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The influence of parasitism on producers and nutrients in mesocosm ecosystems

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ABSTRACT

Pathogens and parasites are increasingly recognized as important components within host populations, communities, and ecosystems. Both density-mediated and trait-mediated impacts of parasites on ecosystems are known and likely operate together to influence ecosystem processes. Despite the assertion that trait-mediated impacts of parasites are pervasive, empirical evidence of these effects is lacking. Our aim is to fill this gap and test whether parasitism can influence ecosystem processes within controlled mesocosm ecosystems. In the host-parasite (snail-trematode) system used, parasites form cysts in second intermediate host tissue and cause minimal direct mortality (minimizing density-mediated parasite impacts). We created mesocosms across a gradient of parasitism and measured water column nutrient concentrations, producer biomass, and invertebrate community composition. We demonstrate that trematode parasitism is correlated with an increase in periphyton dry mass and percent ash-free dry mass. Additionally, water column carbon and phosphorus concentrations were influenced by producers but not parasites. We demonstrate that parasites in the metacercarial stage have limited impact as "ecosystem engineers", but some data suggest parasites may have a subtle influence on ecosystem processes.

1. Introduction

Pathogens and parasites play a significant role in the behavior and physiology of individuals, the stability and dynamics of host populations, and in the assembly and structure of communities (Minchella and Scott, 1991; Morton and Silliman, 2020; Tompkins et al., 2011), but empirical evidence supporting the impact of infection at the ecosystem level is lacking (Buck and Ripple, 2017; Fischhoff et al., 2020; Paseka et al., 2020; Preston et al., 2016; Vannatta and Minchella, 2018). Given the substantial influence of parasites on small scales, it seems plausible that parasitism could have cascading effects on higher levels of biological organization (Buck and Ripple, 2017; Vannatta and Minchella, 2018; Weinstein et al., 2018).

Parasites can constitute a substantial amount of biomass in some ecosystems (Kuris et al., 2008, Preston et al., 2013, but see Paseka, 2017), which may directly contribute to nutrient cycling (Vanni, 2002). This biomass can operate in concert with density-mediated indirect effects (alterations in host population size) and trait-mediated indirect effects (alterations in host behavior and physiology) to influence ecosystem scale processes (Buck, 2019; Buck and Ripple, 2017; Sato et al., 2011; Thomas et al., 1998; Vannatta and Minchella, 2018; Weinstein et al., 2018). In order to demonstrate that parasitic impacts can influence ecosystems, an entire system must have its parasite population manipulated while holding other variables constant.

Ecosystem science deals primarily in two currencies: the flow of energy and the flow of materials (nutrient cycling; Preston et al., 2016). Most research to date has focused on the energetic implications of parasitism in ecosystems (Kuris et al., 2008; Preston et al., 2016; Preston et al., 2013; Sato et al., 2011). However, recent reviews have suggested parasitism must also be considered within the context of ecosystem nutrient cycling (Bernot and Poulin, 2018; Fischhoff et al., 2020; Paseka et al., 2020; Preston et al., 2016; Sanders and Taylor, 2018; Vannatta and Minchella, 2018). Studies have demonstrated links between parasitism and ecosystem nutrient cycling in producer communities (Eviner and Likens, 2010; Hatcher et al., 2012; March and Watson, 2010) as well as in consumer species (Brunner et al., 2017; Holdo et al., 2009; Mischler et al., 2016). Parasites influence nutrient cycling either directly via their own biomass or indirectly by altering nutrient transformation, nutrient transfer, and bioturbation by their hosts (Vannatta and Minchella, 2018). Although ecosystem level effects of parasites via regulation of

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host density have been documented (Buck and Ripple, 2017; Holdo et al., 2009; Whiles et al., 2013), direct parasite biomass effects and indirect parasite-induced changes in host behavior and physiology (trait-mediated impacts of parasitism) are less well understood (Buck, 2019; Buck and Ripple, 2017; Mischler et al., 2016; Vannatta and Minchella, 2018).

In order to assess whether parasitism is correlated with ecosystem processes, we selected a snail-trematode, host-parasite system where parasitism would have a limited impact on host population dynamics. We then experimentally manipulated the number of parasites in the system. Thus, if changes were detected in ecosystem dynamics across the gradient of parasitism, they were likely the result of altered host behavior and physiology, rather than density-mediated effects. We measured the level of parasitism in two ways: infection prevalence (binary infected/uninfected responses to parasitism) and infection intensity (number of parasites per host). We show that despite limited changes in host abundance, parasitism was associated with alterations in producer biomass likely via trait-mediated indirect effects.

