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Herbivore suppression of waterlettuce in Florida, USA

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HIGHLIGHTS

- Introduced and native herbivores reduced biomass and coverage of waterlettuce in Florida.
- *Neohydronomus affinis* is established in Florida and can achieve densities of 6.1 ± 9.4 m^2.
- Further studies should aim to integrate herbicides and biological control agents for waterlettuce.

GRAPHICAL ABSTRACT

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ABSTRACT

Waterlettuce, Pistia stratiotes L. (Araceae: Pistieae) is an invasive free-floating aquatic weed found throughout the world that has been targeted for control using various methods including classical and conservation biological control and, herbicides. In Florida, herbicides are the primary strategy employed by land managers, often without regard to the impact of herbivorous arthropods including Samea multiplicalis Guenee (Lepidoptera: Crambidae), Elophila [=Synclita] obliteralis Walker (Lepidoptera: Crambidae), Argyractis [=Petrophila] drumalis (Dyer) (Lepidoptera: Crambidae), Draeculacephala inscripta VanDuzee (Hemiptera: Cicadellidae), Rhopalosiphum nymphaeae L. (Hemiptera: Aphididae), Orthogalumna terebrantis Wallwork (Acarina: Galumnidae), and Neohydronomus affinis Hustache (Coleoptera: Curculionoidea). A series of field experiments from 2009 to 2012 were conducted at three sites in Florida to quantify the levels of suppression by these species, using an insecticide-check approach to produce restricted and unrestricted herbivory conditions. Four of the species (E. obliteralis, S. multiplicalis, O. terebrantis, and N. affinis) were found at every field site. At the end of the experiment, plots exposed to unrestricted herbivory contained 63.1 % less biomass and covered 32.0 % less surface area compared to plots with restricted herbivory. These results indicate that naturally occurring and introduced species are suppressing the growth of waterlettuce populations in the field in Florida. Future research will examine the synergistic potential of actively managing herbicides and herbivorous arthropods to suppress waterlettuce.

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1. Introduction

Pistia stratiotes L. (Araceae), commonly known as waterlettuce, is a free-floating herbaceous macrophyte that superficially resembles a head of lettuce (Fig. 1). Waterlettuce is considered a worldwide weed and is distributed throughout the subtropics and tropics where it invades and degrades freshwater fish spawning sites and other ecosystem services by restricting light for phytoplankton and submerged aquatic plants, crowding out native floating plants, decreasing dissolved oxygen and pH, while increasing sedimentation (Sculthorpe, 1967; Attionu, 1976; Holm et al., 1977; Dray & Center, 2002). In addition, this plant interferes with recreational activities like boating and fishing, impedes drainage and irrigation, and lowers property values (Cook et al., 1974; Holm et al., 1977). In Florida, waterlettuce is classified as a Category I Plant on the Florida Exotic Pest Plant Council's List of Invasive Plants Species (FLEPPC, 2017) and is also on the Florida Prohibited Aquatic Plants List (Florida Administrative Code, 2008). Category I plants are defined by the Florida Exotic Pest Plant Council (FLEPPC) as "Invasive exotics that are altering native plant communities by displacing native species, changing community structures or ecological functions" Fig. 2.

Beginning in 1899, the United States Congress authorized the U.S. Army Corps of Engineers to prevent waterhyacinth [Martius] Solms. (*Pontederia* [*Eichhornia*] *crassipes* [Pontederiaceae]) from obstructing navigation in Florida rivers. Since this original authorization, the Florida Legislature designated the Florida Fish and Wildlife Conservation Commission (FWCC) as the lead agency through the Florida Aquatic Weed Control Act of 1989 to "direct the control, eradication, and regulation of noxious aquatic weeds and direct the research and planning related to these activities… so as to protect human health, safety, and recreation and, to the greatest degree practicable, prevent injury to plant and animal life and property." Using this authority, FWCC contracts with government and private entities to control aquatic invasive plants, including waterlettuce.

