



Invasive snails alter multiple ecosystem functions in subtropical wetlands

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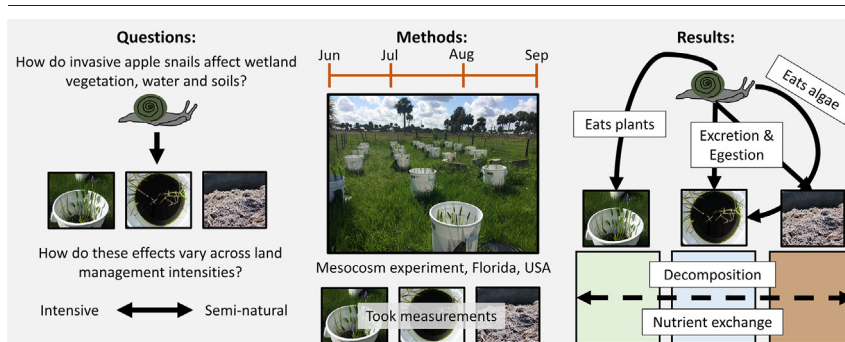
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HIGHLIGHTS

- Apple snail invasions exerted diverse direct and cascading ecological effects.
- Apple snails profoundly altered plant communities and nutrient cycling in the water.
- Snail changes to wetlands could hinder ecosystem service provision.
- Highly human-modified wetlands may be more affected by snail invasions.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Sergi Sabater

Keywords:

Biological invasion
Apple snail
Multifunctionality
Grasslands
Water quality
Plant community
Plant diversity
Ecosystem service

ABSTRACT

Invasive species that compromise ecosystem functioning through direct and indirect (or cascading) pathways are a rising global threat. Apple snails (*Pomacea* spp.) are semi-aquatic freshwater invaders that have exerted devastating ecological and economic impacts on agricultural wetlands and are emerging as a major threat to the structures and functions of natural wetlands. In this research, we conducted a field mesocosm experiment in subtropical wetlands in Florida, USA to investigate how *P. maculata* alter a suite of wetland vegetation, water, and soil processes and how these effects vary across wetlands under two different management intensities. Overall, we found that invasive snails substantially decreased aboveground biomass and vegetation cover and exhibited preferential feeding on wetland plant species. In addition, snails increased water nutrients (e.g., total carbon, nitrogen, phosphorous and dissolved solids), but showed minimal impacts on soil pools and processes. While most effects of invasive *P. maculata* were similar across wetland types, certain responses (e.g., algal biomass) were divergent. Our study provides holistic evidence on multiple direct and indirect consequences of invasive apple snails along the wetland plant-water-soil continuum. By altering plant assemblages and nutrient cycling (e.g., via consumption, egestion, and excretion), *P. maculata* invasion could hamper vital wetland services, which is concerning for these globally vulnerable ecosystems. Differential snail effects across management intensities further suggest the need for tailored actions to mitigate apple snail impacts and conserve wetland ecosystems.

1. Introduction

Biological invasions threaten many essential ecosystem functions and services either directly or indirectly along cascading pathways (Gandhi and Herms, 2010; Pejchar and Mooney, 2009; Vitousek, 1990). For

example, in the Laurentian Great Lakes, the invasive zooplankton, *Bythotrephes longimanus*, caused *Daphnia* populations (i.e., an efficient grazer on phytoplankton) to decrease, which subsequently decreased water clarity and ultimately negatively impacted lake water quality and recreational uses (Walsh et al., 2016). Therefore, to better understand invasion impacts, holistic approaches which examine multiple direct and cascading processes simultaneously are needed (Flood et al., 2020; Gandhi and Herms, 2010; Nuñez et al., 2010; Sin et al., 2008; Strayer, 2012). Such

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understanding is particularly relevant for freshwater systems that are disproportionately important yet vulnerable to invasions (Dudgeon et al., 2006). Specifically, wetlands provide 40 % of the world's ecosystem services but are heavily impacted by invasions due to their decreased resilience to disturbance from global human modification (Zedler and Kercher, 2005) and their status as landscapes sinks (Zedler and Kercher, 2004). Holistic approaches are also relevant to wetland studies as many of their processes are interconnected via subsystems in the water column, at the soil-water interface, and in the sediments (Ehrenfeld, 2010).

Apple snails, a family of South American semi-aquatic snails, are global invaders with the potential to significantly alter wetland ecosystems (Carlsson et al., 2004). Imported to Southeast Asia for cultivation in 1979–1980, *Pomacea* spp. escaped into agricultural wetlands (e.g., rice paddies) where the fecund species consumed and substantially reduced agricultural yields (Halwart, 1994; Horgan et al., 2014; Naylor, 1996). Previous research has predominantly concentrated on control strategies, plant preference trials, and population dynamics of invasive apple snails (Horgan et al., 2014). Yet their effects on an array of wetland structures and functions remain understudied and sometimes can be contradictory, with even fewer studies that explore cascading effects on multiple interlinked processes. For example, Carlsson et al. (2004) found the direct effects of *P. canaliculata* on macrophytes and water nutrients to increase light penetration and phytoplankton growth and ultimately lead to an ecosystem-state transition from clear-water macrophyte-dominated aquatic habitats to turbid, phytoplankton-dominated habitats (de Tezanos Pinto et al., 2007). However, Fang et al. (2010) found that *P. canaliculata* decreased macrophyte biomass, but showed no effects on water N or P levels nor on phytoplankton biomass in a similarly designed experiment. Thus, more holistic research is needed to understand direct and cascading effects that invasive apple snails may cause to wetland ecosystems and how these effects could vary across study contexts (e.g., focal invader species, land management, geographic locations).

Apple snail introductions to wetlands in the Southeast United States highlight further need to address these questions. *Pomacea maculata* (previously known as *P. insularum*), a widespread invader, is the most fecund and potentially destructive apple snail species given its body size, reproductive capacity, and plasticity in life history traits (Barnes et al., 2008). For years, *P. maculata* was misidentified as *P. canaliculata* and thus research is needed to distinguish *P. maculata*'s unique ecological effects on wetlands (Howells et al., 2006). For example, in laboratory feeding trials, *P. maculata* and *P. canaliculata* had similar plant preferences and total biomass consumption, but *P. maculata* had much higher growth and conversion efficiencies with lower mortality, and thus presumably greater destructive ecological effects (Morrison and Hay, 2011). In addition, *P. maculata* has also invaded natural wetlands in the Southeast United States, which may respond differently than the commonly studied rice-growing wetlands in Southeast Asia. For example, natural habitats are often more biodiverse and may have stronger resilience to invasion (the biotic resistance hypothesis; Beaury et al., 2020) and are less enriched with nutrients when compared to agriculturally managed wetlands, another factor that may increase susceptibility to invasion (Davis et al., 2000). Furthermore, wetland responses to invasion may also differ depending on the intensity of the surrounding agricultural land use. Agricultural intensification can simplify landscapes, disrupt succession, lower plant defenses, and decrease nutrient cycling efficiency, all of which increase vulnerability to pest invasion (Altieri and Nicholls, 2004). Previous studies have shown that land-use intensification exerts strong influences on wetland communities, ecosystem structures and functioning (Boughton et al., 2016, 2011; Guo et al., 2021; Jansen et al., 2019), however, few studies have investigated how invasive snail effects would differ across wetlands of varying management intensities.

In this research, we conducted a mesocosm experiment to investigate ecological consequences of *P. maculata* invasion in subtropical wetlands in Florida, USA (Swain et al., 2013). We chose Florida because (1) it is at the forefront of the *P. maculata* invasion in the U.S., (2) wetlands are highly abundant in Florida (i.e., comprising >31 % of the land use), fundamental to the integrity of many ecosystems (e.g., Everglades) and livelihoods of

residents, and largely affected by *P. maculata* (Pierre et al., 2017; Smith et al., 2015; Volk et al., 2017); and (3) wetlands are embedded in a variety of different land uses and management intensities, providing an opportunity to assess agricultural intensification impacts of invasion on wetlands (Boughton et al., 2011). Specifically, we asked two main questions: (1) How do invasive *P. maculata* affect wetland vegetation, soil and water processes and functions? (2) How do invasive *P. maculata* effects vary across different land management practices? We hypothesized that snails would (i) reduce wetland plant biomass and cover; (ii) alter plant communities through preferential feeding; (iii) increase decomposition processes and nutrient cycling in the water and soil; (iv) trigger algal growth and potentially a transition from a clear-water system to a phytoplankton-dominated system; and (v) exert stronger impacts in intensively managed wetlands than semi-natural wetland habitats.