2. Materials and methods

2.1. Summary

We created experimental mesocosms using a snail-trematode system in which one group of caged snails (first host) transmitted parasites to free-roaming snails (second host). A gradient in parasitism was created by altering the proportion of infected caged snails transmitting parasites while keeping the total number of caged snails constant. We maintained our mesocosms for 12 weeks and examined dissolved nutrient concentration and stoichiometry, producer biomass, invertebrate community composition, and free-roaming snail abundance and infection intensities.

2.2. Parasite life cycle

We utilized the trematode parasite, *Echinostoma trivolvis*. *Echinostoma trivolvis* begins its life cycle in the intestinal tracts of waterfowl or muskrats (Olsen, 1974; Fig. 1). Adult parasites release eggs produced via sexual reproduction in host feces which mature in the environment. Once hatched, free-living miracidia penetrate *Helisoma* spp. snails and undergo asexual reproduction. After 4–6 weeks, free-living cercariae burst from *Helisoma* and encyst as metacercariae (parasitic cysts) in any available aquatic gastropod host (tadpoles may also be infected). These metacercariae are ingested by the vertebrate host when the snail is eaten, beginning the life cycle again. In our experiment, we replicated the snail-to-snail transmission pathway.

2.3. Experimental setup

Mesocosms were established at the Ross Biological Reserve in Tippecanoe County, Indiana, USA. Twenty-four mesocosms (150 L; 65 cm wide x 90 cm long x 30 cm deep) were randomly distributed on a concrete platform (see Appendix, Fig. A.1) and established by rinsing 1 L of homogenized sediment from a pond at Purdue Wildlife Area through 1000 μm, Nitex bolt cloth using well water. Bolt cloth removed large debris and unwanted gastropods from sediment. Sediment also served to establish zooplankton and algal communities. This volume of sediment was chosen to cover the base of the mesocosm with a thin layer of sediment and provide a sufficient amount of algal inoculum (Johnson et al., 2007). One cinder block was placed in the center of each mesocosm to generate habitat structure and to add additional surface area for algal growth. Mesocosms were covered with 1 mm window screen lids to prevent colonization of additional organisms and left for two weeks (McCormick and Stevenson, 1989) to allow algal and zooplankton communities to establish. Then, the snail-trematode parasite community components were added along with two 15 × 15 cm ceramic tiles to measure periphyton characteristics (explained further below).

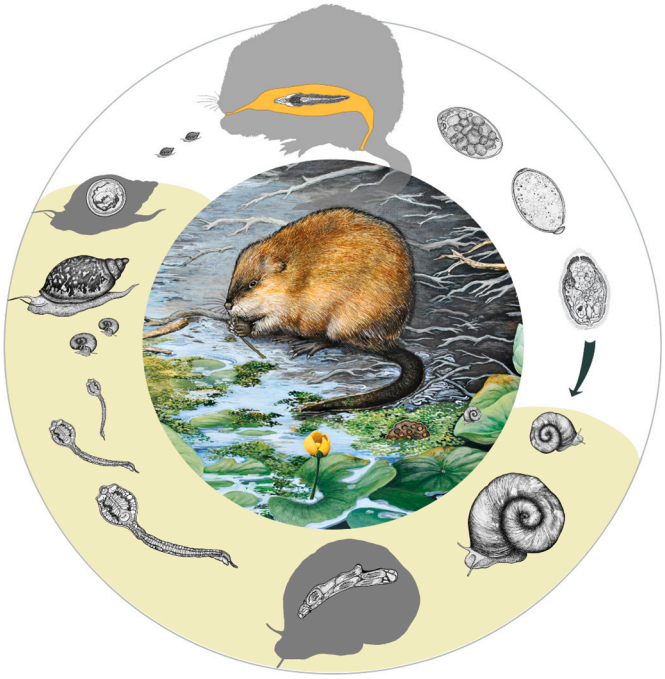

Fig. 1. *Echinostoma trivolvis* life cycle. *Echinostoma trivolvis* adults reside in muskrat intestines. Eggs are released in feces, mature in aquatic environments, and hatch as miracidia. Miracidia penetrate *Helisoma* spp. snails and mature to rediae. Rediae release cercariae which actively seek out gastropod second intermediate hosts such as *Physa* and *Promenetus*. Cercariae enter the second intermediate host and form metacercariae, which develop into adult worms after ingestion by muskrats. The tan, shaded region was replicated within our experimental mesocosms (illustrations by Gabriela Sincich).