Waterlettuce is managed through a combination of chemical, biological, mechanical, and physical techniques, with herbicides the most widely used tactic in Florida. Managers frequently apply a so-called 'maintenance control' strategy, a term defined as 'techniques that are used in a coordinated manner, on a continuous or periodic basis, in order to maintain the target plant population at the lowest feasible level as permitted by the availability of funding and technology' (FFWCC, 2017). This approach usually results in the repeated and wide scale use of herbicides by agencies including FWCC which spent $15 million in FY2018-2019 spraying 63,796 acres of aquatic weeds, including waterlettuce, on public waters (FWC, 2019). This herbicide-centric management strategy ignores the contribution of herbivores and biological control agents despite evidence of the utility of integrating them with herbicide rates and spray patterns to improve overall control and program sustainability (Tipping et al., 2017; Lake & Minteer, 2018; Goode et al., 2022). The lack of integration of biological control with current management strategies for floating aquatic weeds (i.e., waterlettuce and waterhyacinth) may be explained, in part, by skepticism and a lack of understanding of the role of the population level impacts of herbivores.

Several herbivores attack waterlettuce in Florida including the host specific classical biological control agent *Neohydronomus affinis* Hustache (Coleoptera: Curculionoidea) (Dray et al., 1990; Dray and Center, 1992). Several native and introduced polyphagous species are also present including *Samea multiplicalis* Guenee (Lepidoptera: Crambidae), *Elophila* [=*Synclita*] *obliteralis* Walker (Crambidae), *Argyractis* [=Petrophila] *drumalis* (Dyer) (Lepidoptera: Crambidae), *Draeculacephala inscripta* VanDuzee (Hemiptera: Cicadellidae), *Rhopalosiphum nymphaeae* L. (Hemiptera: Aphididae), and *Orthogalumna terebrantis* Wallwork (Acarina: Galumnidae (Dray et al., 1993).

Heretofore, the combined impact of classical and native biological control agents on waterlettuce has not played a role in management decisions (Schaffner et al., 2020). The densities these herbivores attain with their concomitant impacts on waterlettuce in the field are unknown. Therefore, the objective of this research was to quantify biomass production and surface coverage of waterlettuce as it relates to insect densities and field sites across South Florida from 2009 to 2012 by both classical and native biological control agents.

2. Materials and methods

2.1. Experimental setup and locations

Experiments were conducted from one to three years at three sites located in southern Florida (Table 1). A randomized complete block design was used with two treatments and four replications. The treatments were: (1) restricted herbivory where regular applications of insecticides (acephate 0.07 % ai or bifenthrin 0.01 % ai) were applied to plant populations until wet; and (2) unrestricted herbivory where water was applied. Applications of insecticide were applied every 14 to 77 days in response to variations in seasonal insect pressure (summer vs winter) and periodic site restrictions. Neither insecticide inhibited or promoted waterlettuce growth in experimental tanks and both were equally effective against herbivores attacking waterlettuce (unpublished data). Eight PVC floating frames (7.6 cm in diameter) which enclosed one square meter were placed at each site among persistent populations of waterlettuce, secured with a rope to a cinderblock anchor, and

Fig. 1. One square meter floating frames with (A) unrestricted herbivory and (B) restricted herbivory used to measure Mean Relative Growth Rate (MRGR) and percent coverage of waterlettuce (*Pistia stratiotes*).