2. Materials and methods

2.1. Study site

Archbold Biological Station's Buck Island Ranch (27°09'N 81°11'W) is a working beef cattle operation and research laboratory in south-central Florida with over 600 wetlands interspersed within 4170 ha of grasslands. These wetlands range from 0.007 to 41.9 ha in size, contain water 2–10 months of the year, and are interspersed within and influenced by the two surrounding pasture management practices (Boughton et al., 2016). These wetland type differences stem from both historical and contemporary practices. For example, the intensively managed (IM) pastures were annually fertilized with N (likely 56 kg ha⁻¹ as NH₄SO₄ or NH₄NO₃), P (likely 34–90 kg ha⁻¹ of P₂O₅) and potassium (likely 34–90 kg ha⁻¹ of K₂O) from around 1970 to 1987 and currently receive ~56 kg ha⁻¹ of N (either NH₄SO₄ or NH₄NO₃) every two years (Boughton et al., 2016; Ho et al., 2018). Intensively managed pastures are also limed regularly, heavily ditched, have high cattle stocking densities, are grazed during the summer wet season, and are planted with non-native pasture grasses (*Paspalum notatum*). On the other hand, the semi-natural (SN) pastures were never fertilized, have less ditches, are grazed during the winter, and were seeded to some extent with *P. notatum* but are also still dominated by native grasses such as *Andropogon glomeratus* var. *glaucoptis*., *Axonopus* spp., and *Coleataenia longifolia* (Boughton et al., 2016, 2010). Intensively managed wetlands have a greater percent cover of exotic species and are dominated by *Juncus effusus* var. *solutus*, *Persicaria punctata*, and *Pontedaria cordata* while the SN wetland plant community is characterized by grasses (*Coleataenia* spp.), sedges (*Rhynchospora* spp.), and emergent vegetation (e.g., *P. cordata* and *Sagittaria lancifolia*; Boughton et al., 2010; Guo et al., 2021). This habitat dichotomy extends to the regional landscapes, as other cattle ranches and citrus plantations are juxtaposed against the increasingly diminished native Florida scrub habitat. The climate of this region is characterized by a warm dry season from November – May, and a hot, wet season from June – October, with annual average rainfall of 132 cm, 75 % of which typically falls in the wet season. Average minimum and maximum daily temperatures are 16.7 °C and 28.2 °C, respectively. Buck Island Ranch is an established invasion spot for *P. maculata* (Pierre et al., 2017; Swain et al., 2013); however, current severity of the invasion and the snail's ecological impacts have yet to be quantified.

2.2. Experimental design and setup

To examine effects of invasive apple snail, we used a before-after control-impact (BACI) mesocosm experimental design with 2 × 2 factorials crossing two snail treatments (presence and absence of snails) and two wetland types (IM and SN) with 8 replicates per treatment (2 snail treatments × 2 wetland types × 8 replicates = 32 total mesocosms). Mesocosms were created using in situ wetland soils and white trashcans (Uline, 32-gal, height: 68.58 cm, diameter: 55.88 cm, surface area: 0.24 m²) to avoid absorption of excess heat during the experiment and were housed on Buck Island Ranch. Because IM and SN wetlands have varied

characteristics, we collected in situ wetland soils from 8 randomly chosen wetlands (i.e., four from IM and four from SN). In each wetland, we collected soil from four quadrats to account for spatial variation and ensure that collected soils were representative of that wetland. Then, we individually mixed soils from each of the 8 wetlands, removed rocks and snails by sieving (6 mm), and loosely packed the soils into mesocosms to a 20 cm depth (Appendix A: Fig. 1).

In addition, we collected plants from a SN and an IM wetland and transplanted them into the mesocosms. Plant species in our simulated wetland mesocosm were chosen based on their relative abundance within each wetland type, hardiness, and palatability for snails (i.e., plants with more foliage preferred; Boughton et al., 2016, 2013). We placed 12 individual plants in each mesocosm, with a different number for each species depending on the wetland type (i.e., representative of the field densities; Appendix A: Table 1). After planting, we watered mesocosms and covered with a mesh layer (6 mm) for one week to avoid herbivory and allow for plants to establish. Mesocosms were arranged randomly in a grid (4 × 8 mesocosms) in a fenced area to account for microclimate conditions and prevent disturbances. We maintained the mesocosms for more than two months prior to experimental treatment to allow plants to establish and mesocosms to equilibrate. During this period, mesocosms were uncovered, thus receiving natural rainwater; we also watered regularly if needed, replaced dead plants, and removed unexpected plants that sprouted from the seedbank.

After plants fully established, one week prior to the start of the experimental treatment, we filled mesocosms with groundwater to a height of 25 cm above the soil. We used groundwater, since it is the main water source that feeds into these wetlands in the field. To simulate actual wetland water microbial communities, in situ water was collected from the 8 wetlands, and 100 mL was mixed in each mesocosm's water column where we matched the sources of water with wetland soils collected for constructing the mesocosms. Two drainage holes (30 cm above the soil) were drilled on either side of the mesocosm to simulate lateral water movement and prevent overflow.

We collected 140 apple snails (*P. maculata*) from one location (an invaded ditch) at Buck Island Ranch. We selected immature or "juvenile" snails (operculum: 19.5–25.4 mm; Youens and Burks, 2008; Baker et al., 2010) because they are actively growing, have more consistent consumption patterns (Burlakova et al., 2009), and represent our field conditions since this size class was the most abundant from field observations. We introduced 8 snails per mesocosm, (i.e., ~33 individuals/m²) in the snail treatment (total 128), reflecting an upper limit observed in the field (e.g., in Texas freshwater ponds; Howells et al., 2006). Six snails were stored in 90 % ethanol and shipped to Florida Department of Agriculture and Consumer Services for species identification, where they were confirmed as *P. maculata* (by Dr. Mary Cong). Collected snails were monitored in the lab for a week before deployment into mesocosms in case of die-off after capture stress. They were individually labeled (1–128) using white nail polish covered by a layer of cyanoacrylate. We measured all snail dimensions (height, length, and width) 24 h before deployment using digital calipers (\pm 0.01 mm; Youens and Burks, 2008), and wet weight was recorded after blotting the snails with a paper towel and weighing with an electronic scale. We then sorted snails by wet weight (largest to smallest) and evenly divided them among mesocosms to ensure that each received the equivalent level of snails (e.g., similar total biomass, same number of snails with sized structure). We placed a wire mesh cover (6 mm) on top of mesocosms to prevent predation and snail escape and incubated the mesocosms for 14 weeks (from June 22 – September 27, 2018).

2.3. Sample collection and analyses

Throughout the experiment, water, soil, plant and snail measurements were taken from each mesocosm with different frequencies. For soils and snails, we only conducted initial and end measurements due to destructive sampling techniques, whereas for others that were non-intrusive, we conducted sampling and measurements every two weeks. Plant biomass was measured once at the end of experiment after destructive harvesting.

Specifically, water-related measurements were taken every two weeks over the course of the 14-week experiment after introduction of snails (i.e., 8 sampling efforts total). We used an YSI ProDss multi-parameter handheld unit to take in situ water pH, temperature, oxidation reduction potential, chlorophyll *a* (chl_a, a proxy for algal biomass), conductivity, total dissolved solids (TDS), and dissolved oxygen (DO). We calibrated the YSI probe on each sampling date and conducted measurements at similar times during each sampling (i.e., ~10 AM) to avoid confounding effects due to sampling time. Additionally, at each sampling, three 50 mL water samples were collected from different locations in a mesocosm (at 5–10 cm below the water surface), mixed into one 150 mL sample, and stored in a cooler (4 °C) during transportation to the lab. We then filtered water samples (P5 Qualitative Fisherbrand filters) and froze them (–20 °C) until analysis of total water C, inorganic C, organic C and N (Shimadzu TOC-TN analyzer). We acid-digested filtered water samples (11 N sulfuric acid and ammonium persulfate 40 % solution) to determine total water P (USEPA, 1993). For each 20 mL thawed water sample, 0.2 mL of sulfuric acid and 0.2 mL of ammonium persulfate were added, then placed in an autoclave for 30 min at 121 °C and 15–20 psi for 3 h and analyzed for phosphate (SEAL analytical segmented-flow autoanalyzer, WI, USA).