To generate a gradient in parasitism, we placed 5 echinostome infected, caged *Helisoma* in 'high parasitism' treatments (100% prevalence), 2 infected and 3 uninfected, caged *Helisoma* in 'moderate infection' treatments (~ 40% field prevalence at Purdue Wildlife Area), and 5 uninfected, caged *Helisoma* in 'low parasitism/control' treatments (0% prevalence). These prevalence values were chosen based on estimates of snail densities and infection found during field sampling at Purdue Wildlife Area. In a few instances, false-positive and false-negative snails introduced variability within the treatments.

Helisoma spp. snails were collected from Purdue Wildlife Area throughout the field season and screened for echinostome cercariae (identified according to Schell, 1985). Both infected and uninfected "source" snails in the appropriate combination were placed in snail cages (2 L volume) constructed of 1000 μm bolt cloth and PVC to prevent caged snails from becoming lost or laying egg masses within mesocosms. Once a week, caged snails were screened to confirm survival. Additionally, snails were screened to ensure that the appropriate number of snails were still shedding cercariae and that uninfected, caged snails had not developed active infections. During these weekly screenings, dead snails were replaced with live snails according to infection status and treatment type and surviving infected and uninfected snails were placed into separate containers. Snails in each container were mixed, and haphazardly redistributed across mesocosms. This was done to minimize differences related to infection intensity, snail size, and individual host responses to parasitism in caged snails.

Twenty similarly sized, uninfected *Physa* snails were placed in each mesocosm as free-roaming potential hosts for the parasitic cysts. *Physa* were raised in the laboratory for one year prior to mesocosm establishment to ensure that free-roaming snails would not initially harbor parasites. Additionally, gastropods smaller than 1000 μm were able to enter the mesocosms during establishment with pond sediment. This

group primarily included *Promenetus* spp. snails.

2.4. Measurements of ecosystem function

A complete list of response variables is included in Table A.1. Invertebrate communities were assessed at the conclusion of the experiment. Free-roaming snails were stored in a refrigerator in order to slow their metabolism and prevent mortality. Due to personnel and time constraints, absolute size of snails was not recorded. However, *Physa* greater than 7 mm and those less than 7 mm were noted as being within distinct size classes at the end of the experiment. *Promenetus* snails had little variation in size based on visual inspection at the end of the experiment and were not separated into such classes. All snails were crushed and parasitic cysts (metacercariae) were counted by teasing apart host tissue to determine infection intensity. Prevalence was calculated as the number of free-roaming snails containing cysts divided by the total number of free-roaming snails retrieved from each mesocosm.

The remaining invertebrate community was assessed by collecting 1 L of mesocosm water from the surface, middle, and bottom of each tank (3 L total) and filtering the sample through 80 μm, Nitex bolt cloth. Samples were refrigerated and processed within 1 week. Most invertebrates were keyed to family and, because of their distinctive characteristics, cladocerans were keyed to genus (Haney, 2013; Voshell Jr., 2002).

Primary production was measured using the in situ *diel* primary production method. This method uses the change in dissolved oxygen (DO) concentration between the DO maximum and minimum to approximate community respiration and photosynthesis (Howarth and Michaels, 2000). In situ *diel* primary production was calculated by taking dissolved oxygen readings from 1400 to 1600 h and then from 0400 to 0600 h (the photosynthetic maximum and minimum, respectively) within a 24 h period at weeks 0, 6, 9, and 12. Each mesocosm was recorded three times during these sessions and the average DO reading used as the value for that mesocosm. All remaining metrics of primary production were measured at the conclusion of the experiment. Periphyton ash-free dry mass was measured by scrubbing the 15 × 15 cm ceramic tiles into 380 mL of fresh, well water. Solutions were mixed thoroughly, and 50 mL of solution was vacuum filtered onto pre-ashed and weighed 0.7 μm glass fiber filters. These were then dried for at least 48 h at 60C, weighed, ashed at 550C for 4 h, cooled and re-weighed. We additionally calculated % ash-free dry mass as (ash-free dry mass / total dry mass). In contrast to periphyton dry mass or ash-free dry mass which are absolute quantities, % ash-free dry mass emphasizes the quality (nutritional content) of the periphyton such that high values of % AFDM suggest more nutritious periphyton per unit of intake. For chlorophyll α, the second ceramic tile was scrubbed, and 50 mL of the solution filtered onto a 0.7 μm GFF. This filter was placed in a film canister and frozen at —80C until processing. For extractions, filters were cut in half, placed in 10 mL of 90% ethanol for 24 h and processed on a Turner Designs fluorometer using the Chl a-NA module. Surface vegetation was assessed by collecting all floating vegetation with an aquarium net, drying the sample at 60C for 48 h and weighing. Before drying, 10 mL of packed vegetation was used as a subsample to determine the abundance of different floating vegetation species. This subsample was sorted by species, weighed, and included in the total vegetation biomass calculation.