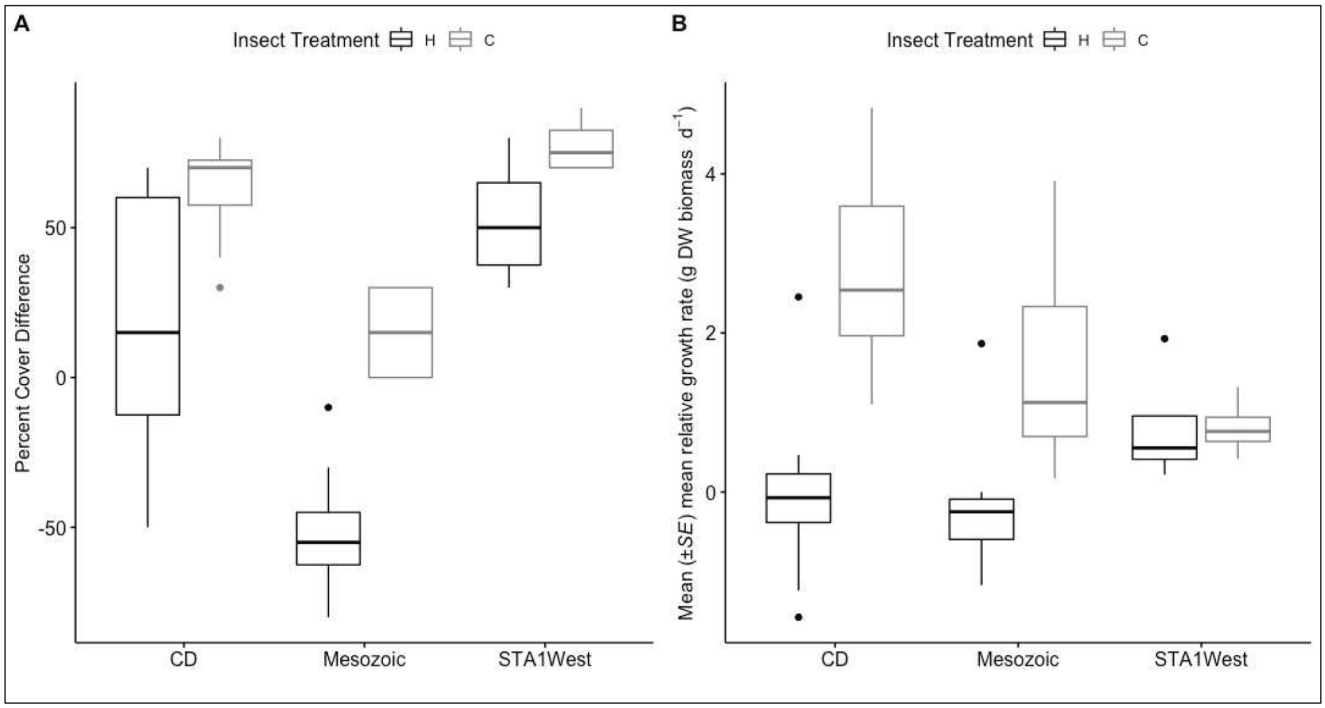

Fig. 2. (A) Percent coverage difference and (B) Mean Relative Growth Rate (MRGR) of waterlettuce (*Pistia stratiotes*) by site. Boxes indicate data between the first and third quartiles and whiskers represent the minimum and maximum values. Treatments with unrestricted herbivory are shaded grey (H = Herbivory) and treatments with restricted herbivory are black (C = Control).

Table 1
Sites, locations (latitude and longitude), trial, dates (day/month/year), and duration (days), for field evaluation studies on the suppression of waterlettuce by herbivores in Florida.

Site	Location (GPS)	Trial	Dates	Duration (days)
Compartment-D	26°28′55.9″N, 80°26′48.1″W	1	11/8/2009 – 10/5/2010	266
		2	7/7/2010 – 16/11/2010	132
		3	21/4/2011 – 18/1/2012	272
Mesozoic	26°33′44.4″N, 80°13′9.13″W	1	29/6/2010 – 10/11/2010	140
		2	20/4/2011 – 18/1/2012	273
STA1-West	26°39′23.5″N, 80°24′3.64″W	1	3/6/2009 – 31/3/2010	301

assigned a treatment. Plastic mesh bags were attached to the underside of each frame to enclose the area to a depth of one meter to prevent plants from washing out from under the frames.

2.2. Sampling

Experimental plant populations were initiated with five similarly sized waterlettuce plants taken from existing populations at each site. Each plant was weighed to record the initial fresh weight (FW) biomass. An additional five waterlettuce plants were collected from the surrounding mat and destructively processed in Berlese funnels to estimate initial herbivore species presence and richness. Those additional five plants per site were then removed from the Berlese, placed in a dryer at 60 °C, and dried to a constant weight to estimate initial dry weight (DW) biomass of experimental plants in the frame at each site.

The experimental plant populations were evaluated for percent coverage (to the nearest 10 %) within the frame by averaging the visual estimates of two observers at the beginning and end of the experiment. Next, five plants were haphazardly chosen from the square, carefully removed, and their FW biomass was recorded and assumed to have a moisture content of 95 %. Plants were then placed back into the frame at their original locations. Sampling was modified when coverage exceeded 50 % whereby the five sample plants removed and evaluated were not replaced back in the square but instead were broken apart by hand and placed in Berlese funnels for seven days to extract and tally internally feeding herbivore arthropods and to determine percent moisture content. Adults and larvae recovered throughout the experiment were identified and distinguished from one another based on morphology (Center et al., 1982). At the end of the experiment, all the plant material inside the frames was harvested, dried to a constant weight as described earlier to determine final DW biomass. Air temperature data used for this analysis were collected using BioSIM 11 to simulate environmental factors based on differences between nearby weather stations using site location characteristics (i.e., latitude, longitude, and elevation) (Régnière, 2014).