For initial and final soil measurements, we collected and homogenized three subsamples from different locations in the top soil layer (0–5 cm depth) of each mesocosm and transported them on ice packs before storing in the lab at 4 °C. We then sieved soils (2 mm) and oven-dried a subsample of soil at 105 °C to calculate gravimetric soil moisture (Robertson et al., 1999). We also ground soils (sieved 2 mm, dried 105 °C) and measured total C and N using a LECO CN628 C/N Determinator (LECO Corporation, MI, USA) and determined soil organic matter (SOM) content using a loss-of-ignition method involving a 4-h high-temperature oxidation in 450 °C muffle furnace (Nelson and Sommers, 2018). We extracted plant-available nutrients (P, calcium, magnesium, potassium, and sulfur) from ground soils (sieved 2 mm, dried 105 °C) using the Mehlich-3 solution (Mehlich, 1984) and measured using inductively coupled plasma spectrometry (ICP) on a Perkin Elmer Avio 200 (Perkin-Elmer, CT, USA).

To determine N mineralization rates, we used an anoxic lab incubation method, modified from White and Reddy (2000). We first measured pre-lab incubation soil inorganic N (ammonium and nitrate) concentrations by weighing 10 ± 0.3 g of soil (field-moist, 2 mm sieved) into 50 mL centrifuge tubes with 40 mL of 2 M KCl. Tubes were shaken (170 rpm) for two hours, filtered (P5 Qualitative Fisherbrand filters) and frozen (–20 °C) until nitrate and ammonium analysis on a SEAL analytical segmented-flow autoanalyzer (WI, USA). Then, we weighed 10 ± 0.3 g of soil (field-moist, 2 mm sieved) into 60 mL glass jars along with 10 mL of deionized water. The jars were purged of oxygen by injecting a continuous flow of N₂ gas for 10 min and then jars were hermetically sealed and placed in a 40 °C incubator for 180 h (~7.5 days). Upon removal from the incubator, we extracted nitrate and ammonium again using the same KCl extraction as described above. We calculated net N mineralization rate by subtracting the initial total inorganic N (nitrate + ammonium) from the final measurement and dividing by total incubation days (7.5). Nitrogen mineralization rates were calculated on a dry soil mass basis using gravimetric soil moisture content.

Plant cover was assessed biweekly using digital photos (Canon PowerShot SX620 HS) taken horizontally above the mesocosm. We then used ImageJ to mask the grass field background in the photos and Easy Leaf Area (Easlon and Bloom, 2014) to analyze green pixel count (plants and leaves) within the mesocosm area. This method may have underestimated plant cover as some of the plants were not green enough to register and some plants grew outside the mesocosm area. However, the method was systematic across all mesocosms and therefore should not influence treatment results.

At the end of experiment, we harvested all plants, which were sorted by species and oven-dried (60 °C) for one week to determine total above-ground plant biomass. Plant species which were not originally included in the experimental design but sprouted over the course of the incubation were grouped together as an "other" category in the analysis. We also

conducted final measurements for snail height, length, width, and wet weight (Youens and Burks, 2008), then euthanized and oven-dried (60 °C) them for 5 days to determine dry weight.

2.4. Statistical analyses

For response variables with discrete initial and final measurements, we used linear mixed-effects models to account for variation due to random effects. Snail treatment (snail absence or presence), wetland type (IM or SN), and initial measurements were treated as fixed effects with wetland ID (8 wetlands) as the random effect. All continuous covariates in models were standardized prior to analysis so effect sizes could be compared. We included an interaction term between wetland type and snail treatment in initial model specification but omitted the interaction if non-significant ($P >$

0.05). We performed separate models for aboveground plant biomass for each wetland type due to complications of different plant species within each wetland type and singular fits with mixed effects models. To assess snail performance, we used the change (final – initial) in snail size measurement (height, length, width, and weight) as the response variable, wetland type as our predictor variable, and wetland ID as a random effect.

To analyze time-series measurements (i.e., probe readings, water chemistry, and plant cover), we used linear mixed-effects models with a random effect of mesocosm ID (out of 32) to account for repeated measurements. All interactions (snail treatment × wetland type × timepoint) were included if found to be significant ($P < 0.05$). Chlorophyll a measurements were highly variable with extreme values (up to 600 $\mu\text{g L}^{-1}$) that complicated the model fit. Because these extreme chl a values were within the range that naturally occurred Buck Island Ranch wetlands (unpublished data, EH

Table 1

Results from linear mixed-effects models. Due to different specification of models (i.e., inclusion of different fixed-effects, interactions, covariates, and timepoint measurements), the response variables have been grouped in similar model categories, rather than the order they appear in the Results section. Interactions were dropped from models if $P > 0.05$ and are labeled as such in the table. Bolded coefficients are statistically significant ($P < 0.05$) with asterisks indicating different levels of significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). The intercept is indicated for each model, with abbreviations referring to the factors of each treatment (IM = intensively managed wetland type treatment; NS = no snail treatment; TF = final timepoint measurement; T1 = initial or first out of 8 timepoint measurements). Response variables on the log or logit-scale are indicated.

Response variable	Intercept (IM - NS - T1)	Snail	Wetland type	Timepoint	Snail × Wetland type	Wetland type × Timepoint	Snail × Timepoint	Snail × Wetland type × Timepoint
Water responses								
Total N (mg L^{-1})	3.81	2.07**	1.33	0.39*	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$
Total C (mg L^{-1})	23.93	0.71	0.35	0.19	$P > 0.05$	$P > 0.05$	1.28***	$P > 0.05$
Organic C (mg L^{-1})	22.91	-0.52	0.99	-0.52**	$P > 0.05$	$P > 0.05$	1.63***	$P > 0.05$
Inorganic C (mg L^{-1})	1.03	1.21	-0.65	0.71***	$P > 0.05$	$P > 0.05$	-0.34*	$P > 0.05$
DO (mg L^{-1}) ⁺	5.1	-1.51**	0.31	0.07	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$
TDS (mg L^{-1})	37.85	1.59	8.51	10.81***	$P > 0.05$	$P > 0.05$	5.34*	$P > 0.05$
chl a ($\mu\text{g L}^{-1}$) ⁺⁺	75.5	-14.66	-41.48	115.39***	22.08	-116.96**	-80.23*	141.36*
Plant responses								
Plant cover (logit-scale)	-1.92	-0.02	-0.72***	0.17***	0.46*	-0.03	-0.21***	-0.003
Response variable	Intercept (IM - NS - TF)	Initial covariate	Snail	Wetland type	Snail × Wetland type			
Soil responses								
Total C (g mg^{-1})		52.52	0.56	-11.49	$P > 0.05$	-	-	-
Total N (g mg^{-1})		3.73	0.7**	-0.03	-0.45	$P > 0.05$	-	-
C:N ratio		14.33	0.56	0.39	-1.3	$P > 0.05$	-	-
N mineralization (log-scale, $\text{mg kg}^{-1}\text{d}^{-1}$)		1.45	-0.05	0.05	-0.32	$P > 0.05$	-	-
Organic matter (logit-scale, %)		-2.23	0.03	-0.14*	-0.3	0.16*	-	-
Ca (mg kg^{-1})		714.34	22.92	-31.27	-265.82*	$P > 0.05$	-	-
P (mg kg^{-1})		19.74	2.33	-0.25	8.93	$P > 0.05$	-	-
Mg (log-scale, mg kg^{-1})		4.63	-0.02	0.08	-0.51*	$P > 0.05$	-	-
S (mg kg^{-1})		15.55	0.32	-0.03	1.88	$P > 0.05$	-	-
K (mg kg^{-1})		25.76	5.54*	8.68*	2.84	$P > 0.05$	-	-
Water responses								
Total P (mg L^{-1} , log-scale)		-3.4	0.04	2.43***	-0.24	-1.34**	-	-
Response variable	Intercept (IM - NS - TF)	Snail	Wetland type	Snail × Wetland type				
Plant responses								
Total biomass (g)	109.03	-65.5***	-53.73***	31.14***	-	-	-	-
<i>P. hemitomon</i> (g)	16.44	1.71	-15.25***	$P > 0.05$	-	-	-	-
<i>P. cordata</i> (g)	81.08	-57.76***	-58.31***	36.5***	-	-	-	-
Other (g)	7.92	-8.01***	0.19	$P > 0.05$	-	-	-	-
<i>A. muehlenbergianum</i> (g)	0.94	-0.41	-	-	-	-	-	-
<i>B. carolianna</i> (g)	7.36	-7.36**	-	-	-	-	-	-
<i>J. angusta</i> (g)	1.29	-1.29***	-	-	-	-	-	-
<i>S. lancifolia</i> (g)	13.1	3.16	-	-	-	-	-	-
<i>A. philoxeroides</i> (g)	3.94	-2.42**	-	-	-	-	-	-
Response variable	Intercept (IM)	Wetland type						
Snail responses								
Height change (mm)	3.09	-1.33**	-	-	-	-	-	-
Length change (mm)	3.94	-1.75	-	-	-	-	-	-
Width change (mm)	3.09	-1.41*	-	-	-	-	-	-
Weight change (g)	2.26	-0.81	-	-	-	-	-	-

⁺ The model for DO contained a temperature covariate that is not included in this table.