Water nutrient concentration and stoichiometry were measured using a Shimadzu TOC/TNM-L analyzer and a SEAL AQ2 autoanalyzer. Water samples, conductivity and pH were taken at week 0, 6, 9, and 12. Due to logistical constraints, samples were frozen before filtration. This is unlikely to have impacted our study as analyses were done relative to other treatments within this study. Carbon, nitrogen, and phosphorus were measured only for dissolved nutrient components (total dissolved organic carbon, total dissolved nitrogen, and total dissolved phosphorus) by filtering samples through 0.7 μm glass fiber filters.

2.5. Statistical analysis

Analyses were done using linear regression with *Physa* mean infection intensity (mean number of metacercariae per *Physa*) or prevalence of free-roaming snails (Number of *Physa* and *Promenetus* infected/ Number of *Physa* and *Promenetus* total) as a predictor. These predictors were chosen as parasitic influences may manifest in a binary manner (where infected and uninfected snail behavior are categorically different) or in an intensity dependent manner (where more parasites in a host generates a gradient in parasitic influence). Nonparametric statistics were used to predict *Physa* prevalence as this data continued to violate assumptions of linear models. For time series nutrient data, linear models were produced with time as an additional predictor variable with an interaction term. Models examining nutrient concentration were done for weeks 6, 9, and 12 when parasitism could reasonably have had an effect on overall nutrient concentration. For analyses examining the change in nutrient concentration, week 0 was included to account for the starting point of each mesocosm. For stoichiometric analysis, C, N, or *P* values below the detection limit were set to one half the detection limit (Halvorson et al., 2017). Invertebrate community data were assessed using non-metric multidimensional scaling (NMDS) with the vegan package in R. Values were log transformed as needed to satisfy statistical assumptions. Supplemental structural equation models are presented within the appendix to further explore the roles of direct, density-, and trait-mediated parasitic impacts on periphyton. However, small samples sizes associated with the number of coefficient estimates necessitates these models be treated in a preliminary manner. All analyses were done in R version 3.6.3 (R Core Team, 2019).

3. Results

3.1. Infection metrics

Among all 24 mesocosms (8 experimental units per low, moderate, and high parasitism) over 1250 free-roaming snails were crushed and examined for parasitic infection. These yielded over 19,000 metacercariae. Prevalence and infection intensity in free-roaming *Physa* and *Promenetus* snails was significantly, positively correlated with our treatment groups (Fig. 2).

3.2. Community metrics

Free-roaming snail abundance was negatively correlated with *Physa* infection intensity (Fig. 3). However, invertebrate community composition did not vary consistently by treatment group (PERMANOVA Adjusted $r^2 = 0.096$, $F_{2,\ 21} = 1.118$, $p = 0.346$, Fig. A.2). Additionally, the number of *Physa* greater than 7 mm was not significantly associated with *Physa* infection intensity or prevalence in free-roaming snails.

3.3. Primary production

In situ *diel* primary production did not vary consistently in response to parasitism ($p = 0.5361$, Fig. A.3). Chlorophyll α also showed no significant relationship to parasitism (Fig. 4b). However, the percent of periphyton ash-free dry mass increased significantly in relation to infection prevalence (Fig. 4a). Additionally, periphyton dry mass increased significantly with *Physa* infection intensity (Fig. 4c).