2.3. Statistical analysis

Different analyses were used to identify causal relationships of mean relative growth rate (MRGR) and percent coverage, and herbivore densities with the site, treatment, trial year, and mean temperature. The MRGR of waterlettuce was calculated as $(W_2 - W_1)/(t_2 - t_1)$, where W_1 and W_2 are the DW biomass at the beginning (t_1) and end (t_2) of the sampling period. The percent coverage difference from the beginning to the end of the experiment for each site and year was calculated as $t_2 - t_1$ where t_2 and t_1 are the end and beginning of the experiment, respectively. Data were tested for normality and equality of variances using the Shapiro-Wilk test. The MRGR and percent coverage difference was analyzed using a generalized linear mixed model (GLMM) with the block as a random effect.

The residuals of the GLMM for MRGR and differences in plant coverage were normally and approximately normally distributed, respectively. Therefore, a Type II ANOVA was used with a Satterthwaite

correction to approximate the independent degrees of freedom and to investigate the regressor effects (Table 2). To investigate differences between treatments for each site/trial year combination, a paired t-tests was used when the data where normally distributed, or paired Wilcoxon signed-rank tests when the data were not normally distributed, to determine significant differences between means (Table 3). Herbivore abundance data were not normally distributed and could not be successfully transformed, therefore a PERMANOVA, i.e., permutational multivariate analysis of variance (Anderson 2001), using unique sums of squares was performed to obtain measures of significance (Table 4).

3. Results

The linear mixed model predicting the MRGR of waterlettuce explained 72 % of the total variation with all the predictor variables showing significance except for the interaction between year and treatment (Table 2). In ranked order, the most influential factors as described by the total sums of squares were treatment (43.1 %), year (11.8 %), site (9.7 %), temperature (9.1 %), and the site × treatment interaction (7.9 %) (Table 2). Overall, populations that experienced unrestricted herbivory contained 63.1 % less biomass compared to plots with restricted herbivory. The interaction was the result of changes in magnitude to the response of the treatments within both site and treatment (Table 3). This is represented by differences in biomass that, while remaining relatively consistent in rank between treatments (i.e., unrestricted herbivory usually significantly suppressed biomass production), also varied among sites and even within sites over years (Table 3).

The linear mixed model predicting the percent surface coverage of waterlettuce explained 82 % of the total variation with all the predictor variables showing significance except for the interaction between year × treatment (Table 2). The surface coverage of waterlettuce was influenced primarily and similarly by treatment and site and to a lesser extent for year, the interaction between site × treatment, and temperature (Table 2). Plots with unrestricted herbivory covered 32.0 % less surface area compared to plots with restricted herbivory. The interaction term was caused by a change in magnitude in coverage between treatments at the Mesozoic site, which was much greater than between treatments at the other sites (Table 3).

Neohydronomous affinis adults and larvae, *S. multiplicalis* larvae, *E. obliteralis* larvae, and O. *terebrantis* mites were present at each of the three sites (Table 3, Fig. 3). Within the restricted herbivore treatment, herbivores were present and were observed feeding on the plant material, albeit at a lower densities (Table 3). Trial year did not affect insect densities (Table 4). Treatment and the interaction between trial year and treatment affected each of the insect response variables (Table 4). *Neohydronomus affinis* adults and larvae and *E. obliteralis* larval densities were affected by site and the interaction between site and treatment (Table 4) while *O. terebrantis* was affected by temperature (Table 4). For example, densities of *N. affinis* larvae and adults were much higher at STA1-W and continued to increase while those at Compartment-D and Mesozoic were consistently lower (Fig. 3, Table 3). Adult Lepidopteran and Hemipteran counts for both the unrestricted and restricted herbivory treatments were likely underrepresented due to the sampling technique (i.e., Berlese funnels) and their proclivity to abscond following site sampling/disturbance.