⁺⁺ The model for chl a included two timepoint measurements (T1 and T2) where the the four initial measurements were categorized as T1 and the four final measurements were categorized as T2. Thus, for the chl a model, the timepoint variable has only two factors (T1 and T2) and T1 is the intercept.

Boughton), we did not remove these potential outliers. Instead, we divided the 8 timepoints into two distinct time periods (i.e., the first four weeks, i.e., “TP1”, or the last four weeks, i.e., “TP2”) and performed a linear mixed-effects model with wetland type, snail presence, and time period (TP1 vs. TP2) as predictors and mesocosm ID as the random effect. Also, for water N, prior to model fitting, we substituted zeros with $\frac{1}{2}$ of the detection limit following Dent and Grimm (1999). In the model fitting, we used a beta distribution (data bound by 0, 1) for soil organic matter and plant cover data.

We checked assumptions of normality visually and log-transformed response variables when necessary. All statistical analyses were performed in R (R Core Team, 2021) using packages tidyverse (Wickham et al., 2019) to manipulate data and create figures, lme4 (Bates et al., 2015) to run linear mixed-effects models, lmerTest (Kuznetsova et al., 2017) to generate P values for linear mixed-effects models, glmmTMB (Brooks et al., 2017) to run linear mixed-effects models with a beta distribution and gridExtra (Aguie, 2017) to create figures. All figures depict raw means and standard deviations calculated from the treatments (crossing snail and wetland type) averages at indicated timepoints (e.g., initial, final, or across 8 collection timepoints for certain variables). Within the results, we described differences in treatment effects using percent change for better comparisons and described level of significance from statistical analyses using a “language of evidence” as per Muff et al. (2022). Statistical model results are summarized in Table 1.

3. Results

3.1. Snail performance

Invasive apple snail size increased over time, and there was moderate evidence that snail performance was greater in IM than SN mesocosms (Fig. 1). On average, IM wetland snail height, length and width increased by 3.09, 3.94, and 3.09 mm, respectively, over the incubation period (Fig. 1). In contrast, increases in snail size in SN wetland mesocosms were 1.33, 1.75, and 1.41 mm lower in height ($P < 0.01$), length ($P = 0.06$) and width ($P < 0.05$), respectively, than those in IM. There was little evidence that wetland type affected snail weight change (0.85 g difference, $P = 0.16$). Out of 128 snails deployed, 15 died by the end of the experiment (~12 % mortality rate), which occurred mostly in the IM treatments (i.e., 11 out of 15 mortalities).

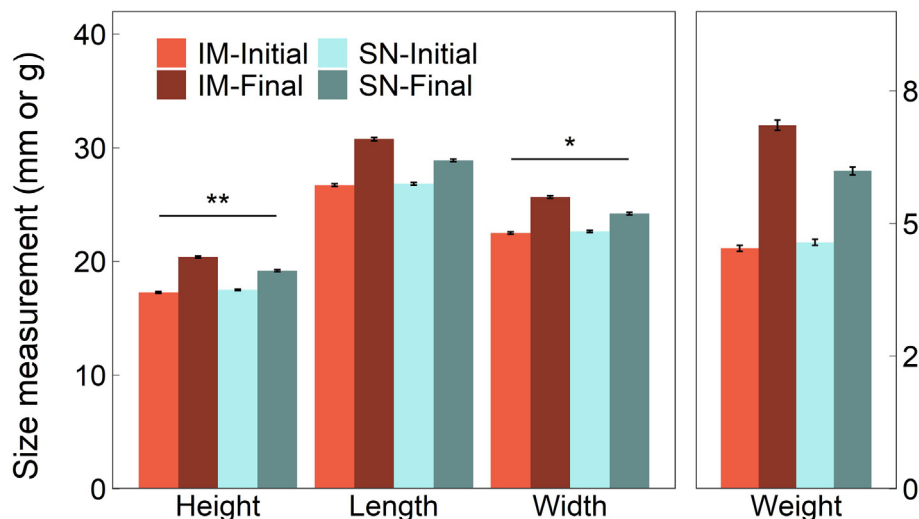


Fig. 1. Over the course of the 14-week experiment, apple snails' size measurements (height, length, width and weight; unit: mm for height, length and width, and g for weight) increased. Bars show treatment means (\pm SE) with colors differentiating intensively managed (IM) and semi-natural (SN) wetland types and timepoints (initial and final). The changes over time in snail height and width were significantly ($P < 0.05$) greater in IM wetlands compared to SN wetlands, as indicated by the lines and level of significance above the bars (* $P < 0.05$, ** $P < 0.01$).

3.2. Snail effects on plant cover, biomass and species composition

Snail presence showed very strong evidence for a substantial negative effect on plant cover in mesocosms over time ($P_{\text{snail} \times \text{timepoint}} < 0.001$), emerging at the second time measurement (Fig. 2b). However, there was no evidence that snails exerted different effects on plant cover across wetland types over time ($P_{\text{snail} \times \text{wetlandtype} \times \text{timepoint}} > 0.05$, Fig. 2b). Despite this, after 14 weeks, plant cover in IM no snail treatments was on average 3.2 times greater than that in snail treatments while plant cover in SN no snail treatments was 2.6 times greater than snail treatments (both $P < 0.05$, Fig. 2b). Additionally, after 14 weeks, there was very strong evidence that snail presence greatly decreased aboveground biomass compared to no snail treatments, although it was to a similar extent between the two wetland types (Fig. 2a). For example, when compared to mesocosms without snails, aboveground biomass was 62 % lower in SN mesocosms with snails ($P_{\text{snail} \times \text{wetlandtype}} < 0.001$) and 60 % lower in IM mesocosms with snails ($P < 0.001$, Fig. 2a).

Snails also showed preferential effects on individual plant species (Fig. 2c) which further caused alterations in plant composition (Fig. 2d). For example, there was strong evidence that snails decreased *A. philoxeroides* from the IM mesocosms by 61 % ($P < 0.01$, Fig. 2c). In SN mesocosms, snails completely eradicated *B. caroliniana* ($P < 0.01$) and *J. angusta* ($P < 0.001$, Fig. 2c) while there was only weak evidence that *S. lancifolia* increased by 24 % in snail treatments ($P = 0.07$, Fig. 2c). There was no evidence that *P. hemitomon*, which was present in both wetland types, was affected by snail treatment ($P > 0.05$, Fig. 2c). *P. cordata*, a species found in both wetland types, showed the most drastic declines due to snails with very strong evidence, decreasing by 71 % ($P < 0.001$, Fig. 2c) in IM mesocosms and 93 % in the SN mesocosms ($P_{\text{snail} \times \text{wetlandtype}} < 0.001$, Fig. 2c). However, the effect size overall appears larger for IM wetlands (Fig. 2c), likely because there was more plant biomass in these mesocosms due to the species and number of individuals originally planted (Appendix A: Table 1).

3.3. Snail effects on soil nutrient pools and processes

After 14 weeks of incubation, N mineralization rates increased across all treatments (Fig. 3a). While snails appeared to increase N mineralization rates compared to no snail treatments in SN wetlands by 12 %, there was no evidence for the statistical significance of this relationship