3.4. Nutrient concentration and stoichiometry

Dissolved organic carbon (DOC) and total dissolved phosphorus (TDP) concentrations in the water column were not influenced by parasitism. However, DOC and TDP were significantly related to surface vegetation biomass (Fig. A.4). Unfortunately, variable starting conditions for total dissolved nitrogen (TDN) obscure the influence of parasitism (Fig. A.5 and Table A.2). Absolute values of DOC and TDN match

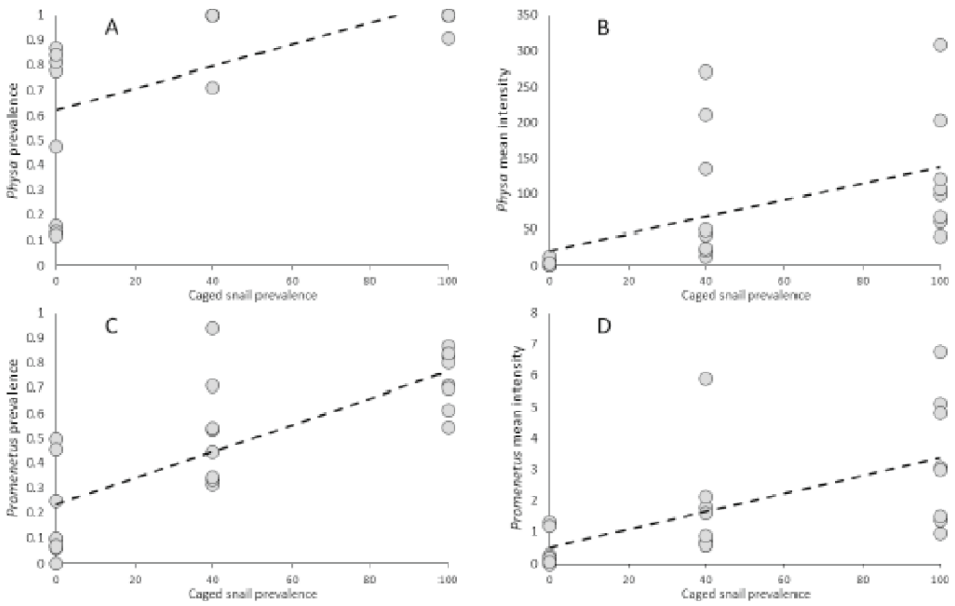

Fig. 2. Caged snail treatments were a significant linear predictor of both *Physa* (Median-based linear model $p < 0.0001$; see code files for further details) and *Promenetus* prevalence (Adjusted $r^2 = 0.5901$, $F_{1, 22} = 34.11$, $p < 0.0001$; Promenetus prevalence = (0.005 * caged-snail prevalence) + 0.234) and *Physa* (Adjusted $r^2 = 0.5461$, $F_{1, 22} = 28.68$, $p < 0.0001$; ln(*Physa* infection intensity) = (0.040 * caged-snail prevalence) + 1.159; data shown untransformed) and *Promenetus* infection intensity (Adjusted $r^2 = 0.4777$, $F_{1, 22} = 22.03$, $p = 0.0001$; ln(*Promenetus* infection intensity) = (0.010 * caged-snail prevalence) + 0.354; data shown untransformed).

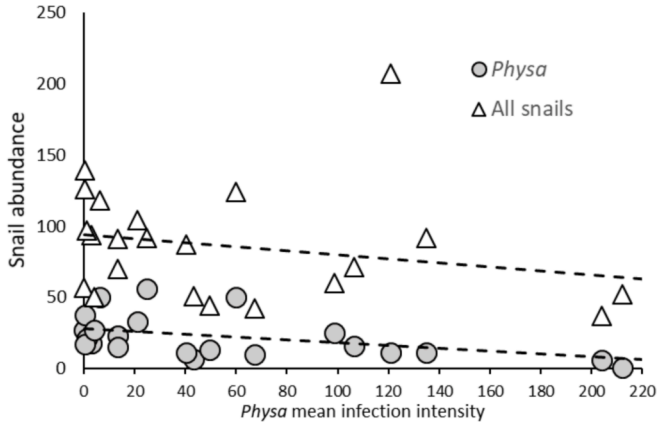

Fig. 3. *Physa* and total snail abundance within mesocosms. Abundance was negatively correlated with *Physa* mean infection intensity (*Physa*: Estimate = -0.0081 ± 0.0014, $F_{1, 22} = 31.61$, $p < 0.0001$; All snails: Estimate = -0.0025 ± 0.0011, $F_{1, 22} = 0.0299$).

measurements and ranges from other systems (Hessen, 1992; Johnson et al., 2006; Mischler et al., 2014). However, TDP in our experiment was low compared to others (Mischler et al., 2014).

