Museum, Division of Invertebrate Zoology. (Available from: https://www.floridamuseum.ufl.edu/iz/resources/florida-snails/, Accessed July 2022)

Tonn, W. M., P. W. Langlois, E. E. Prepas, A. J. Danylchuk, and S. M. Boss. 2004. Winterkill cascade: Indirect effects of a natural disturbance on littoral macroinvertebrates in boreal lakes. Journal of the North American Benthological Society 23:237–250.

Trexler, J. C., E. E. Gaiser, J. S. Kominoski, and J. L. Sanchez. 2015. The role of periphyton mats in consumer community structure and function in calcareous wetlands: Lessons from the Everglades. Pages 155–179 *in* J. A. Entry, A. D. Gottlieb,

K. Jayachandran, and A. Ogram (editors). Microbiology of the Everglades ecosystem. CRC Press, Boca Raton, Florida.

Trexler, J. C., and W. F. Loftus. 2016. Invertebrates of the Florida Everglades. Pages 321–356 *in* D. P. Batzer and D. Boix (editors). Invertebrates in freshwater wetlands: An international perspective on their ecology. Springer, Berlin, Germany.

Trexler, J. C., W. F. Loftus, and S. A. Perry. 2005. Disturbance frequency and community structure in a twenty-five year intervention study. Oecologia 145:140–152.

Turchin, P. 2003. Complex population dynamics: A theoretical/empirical synthesis. Monographs in population biology. Volume 35. Princeton University Press, Princeton, New Jersey.

Turner, A. M., J. C. Trexler, C. F. Jordan, S. J. Slack, P. Geddes, J. H. Chick, and W. F. Loftus. 1999. Targeting ecosystem features for conservation: Standing crops in the Florida Everglades. Conservation Biology 13:898–911.

Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27: 337–363.

Werner, E. E., D. K. Skelly, R. A. Relyea, and K. L. Yurewicz. 2007. Amphibian species richness across environmental gradients. Oikos 116:1697–1712.

Whiles, M. R., and B. S. Goldowitz. 2005. Macroinvertebrate communities in central Platte River wetlands: Patterns across a hydrologic gradient. Wetlands 25:462–472.

Wilbur, H. M. 1997. Experimental ecology of food webs: Complex systems in temporary ponds. Ecology 78:2279–2302.