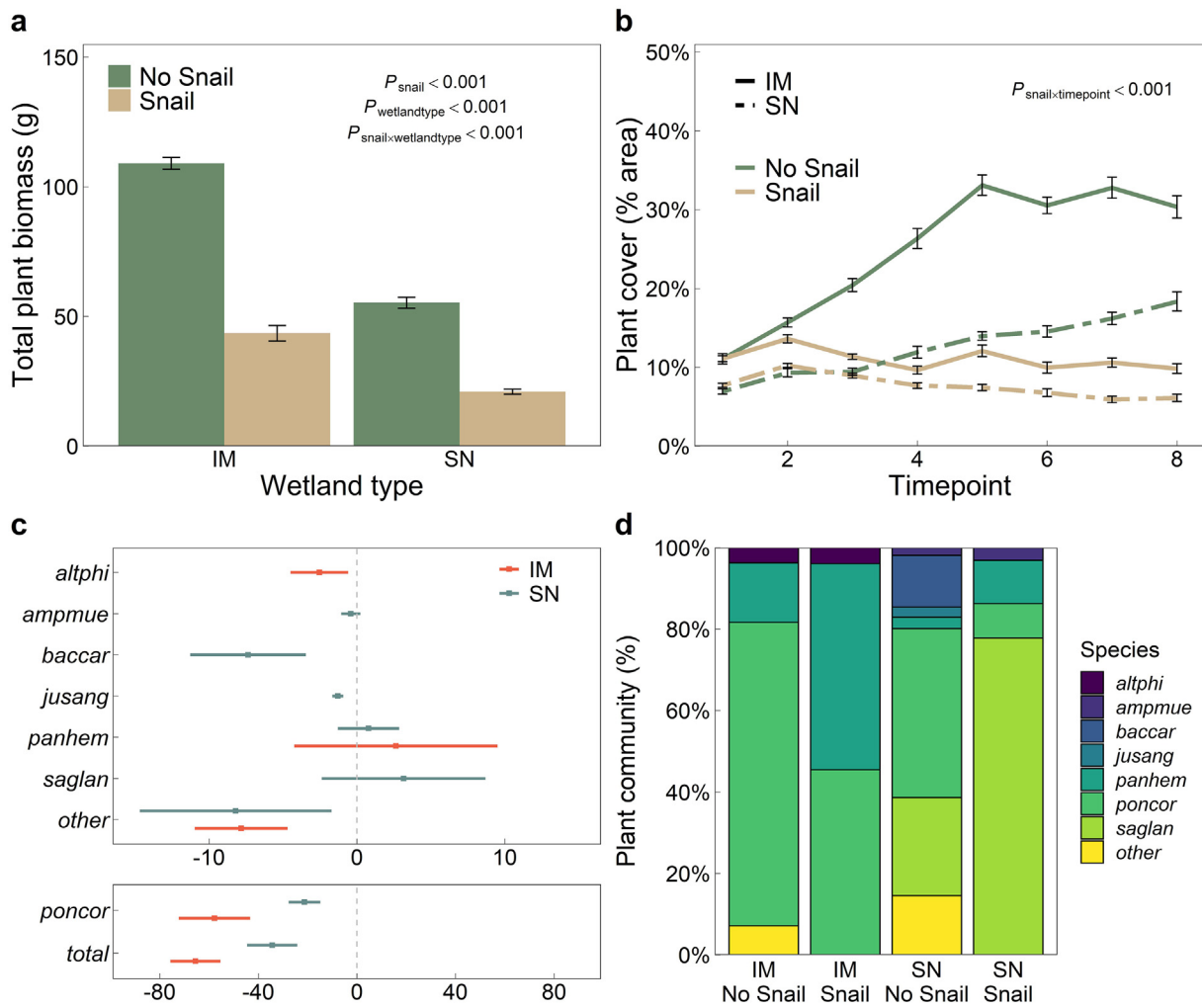


Fig. 2. Depicts changes by snail and wetland type to mesocosm plant communities. Means (\pm SE) of (a) final total aboveground plant biomass across wetland types (x-axis) and (b) percent mesocosm area covered by plants (plant cover) over the 8 timepoints of the 14-week experiment. Varied colors show snail vs. no snail treatments (for both a and b) and line types (b) show intensively managed (IM) and semi-natural (SN) wetland types. Significant results from models are displayed in text, however for plant cover, only significant interactions with timepoint are shown (see Table 1 for full model results). Panel c and d show snail effects on individual plant species in IM and SN wetlands. Plant species names have been abbreviated for figure clarity (see Appendix A: Table 1). For panel c, effect sizes of snail treatment (i.e., difference from its corresponding wetland type no snail treatment) on aboveground biomass for each plant species are depicted. Horizontal lines are 95 % confidence intervals. Total plant biomass (labeled total) is the average summation of plant biomass from all plant species within each mesocosm. Due to the high negative effect size of snail treatment on *poncor* (i.e., *P. cordata*) and total plant biomass, this data was plotted on a separate scale. In panel d, stacked bar charts show plant community composition changes across snail and wetland type treatments (x-axis) with varied colors for different plant species. Percent values are calculated as final dry weight (g) of a species / final total plant biomass dry weight (g) \times 100.

($P_{\text{snail} \times \text{wetlandtype}} = 0.15$, Fig. 3a). We also found that IM wetlands had an average N mineralization daily rate of $4.28 \text{ mg kg}^{-1} \text{ d}^{-1}$ and there was weak evidence that this was greater than SN treatments by 28 % ($P = 0.06$, Fig. 3a). Our results also showed that snail presence decreased SOM by 11.8 % ($P < 0.05$) in IM wetlands and slightly increased SOM by 2.7 % ($P_{\text{snail} \times \text{wetlandtype}} < 0.05$) in SN wetlands compared to no snail treatments (Fig. 3b). There was no evidence that soil C, N, C:N ratios, P or sulfur were affected by wetland type or snail treatments. There was moderate evidence that potassium (K) increased in snail treatments (34 % increase, $P = 0.05$), but there was no evidence that snail effects on K concentration differed across wetland types ($P_{\text{snail} \times \text{wetlandtype}} > 0.05$, Fig. 3c).

3.4. Snail effects on water nutrient and physicochemical responses

In the first time period (1–8 weeks or TP1) of the experiment, there was no evidence that snail and wetland type affected chl_a concentrations (all $P > 0.05$, Fig. 4a). However, there was moderate evidence that snail effects

emerged during the second time period (i.e., weeks 9–14 or TP2, $P_{\text{snail} \times \text{timepoint}} = 0.05$, Fig. 4a) and diverged substantially across wetland type ($P_{\text{wetlandtype} \times \text{timepoint}} < 0.01$, $P_{\text{wetlandtype} \times \text{snail} \times \text{timepoint}} < 0.05$, Fig. 4a). For example, by TP2, chl_a concentrations in IM snail treatments were 50 % lower than IM no snail treatments, whereas chl_a in SN snail treatments were 211 % higher than SN no snail treatments (Fig. 4a). Snail presence also appeared to decrease DO levels (Fig. 4b), however there was no evidence for snail differences across wetland type or changes over time (all $P > 0.05$). There was very strong evidence that TDS in the water column increased with time for all treatments ($P < 0.001$), with moderate evidence of higher increases in snail treatments ($P_{\text{snail} \times \text{timepoint}} < 0.05$, Fig. 4c). By the final timepoint, there was very strong evidence that TDS in snail treatments was on average 37 % higher than no snail treatments ($P < 0.001$), regardless of wetland type ($P > 0.05$, Fig. 4c).

Total water P increased in the snail treatments ($P < 0.001$), with substantially higher increases observed in IM (~1034 %) vs. SN (198 %) wetland mesocosms ($P_{\text{snail} \times \text{wetlandtype}} < 0.01$, Fig. 4d). By week 14, there was

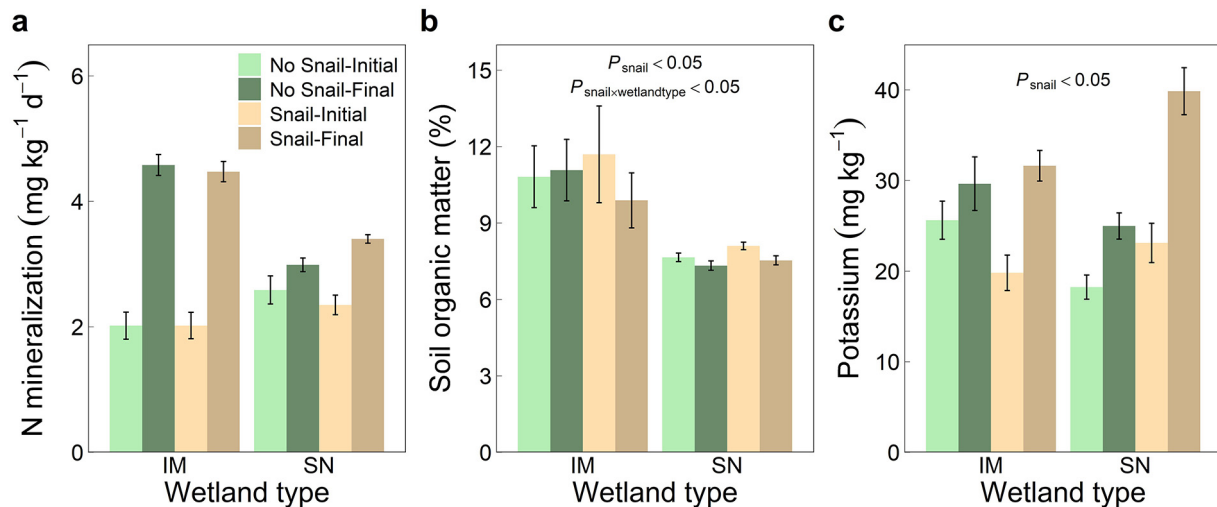


Fig. 3. Snail effects on mesocosm soils for intensively managed (IM) and semi-natural (SN) wetland types (x-axis). Bar plots show treatment means (\pm SE) of (a) N mineralization daily rates ($\text{mg kg}^{-1} \text{d}^{-1}$) calculated from our 10-day lab incubation, (b) treatment effects on soil organic matter (%), and (c) potassium concentrations (mg kg^{-1}) in mesocosm soils. For all three panels, colors show initial and final timepoint concentrations in no snail versus snail treatments. Model significant results are depicted.