Stoichiometry was highly variable within mesocosm water samples. Over time C:N, C:P, and N:P ratios all increased, but none of these changes were significantly related to parasitism (Figs. A.6 – A.8). Molar DOC:TDN began near 15 and ended near 30, DOC:TDP ratios began near 400 and ended near 800, and TDN:TDP ratios remained near 30 throughout the experiments duration.

4. Discussion

In order to test whether parasitism was correlated with an impact on an ecosystem, we selected a system where parasitism would have a limited impact on host population dynamics. That is, the effect of metacercarial parasites on host abundance is small. Thus, if changes were detected in ecosystem dynamics when parasitism was present, they were likely the result of parasite biomass or the indirect result of parasite-induced changes in host behavior and physiology (trait-mediated effects). Unfortunately, snail abundance was significantly correlated with infection intensity. This limits our ability to distinguish between the role of density and trait-mediated impacts of parasitism. Despite this, parasitism had a significant, positive impact on the dry mass of periphyton.

Intensity and prevalence data show that our experiment successfully created a gradient in parasitism, but the specific mechanisms by which parasite biomass influences nutrient concentrations and producer biomass remain unclear. Four non-mutually exclusive mechanisms could explain our results: 1) the decrease in host density had a cascading influence on producers (Holdo et al., 2009), 2) cercariae which are unsuccessful at finding a snail host may contribute energy and nutrients to these systems by their death (Kuris et al., 2008; Lambden and Johnson, 2013; Preston et al., 2013), 3) infection with trematode metacercariae (in free-roaming snails) and/or rediae (in caged snails) may influence the C, N, and P excretion rate in hosts (Bernot, 2013; Mischler et al., 2016), and/or 4) metacercarial infection may alter snail foraging patterns and movement (Keeler and Huffman, 2009; Mouritsen and Poulin, 2005; Webber et al., 1987). Although these variables were not directly measured here, we explore how these factors may have influenced our results below.

Disease is known to have various top-down effects on producers (Buck and Ripple, 2017; Holdo et al., 2009). The significant, negative association between host abundance and infection intensity in our system, although small, could influence producer biomass. As total periphyton dry biomass increased with infection intensity and not prevalence, it is most likely that reductions in host density or a reduction in foraging (a host trait) due to high infection intensities drove this association. Mortality associated with metacercarial infection may result from damage to snail tissue as the cercariae enter the mantle cavity or from encystment of the metacercariae around the snail's heart. Metacercariae are often seen in the heart cavity during dissection (personal observation) which could limit the flow of hemolymph and stress animals. Kuris and Warren (1980) found that metacercariae were only considered a mortality factor when densities reached near 250 metacercariae in a snail. However, these relationships were size-dependent with larger snails surviving higher parasite doses. Despite our mean infection intensities remaining largely below 150 metacercariae our data suggest that metacercariae can have a limited influence on host abundance. In one of the few field surveys examining metacercarial intensity, Zimmermann et al. (2017) found an average intensity of 80 metacercariae in some locations, which is similar to the values we observed in our 40% and 100% prevalence caged-snail treatments.