4. Discussion

This is the first field study to document the suppressive effect of multiple herbivores on biomass accumulation and surface coverage of waterlettuce in the United States.. Plots with unrestricted herbivory contained 63.1 % less biomass and covered 32.0 % less surface area compared to plots with restricted herbivory (Fig. 2). The decrease in waterlettuce biomass was comparable to the reduction of biomass of waterhyacinth (58.2 %) from herbivory by a suite of classical biological control agents and generalist herbivores (Tipping et al., 2014). Conversely, while waterlettuce surface coverage was consistently lower in the unrestricted herbivory treatment, waterhyacinth surface coverage was not (Tipping et al., 2014). Different plant architectures, morphological plasticity (the ability to modify anatomical traits independent of genotype in response to environmental variation) and feeding mode and damage by herbivores may explain the treatment differences in coverage found between waterlettuce and waterhyacinth.

Of the handful of herbivore taxa known to directly feed on living waterlettuce in the United States (Dray et al., 1993), including the classical biological control agent, *N. affinis,* and the adventive mite, *O. terebrantis*, four were found throughout this study (Table 3). Of these, *S. multiplicalis* and *E. obliteralis* have been reported as the most damaging in Florida; likely due to their potential population densities and the size and burrowing activity of the larvae (Dray et al., 1993; Wheeler and Halpern 1999). However, when released in Australia and in Argentina, *S. multiplicalis* populations and their associated damage were described as sporadic (Sands and Kassulke, 1984; Cabrera and Maestro, 2016), possibly due to parasitism and disease (Knopf and Habeck, 1976; Newton and Sharkey, 2000).

All herbivores reported in this study feed internally as immatures and thus are unable to abscond from mats following herbicidal treatment and ultimately die with the plant. Although not found in this study, both *D. inscripta* and *R. nymphaeae* are commonly found on waterlettuce in the field in Florida (Dray et al., 1993). Following egg eclosion, all *D. inscripta* and *R. nymphaeae* life stages are highly mobile and feed externally and can likely disperse to unsprayed plants following herbicide treatment.

Lepidelphax pistiae Remes Lenicov (Hemiptera: Delphacidae), is a waterlettuce specific, classical biological control agent that was considered for release in Florida (Cabrera et al., 2014; Goode et al., 2019). *Lepidelphax pistiae* significantly reduced waterlettuce growth and flower production alone and in conjunction with *N. affinis* (Cabrera et al., 2014; Cabrera and Maestro 2016; Goode et al., 2019). All *L. pistiae* life stages except the egg stage, are highly mobile and can readily migrate to nearby untreated refugia. However, because of questions regarding the origin of waterlettuce (Evans, 2013; Madeira et al., 2022) additional releases of classical biological control agents are not recommended.

The presence of herbivores within the restricted herbivory treatment was likely due to the interval between insecticide treatments, which ranged from 14 to 77 days. Within ~ 50 days of an insecticide treatment, herbivores, particularly *S. multiplicalis*, can re-populate waterlettuce (J. R. Foley, pers. obs). *Samea multiplicalis* larvae were affected least by site and among the herbivores found least affected by treatment. The

Table 2
Results of the ANOVA for plant variables with site, year, and treatment as main factors.

Response Variable	r2 (%)	Site (S)		Trial Year (Y)		Treatment (T)		S X T		Y X T		Temperature (C°)	
		df	TSS (%)	df	TSS (%)	df	TSS (%)	df	TSS (%)	df	TSS (%)	df	TSS (%)
MRGR	72	2	9.7**	2	11.8**	1	43.1**	2	7.9**	2	1.6	1	9.1**
% Cover	82	2	24.6**	2	4.8**	1	28.4**	2	4.3**	2	2.4	1	3.8**

Presented are the degrees of freedom (df), the rounded percentage of variance explained by each factor (TSS = (100x factor SS/total SS)).
* $t = 0.05$.
** $t = 0.01$.

Table 3
Mean (±SE) of variables for the different sites and years for all sample dates.