moderate evidence that snail treatments had increased total water N compared to no snail treatments ($P < 0.05$); although there was no evidence that snail effects differed across wetland types nor showed any trend over time (Fig. 5a). Snail treatments also increased total water C and total organic C concentrations over time (both $P_{\text{snail} \times \text{timepoint}} < 0.001$, Fig. 5b, c), however there was moderate evidence that total inorganic C decreased in snail treatments ($P_{\text{snail} \times \text{timepoint}} < 0.05$, Fig. 5d). By the final measurements, our results showed that total C was 48 % greater ($P < 0.001$, Fig. 5b) and total organic C was 77 % greater ($P < 0.001$, Fig. 5c) in snail compared to no snail treatments, but we found no evidence that snail effects on water C measurements differed across wetland types (all $P > 0.05$, Fig. 5d).

4. Discussion

Our study demonstrates that *P. maculata* exerted direct and cascading ecological effects across the plant-water-soil interface (Fig. 6) by altering plant communities and nutrient cycling. While most snail effects were consistent across wetland types, certain responses (e.g., chl_a) were divergent, suggesting that management strategies may mediate how invasive apple snails impact wetland ecosystems. In tandem, our findings are relevant for managed and natural wetlands that are experiencing similar apple snail invasions across the globe and imply that *P. maculata* invasion may also compromise vital wetland ecosystem services.

4.1. Plants biomass and community

Similar to previous work revealing negative effects of different apple snail species on plants (Carlsson et al., 2004; Fang et al., 2010; Horgan et al., 2014; Wang and Pei, 2012), excessive direct snail feeding likely decreased total plant biomass and cover in our experiment. However, plant biomass decreases did not vary by wetland type. Instead, snail consumption preferences appeared to exert greater control across wetland types, such as eradicating certain species (e.g., *B. caroliniana*, *J. angusta*) in SN wetlands. In fact, strong snail preference for some species (e.g., *P. cordata*) may have led to greater snail size increases in IM wetlands, where these plants were found in greater quantities. However, our findings are inconsistent with prior studies of apple snail plant preference feeding trials (Baker et al., 2010; Burlakova et al., 2009; Morrison and Hay, 2011), many of which used the same species as our experiment. Herbivores typically prefer plants that are more edible, for example those containing less chemical defenses and lignin content, or higher in nutritional value (Liu et al., 2022). Yet our results showed *P. cordata* to be a highly preferred plant species (i.e., different from other work), even though it is not the most palatable

plant species in our mesocosms (Polisini and Boyd, 1972; Sonnier et al., 2020). This may indicate adaptable apple snail population-level dietary preferences or variable palatability for the same plant species (Morrison and Hay, 2011). In addition, during our experiment, we often observed *P. maculata* clinging to *P. cordata* stems while consuming *P. cordata* leaves, suggesting the plants were attractive or accessible to snails by functioning as habitat (Nicotri, 1980). While apple snails may ultimately prefer plants that are more palatable (e.g., high N content, less dry matter content; Wong et al., 2010), plants that function as habitat may also exert some secondary influence on snail diets (Duffy and Hay, 1991).

Regardless, preferential feeding by invasive apple snails could alter plant community composition (Fig. 2d; Howe et al., 2002), and ultimately compromise wetland biodiversity by eradicating native plant species. As large sources of plant diversity, wetlands can serve as critical habitat refugia, support specialist herbivores, and provide high value supplementary forage for livestock if agriculturally managed (Sonnier et al., 2020; Zedler and Kercher, 2005). Of particular broad-reaching concern is apple snail potential preference for plant seedlings (Naylor, 1996). In our mesocosms, seedlings emerged from the soil seedbank (i.e., classified as “other” species) in the no snail treatments, however, no “other” species were found in snail treatments, even though all mesocosms were constructed using the same wetland soils and thus had the same seedbank. Herbivores may prefer seedlings as they may be more palatable than adult plants (Fenner et al., 1999). Such preferences can increase plant competition and alter recruitment (Hanley and Sykes, 2009), which has implications for rare or vulnerable species in wetland habitats (Flinn et al., 2008).

4.2. Nutrient cycling

Increases in N, P, C and TDS in the water column suggest invasive snails accelerated nutrient cycling. This can occur directly when snails consume plant tissues converting them into dissolved organic matter and labile nutrients (Belova, 1993; Li et al., 2014); and/or at the same time, indirectly when snail feeding decreases plants' ability to uptake nutrients for maintenance and growth (Dhir et al., 2009). Direct effects through snail egestion (feces) and excretion could increase N and/or P in water, however amounts may vary across species, food source, environment, size and life stages of organisms (Li et al., 2009; Moslemi et al., 2012). While *P. maculata* egestion/excretion rates are overall understudied, some limited evidence in a lab-based study revealed similar ammonia excretion rates to other freshwater snails (Deaton et al., 2016). On the other hand, aquatic herbivores with voracious feeding habits and/or those acting as ecosystem engineers (similar to *P. maculata*) have enacted significant nutrient cycling changes in