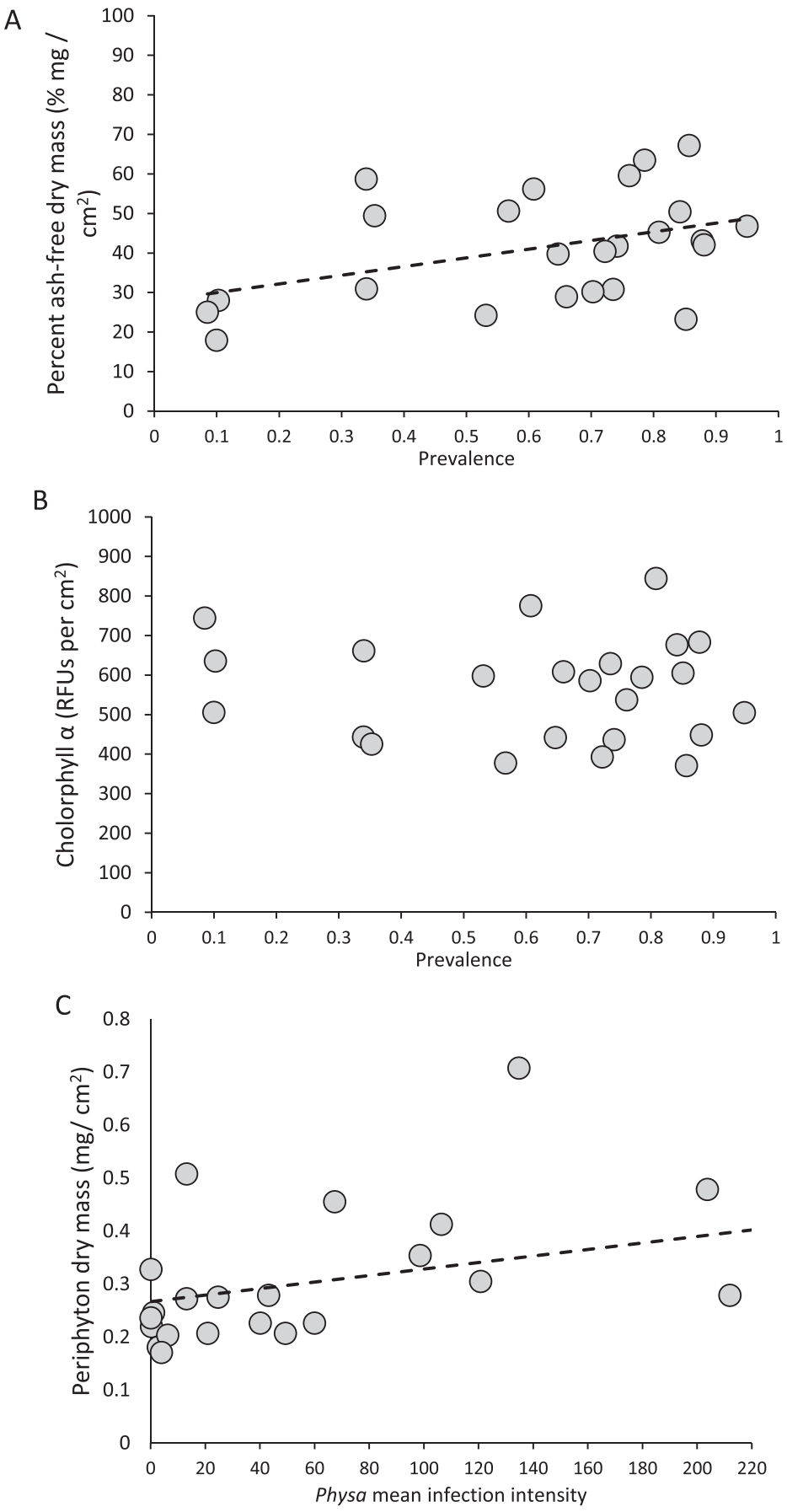

Fig. 4. Influence of free-roaming snail prevalence on A) the percent of periphyton ash-free dry mass and B) Chlorphyll α RFUs. Influence of mean infection intensity on C) Periphyton dry mass (mg/cm^2). Ash-free dry mass has a linear relationship with prevalence (Adjusted $r^2 = 0.1377$, $F_{1, 22} = 4.673$, $p = 0.042$; % AFDM = (21.98 * prevalence) + 27.774), chlorophyll α had no relationship with prevalence (Adjusted $r^2 = -0.040$, $F_{1, 22} = 0.113$, $p = 0.740$), and periphyton dry mass was positively correlated with infection intensity (Adjusted $r^2 = 0.1972$, $F_{1, 22} = 6.651$, $p = 0.0171$; ln(Periphyton dry mass) = (0.002 * infection intensity) - 1.377; data shown untransformed).

These results suggest that at field prevalence, metacercariae could have a cryptic influence on host density which is currently unrecognized. However, whether this change stems from altered host fecundity or mortality remains unknown. Our preliminary structural equation model suggests that host density and trait-mediated indirect effects act jointly to influence periphyton dry mass but that trait-mediated effects have a stronger influence on periphyton dry mass (Fig. A.9). Additionally, trematode cercariae can produce a substantial amount of biomass within certain systems (Kuris et al., 2008; Preston et al., 2013). It remains possible that decomposing cercariae supply a fraction of periphyton nutrient requirements, but our structural equation model suggests this is a weak driver of periphyton dry mass.