Site	Trial	Trt[a]	Surface coverage (%)	Area biomass (Kg DW m^{-2})	*N. affinis* adults and larvae (# plant −1)	*O. terebrantis* (# plant −1)	*S. multiplicalis* larvae (# plant −1)	*E. obliteralis* larvae (# plant −1)
STA1West	1	H	81.2 ± 4.3	0.6 ± 0.2	24.35 ± 3.8**	133.5 ± 50.5**	24.0 ± 4.2*	3.3 ± 1.2
		C	86.0 ± 4.6**	1.3 ± 0.2**	0.65 ± 0.3	12.5 ± 6.9	92.1 ± 32.0	0.6 ± 0.3
CD	1	H	16.4 ± 2.2	0.6 ± 0.2	0.0 ± 0.0	41.9 ± 28.4	4.8 ± 2.9	0.8 ± 0.5
		C	41.0 ± 7.2**	3.4 ± 1.0	0.5 ± 0.5	31.1 ± 8.5	62.5 ± 23.4	0.3 ± 0.3
	2	H	66.1 ± 4.5	1.8 ± 0.3	1.4 ± 0.4	55.8 ± 13.9	38.4 ± 6.0	0.1 ± 0.09
		C	89.4 ± 3.4**	3.8 ± 0.6*	0.9 ± 0.6	30.0 ± 8.2	48.3 ± 13.6	0.0 ± 0.0
	3	H	61.9 ± 8.2	3.0 ± 0.9	1.3 ± 0.1	0.0 ± 0.0┼	9.9 ± 2.6	0.9 ± 0.4
		C	82.5 ± 7.8**	9.4 ± 3.0*	0.0 ± 0.0	0.0 ± 0.0┼	8.9 ± 4.2	0.0 ± 0.0
Mesozoic	1	H	61.6 ± 5.3	2.2 ± 0.5	8.1 ± 3.1**	112.4 ± 40.1**	36.6 ± 5.1**	10.8 ± 3.0**
		C	95.6 ± 1.3**	3.9 ± 0.8	0.1 ± 0.1	3.1 ± 1.8	13.4 ± 4.6	0.0 ± 0.0
	2	H	44.9 ± 5.8	1.0 ± 0.2	1.2 ± 0.5	0.3 ± 0.1	6.8 ± 2.5**	0.9 ± 0.5
		C	94.2 ± 2.3**	3.1 ± 0.8	0.0 ± 0.0	0.2 ± 0.1	1.3 ± 0.8	0.0 ± 0.0

a Trt = experimental treatments where C was the restricted herbivory and H was the unrestricted herbivory by biological control agents.
*, ** $t = 0.05$ and 0.01, respectively, when comparing means between treatments within variables site and trial.
┼ indicates no difference between treatments for all observed responses in the site/trial year combination.

Table 4
Results of PERMANOVA for insect variables with site, year, and treatment as main factors.

Response Variables	r^2 (%)	Site (S)		Trial Year (Y)		Treatment (T)		S X T		Y X T		Air Temperature (C°)	
		df	TSS (%)	df	TSS (%)	df	TSS (%)	df	TSS (%)	df	TSS (%)	df	TSS (%)
# *N. affines* A and L	32.8	2	6.0**	2	16.1	1	11.4**	2	6.1**	2	15.1**	1	0.1
# *O. terebrantis*	23.2	2	0.6	2	8.8	1	5.7**	2	1.8	2	4.4**	1	3.0**
# *S. multiplicalis* L	22.2	2	1.3	2	9.7	1	1.8**	2	0.5	2	7.6**	1	1.2
# *E. obliteralis* L	24.1	2	4.8*	2	4.4	1	7.8**	2	4.5*	2	3.9*	1	0.3

Presented are the degrees of freedom (df), the rounded percentage of variance explained by a factor (TSS = (100x factor SS/total SS)).
A = adults; L = larvae.
* $p = 0.05$.
** = 0.01.