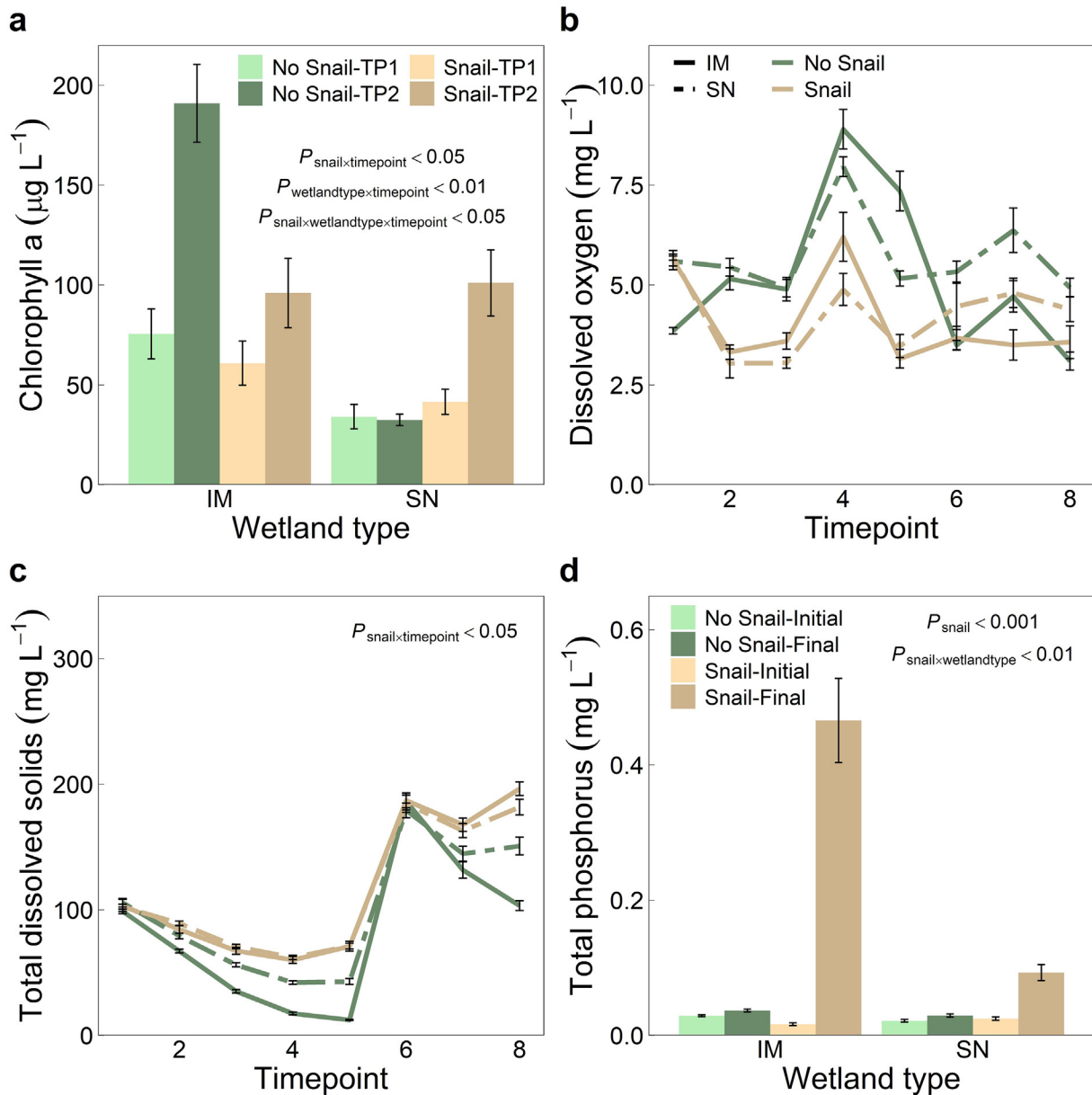


Fig. 4. Means (\pm SE) of (a) chl a concentrations ($\mu\text{g L}^{-1}$) in the water column are depicted in two time periods: “TP1” (i.e., timepoint measurements 1–4 averaged) and “TP2” (i.e., timepoint measurements 5–8 averaged) with intensively managed (IM) and semi-natural (SN) wetland types shown on the x-axis. Snail vs. no snail treatments in each timepoint are indicated by the varied colors. Treatments means of (b) dissolved oxygen (mg L^{-1}) and (c) total dissolved solids in the water column are shown across the 8 timepoints. The different line types indicate wetland types IM and SN and varied colors show snail and no snail treatments. Means (\pm SE) (d) of total phosphorus concentration (mg L^{-1}) in the water column for initial and final timepoints with x-axis and colors labeled as panel a. Significant results from models are displayed, however for DO and TDS, only significant interactions with timepoint are shown (see Table 1 for full model results).

different water bodies (Matsuzaki et al., 2007; Moslemi et al., 2012; Ozersky et al., 2015). For example, invasive snails (*Potamopyrgus antipodarum*) were found to greatly control N and C cycling in the water column of a stream in Yellowstone National Park, by consuming around 75 % of the total gross primary production while also contributing to most of the ammonium regeneration (Hall et al., 2003). Additionally, *P. maculata*'s destructive feeding habits, such as breaking off large pieces of the plant, can limit plant growth (Monette et al., 2016), and may also indirectly affect water and soil processes when partially-consumed organic particles are readily degraded and converted into labile nutrients (Jabłońska et al., 2021; Thorén et al., 2004). Our steady increases in water nutrients and C, particularly organic C, in snail treatments may reflect this plant decomposition (Guo et al., 2023; Kayranli et al., 2010). In fact, the higher water P in snail treatments for IM wetlands was likely due to higher P concentrations in IM plant litter from legacy soil P effects from fertilization (Sonnier et al.,

2020; Guo et al., 2023, Appendix A: Fig. 2). Ultimately, with little change in soil nutrient or C storage, these snail-induced water N, P, and C increases pose a risk for downstream waters as they may be leached from the wetlands.

Although water nutrient changes due to snail invasion were similar in both IM and SN mesocosms (besides additional amplified P in IM wetlands), algal biomass response differed by wetland type. Over time, chl a concentrations decreased in IM snail treatments compared to no snail treatments whereas chl a increased in SN snail treatments. This was surprising because increased water P concentration, such as that observed in IM snail treatments, is a known trigger for algal growth (Schindler, 1974). Instead, cascading nutrient increases caused by snails in IM treatments in the first time period may have spurred initial algal growth, but over time, algal die-off occurred (e.g., from lower nutrients; Paerl and Otten, 2013). However, this could also cause excessive oxygen depletion or fluctuations

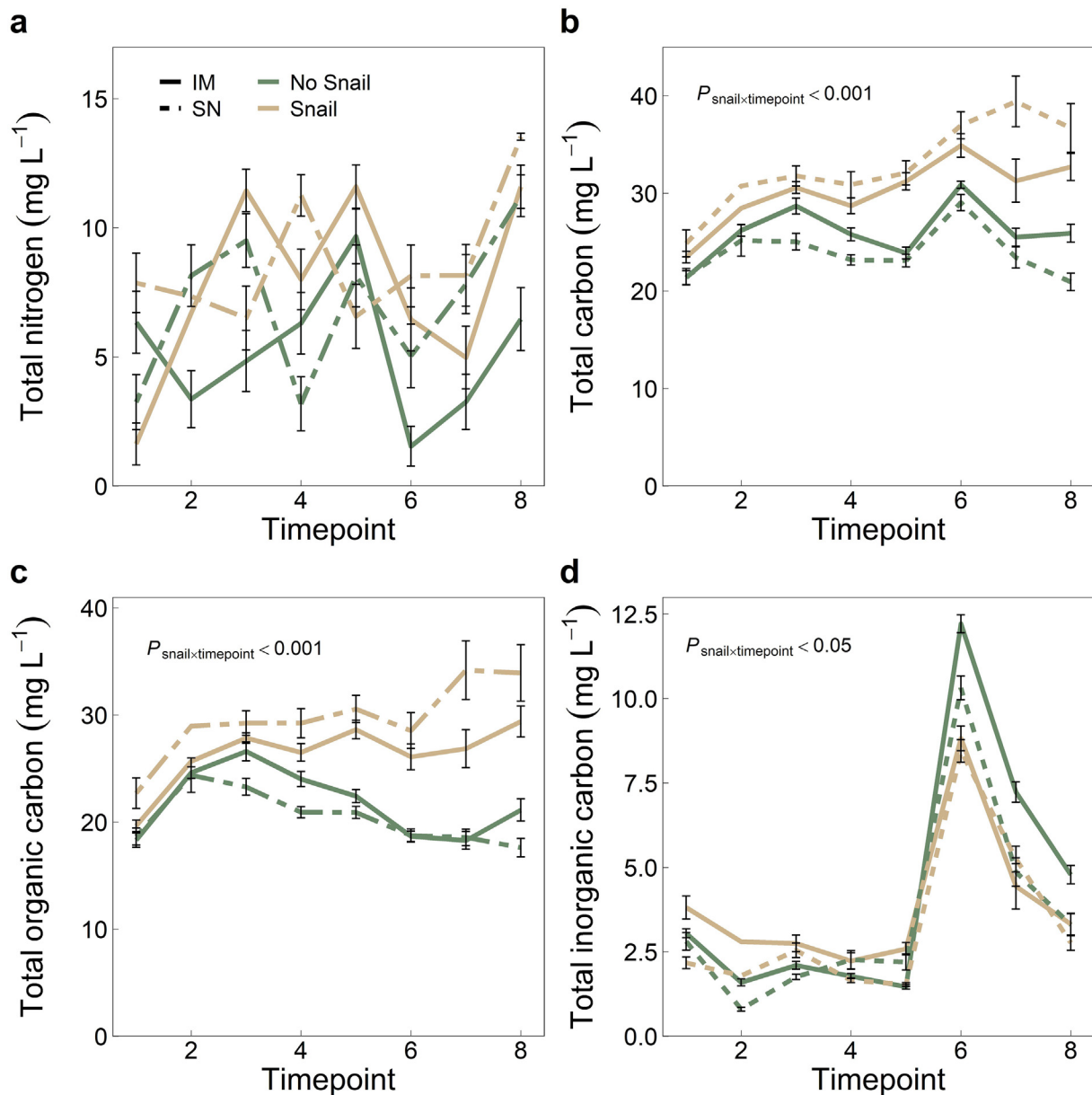


Fig. 5. Means (\pm SE) of total nitrogen (a), total carbon (b), total organic carbon (c) and total inorganic carbon (d) in the water column across the 14-week experiment. Water measurements were taken on each of the 8 timepoints (x-axis), with colors differentiating snail treatments and line types showing intensively managed (IM) and semi-natural (SN) wetland types. Significant results from models are depicted, however only significant interactions with timepoint are shown (see Table 1 for full model results).

(Paerl and Otten, 2013), and we did not observe extreme DO fluctuations or significant differences in DO across wetland types (Fig. 5b). Alternatively, snail feeding preferences may have affected algae growth, such that snails preferred eating certain algal species (Fang et al., 2010) that were more common in IM wetlands, or because snail-preferred plants (e.g., *B. caroliniana* or *J. angusta*) were only available in SN wetlands, snails grazed more on algae (than plants) in the IM wetlands. Yet other work has found minimal differences in *P. canaliculata* diet composition (percent detritus, macrophytes, algae, cyanobacteria, etc.) across different habitats (Kwong et al., 2010). Regardless, an ecosystem state-transition from clear-water and macrophyte-dominated to turbid and phytoplankton-dominated as we hypothesized did not occur in the snail treatments.