Although many species of trematode metacercariae are assumed to have little impact on their hosts (Keeler and Huffman, 2009; Kuris and Warren, 1980), a number of studies have documented that metacercariae can remain metabolically active, even after encystment (Keeler and Huffman, 2009; Lowenberger et al., 1994; Siddiqui and Nizami, 1981; Thomas and Gallicchio, 1967). Lambden and Johnson (2013) showed that in the transition from free-living cercariae to encysted metacercariae, *Echinostoma trivolvis* (the parasite used in this study) will increase its dry mass by 80%. This mass increase suggests metabolic activity as *E. trivolvis* transitions from cercariae to metacercariae, which could alter nutrient excretion in the current system as seen in other metacercarial systems (Mischler et al., 2016). Additionally, infections in caged snails could alter nutrient inputs into the system. Sporocysts (a parasitic life stage comparable to rediae) are known to influence host nutrient excretion rates (Bernot, 2013). Although it is possible that *E. trivolvis* metacercarial or redial infection generates a similar increase in N excretion that could contribute to changes in periphyton, we did not measure periphyton C, N, or P and the water chemistry analyses do not support this explanation. Almost all N in our mesocosms was in the dissolved organic instead of dissolved inorganic form (see mesocosm.master.csv in the data repository) indicating that available N is not coming from excretion.

In addition, the percent of periphyton represented as ash-free dry mass (% AFDM) increased with parasite prevalence. In contrast to strict mass measures, % AFDM is a measure of periphyton quality, not quantity. The increase in % AFDM with prevalence is likely related to host movement in the presence of parasites and our structural equation model further supports a trait-mediated driver of this relationship (Fig. A.10). For example, Webber et al. (1987) found that metacercarial infection can alter the activity of infected individuals. In our system, *Physa* show vigorous shell shaking responses, surface from the water, and spend less time foraging in the presence of parasites (Vannatta and Minchella, 2018) which may increase bioturbation and limit foraging. During the experiment, snails were mostly observed near the water surface. As periphyton near the surface is sloughed during shell shaking, this material can accumulate as particulate organic matter at the tank bottom where the periphyton tiles were located (Evans-White and Lamberti, 2005; Grimm, 1988; Halvorson et al., 2017; Halvorson and Atkinson, 2019; Morales and Ward, 2000) Particulate organic matter can trap other particles and create a substrate for nutritious bacterial growth (Mulholland et al., 1991). Thus, increased bioturbation may lead to an increasing proportion AFDM in periphyton, but not increasing photosynthetic activity. This would also not dramatically influence nutrient concentrations in the water column as the periphyton near the water's surface is very thin and well oxygenated. Thus, the material transported to the tank bottom is unlikely to release new nutrients but simply settles near the bottom of the mesocosm and accumulates. These assertions are supported as the additional AFDM was not coupled with any change in chlorophyll or nutrient concentration in our system.

5. Conclusion

In summary, we show that parasitism is associated with altered producer biomass which may have cascading impacts on ecosystems. Mechanistically, parasitism may alter the accumulation of particulate organic matter through parasite-induced changes in host foraging and bioturbation. Metacercariae, the parasitic stage used in this experiment, are commonly considered to have little ecological significance. Trematodes in general, and metacercariae in particular, are common within ecosystems, can reach high densities, are distributed widely within habitats, persist for long periods of time, and may impact resources (as suggested in this study). All of these characteristics can be important for ecosystem function. We have demonstrated that parasitism can be an important factor structuring mesocosm ecosystems. However, studies at larger (field manipulations) and smaller scales (examining specific mechanistic pathways) are needed in this snail-trematode system in order to better understand the magnitude of the impact. Additionally, alterations in the nutrient status of an ecosystem could alter the importance of parasitism. As such, examining parasitism across a gradient of nutrient inputs must also be considered. This study documents the importance of considering parasites not only at the individual, population, and community levels, but also as integral components of ecosystems.

Data availability

All relevant code and data for this experiment will be publicly available on GitHub (https://github.com/vanna006).

Author's contributions

JTV and DJM conceived the ideas and designed methodology; JTV collected the data; JTV analyzed the data; JTV and DJM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors have no competing interests to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fooweb.2021.e00204.

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