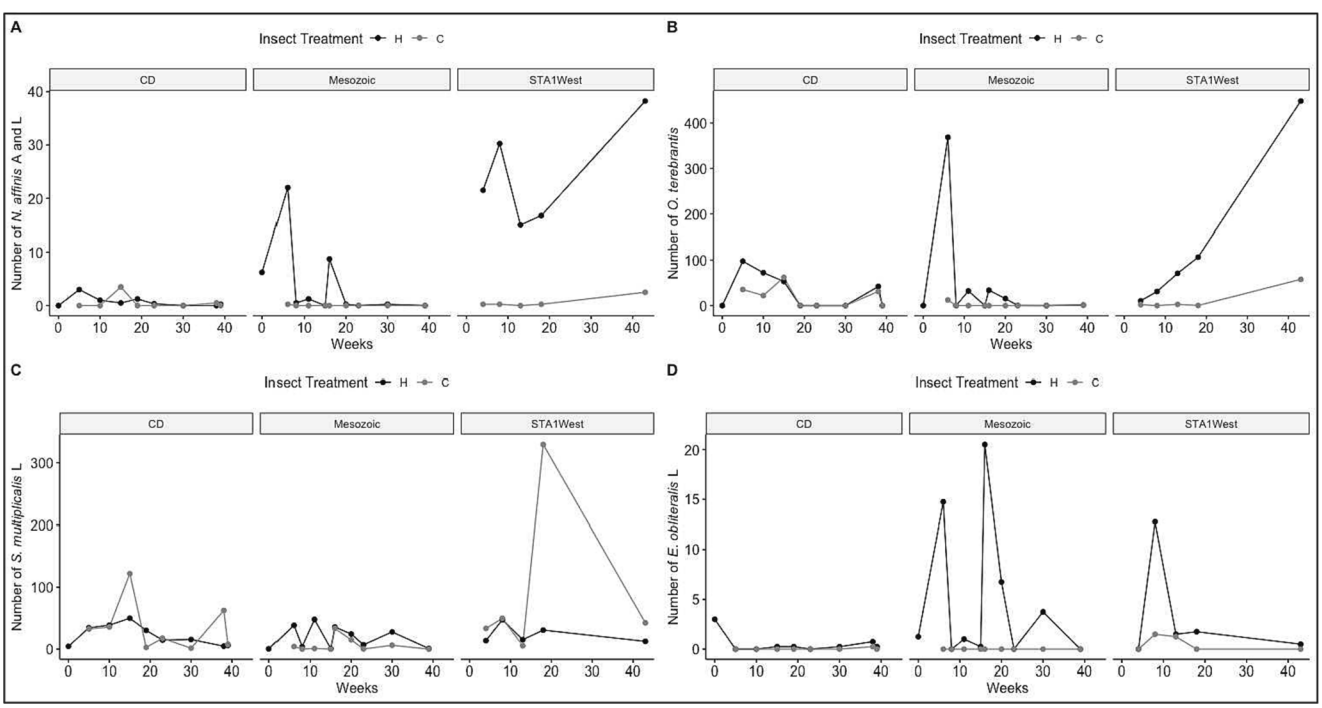

Fig. 3. Number of (A) *Neohydronomus affinis* (B) *Orthogalumna terebrantis* (C) *Samea multiplicalis* and (D) *Elophila obliteralis* over time (weeks) per site. Treatments with unrestricted herbivory are shaded grey (H = Herbivory) and treatments with restricted herbivory are black (C = Control).

relatively rapid recolonization of waterlettuce by *S. multiplicalis* following an insecticide treatment may be explained by the preference of adults to seek undamaged plants for oviposition (Taylor and Forno, 1987) as well as their broad host range whereby they can utilize alternative untreated host plants like *Salvinia rotundifolia* Willd., *Azolla caroliniana* Willd., and waterhyacinth. Conversely, *N. affinis* was affected

the most by site, treatment, and the interaction between site and treatment. *Neohydronomus affinis* can only feed and complete development on waterlettuce (Dray et al., 1990), which could limit its ability to repopulate plants following local extirpation (i.e., insecticide and herbicide).

Management of aquatic invasive plants relies on continuous and consistent funding to keep plant populations from obstructing navigable waterways and control structures (Schmitz et al., 1993, Schardt, 2016, Gettys et al., 2020). Biological control organisms, when combined with reduced herbicide application rates, can work synergistically to suppress waterhyacinth by increasing their susceptibility to herbicides which, in turn, decreases the number of herbicide applications required to reach management goals (Tipping et al., 2017, Goode et al., 2022). Whether the impact of herbivores on waterlettuce can produce similar synergies with herbicides awaits further studies. In the meantime, land managers should direct applicators to conserve waterlettuce herbivores by leaving unsprayed refugia whenever and wherever feasible.

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CRediT authorship contribution statement

Jeremiah R. Foley: Methodology, Formal analysis, Investigation, Writing – original draft, Visualization. **Jacob Williams:** Formal analysis, Writing – review & editing, Visualization. **Eileen Pokorny:** Investigation, Resources, Writing – review & editing. **Philip W. Tipping:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision.

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.

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