4.3. Soil properties and processes

Soil properties and processes were less affected by snails. For example, SOM content changes in snail treatments (Table 1) were more likely caused

by differences in initial SOM content in snail vs. no snail treatments (Fig. 4b). On the other hand, significant soil K concentration increases in snail treatments probably stem from snail feeding and increased decaying plant litter inputs (Chimney and Pietro, 2006; Staaf, 1980). However, overall, snail effects on soil may have been minimal because nutrients were lost from the water column via microbial processes or via the overflow holes in the mesocosm (in order to mimic the natural water flow of wetlands) before sedimentation could occur. This may be concerning for wetland nutrient retention and C storage as N, P and C released from decaying litter and snail egestion/excretion products are not retained in the wetland system.

4.4. Management implications

Direct and cascading ecological effects by invasive apple snails may ultimately hinder wetlands' capability to provide ecosystem services for both natural and human-managed habitats. For example, snail feeding decreased plant diversity and lowered primary productivity, which contributes to

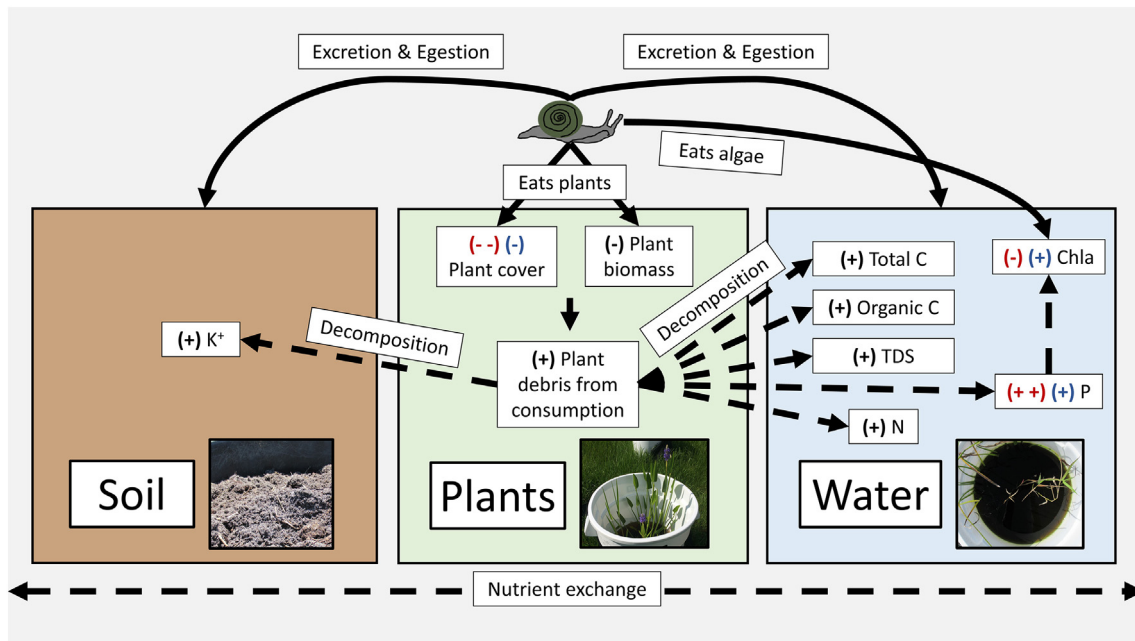


Fig. 6. Potential direct (solid arrows) and cascading (dashed arrows) effects by snails on soil, plant, and water responses in wetland mesocosms. Positive and negative signs by response measurements indicate a positive or negative effect by snail with red showing intensively managed (IM), blue showing semi-natural (SN) responses, and black showing the response of both wetland types. Double positive or negative signs indicate a stronger or amplified effect in a specific wetland type (i.e., water P or plant cover). There is moderate to very strong evidence for all effects shown (all $P < 0.05$). Photos & snail: C. M. O'Neil. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

habitat and food for other organisms, and, in our region, can be a vital forage source for livestock (Sonnier et al., 2020). Invasive apple snails also accelerated nutrient cycling by releasing C stored in plants and increasing nutrients such as N and P in the water column, with little change in soils, thus potentially compromising wetland C storage and nutrient retention. A major environmental concern in South Florida is non-point source P losses from grazing lands. Ranches have been targeted for adopting best management practices (BMPs) to improve P control strategies (Bohlen and Villapando, 2011). However, reduced wetland nutrient retention capacities and increased N or P loss caused by abundant invasive apple snails may compromise effectiveness of BMPs, thus potentially negatively impacting downstream water quality, the Everglades and coastal ecosystems.

Our findings also have broader relevance for other wetlands worldwide undergoing similar apple snail invasions. Higher water P levels and greater plant cover loss in IM snail treatments suggest that intensively managed wetlands may be more vulnerable to invasion. Thus, highly modified wetlands, a habitat type increasing globally (Zedler and Kercher, 2005), should be considered a priority for control of invasive apple snails. Further, direct and cascading effects on multiple wetland functions highlight the importance of developing dynamic management strategies to reduce current snail populations and mitigate further spread. In that regard, the biotic resistance hypothesis (i.e., resilience to invasion through native biodiversity) and fluctuating resource hypothesis (i.e., unused resources in ecosystems increase susceptibility to invasion) are important considerations when making management decisions (Brown and Barney, 2021; Burke and Grime, 1996; Davis et al., 2000). Thus, a renewed focus on reducing nutrient enrichment to ecosystems and encouraging healthy native species communities may prove best for ameliorating invasion effects (Brown and Barney, 2021).

4.5. Caveats

While our results hold value in a highly controlled but biologically complex mesocosm experiment, scaling up findings to landscapes must be met with some caution. Experimental duration, wetland size, predator presence,

and snail density are additional factors that fluctuate in field conditions and could further affect wetland responses to snails. In addition, artificial and structural mesocosm elements such as the water overflow holes may not have sufficiently mimicked field wetland overland flow, thus affecting nutrient loss. It is also possible our constructed soil profile had less capacity to store and cycle nutrients compared to field soils. Despite this, mesocosm experiments are still useful in teasing out direct and indirect effects of apple snails in dynamic systems such as our studied wetlands, which otherwise would be difficult in field conditions.

5. Conclusions

Our research reveals that invasive apple snails exerted profound impacts on wetland plant communities and nutrient cycling. Wetlands at Buck Island Ranch are hotspots for ecosystem services, which is common for many isolated wetland habitats across human-modified landscapes (Swain et al., 2013; Zedler and Kercher, 2005). Therefore, snail invasion consequences as revealed in Florida's natural and managed ecosystems could have broad implications for other wetlands around the globe that are experiencing invasive *Pomacea* spp. Future studies should consider holistic approaches, like ours, to better quantify and predict invasion effects on subtropical wetlands. Additionally, longer-term studies are needed to understand how ecosystems may bounce back or stabilize from the initial dramatic changes we observed in our 14-week experiment. Overall, our research demonstrates that apple snail invasions threaten wetland structures and functions through direct and cascading pathways and highlights the necessity for strategies to control and mitigate impacts.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.160939>.

CRediT authorship contribution statement

All authors contributed to Conceptualization, Methodology, Investigation, and Manuscript review and editing. **Chase M. O'Neil:** Data collection, Formal analysis, and Writing of the original manuscript draft; **Yuxi Guo:** Data collection; **Steffan Pierre:** Data collection; **Elizabeth H. Boughton:**

Resources **Jiangxiao Qiu**: Formal analysis, Resources, and Funding acquisition.

Data availability

All underlying data and code from this work will be fully accessible and archived in a public repository after manuscript acceptance.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Marx Gedeon, Ariel Johnson, Tiehong Song, Claudine Alcida, Amy Wiedenfeld, and all the Buck Island Ranch research staff, including Grégory Sonnier, Amartya Saha and Haoyu Li, who helped construct mesocosms or collect data in the field and lab. We also thank Hilary Swain for helpful discussions and research advice. Funding support of this work comes from USDA National Institute of Food and Agriculture, Hatch (FLA-FTL-005640), McIntire-Stennis (FLA-FTL-005673) and AFRI Foundational and Applied Science Program (GRANT13070634) projects. This research is a contribution of the Long-term Agroecosystem Research Network. The LTAR is supported by the United States Department of Agriculture.

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