



Invasive Floating Fern Limits Aerial Colonization and Alters Community Structure of Aquatic Insects

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Abstract

Aquatic insects are important to the transfer of energy in freshwater wetlands. They link primary producers and organic matter to higher trophic levels, and pass energy from the aquatic environment to the terrestrial ecosystem via predation of adults. Introduction of the invasive free-floating aquatic fern giant salvinia, *Salvinia molesta* Mitchell, threatens aquatic insect communities and life cycle completion, specifically colonization, through mat formation and habitat changes. We examined how aerial colonization and assemblage structure of aquatic insects were affected by giant salvinia coverage. Mesocosms were established with three giant salvinia coverages, 25%, 50%, and 100%, and a native submerged macrophyte, 0% coverage; and environmental conditions and community structure were sampled monthly, over four months. After four weeks, all giant salvinia coverages reduced dissolved oxygen, pH, and light availability in the aquatic environment. In the 100% cover treatment, aquatic insect colonization was impeded, resulting in communities with lower abundance and richness, which were dominated by a coleopteran. The 25% and 50% giant salvinia coverages changed habitat complexity, which yielded different aquatic insect communities from the 0% and from 100% coverages. Regardless of the coverage, giant salvinia changed environmental conditions and putatively the 100% coverage disrupted the aquatic insect life cycle by limiting aerial colonization. This inability to complete their life cycle means aquatic insects cannot replenish themselves, leading to a diminished species pool and reduced energy potential. Our results highlight new, previously unreported, negative impacts from giant salvinia on ecosystem structure and function.

Keywords Dispersal · Disturbance · Energy transfer · Macroinvertebrate · *Salvinia molesta* · Submerged macrophyte

Introduction

In freshwater wetlands, aquatic insects are highly abundant and are closely associated with submerged macrophytes. Aquatic insect abundance, diversity, and biomass in lentic systems has been attributed to submerged macrophyte architecture and biomass (Warfe and Barmuta 2004; Rennie and Jackson 2005). Submerged macrophytes fill the water column, providing important substrate for aquatic insects to evade predation and acquire resources (Walker et al. 2013), and plant leaves with large surface area and branching offer

the greatest quantity of habitat and biomass (Warfe and Barmuta 2006; Hinojosa-Garro et al. 2010). Diverse macrophyte communities generate the critical habitat complexity, thus the structure of insect communities in wetlands can be directly related to macrophyte diversity (McAbendroth et al. 2005; Ferreiro et al. 2011; Thornhill et al. 2017).

Aquatic insects are an important component in the trophic structure of freshwater ecosystems. Within trophic webs, aquatic insects directly consume primary producers and organic matter, and serve as a resource for a variety of invertebrate and vertebrate predators, such as fish and waterbirds (Cummings 1973; Hershey et al. 2010; Tapp and Webb 2015; Mermillod-Blondin et al. 2020). Aquatic insect life history involves an egg and larval, or nymph, phases in the aquatic environment and an adult phase where they emerge from the water and disperse aerially (Merritt and Cummins 1996). Insects can be semi-aquatic, where the adult life stage cannot reenter the water after exiting, or fully aquatic, where adults live in the aquatic environment and can briefly exit the water

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then re-enter again. Aerial dispersal allows these invertebrates to colonize new locations, maintain communities, avoid drought, reproduce, and lay eggs (Blakely et al. 2006; Batzer and Boix 2016; Jourdan et al. 2019). During their adult phase aquatic insects are susceptible to predation by terrestrial organisms, such as birds (Murakami and Nakano 2002; Epanchin et al. 2010), bats (Salvarina et al. 2018), reptiles and amphibians (Sabo and Power 2002), and arthropods (Paetzold and Tockner 2005; Chari et al. 2020), therefore, they can directly transfer energy from the aquatic ecosystem to the terrestrial environment. Disruptions to aquatic insect communities potentially pose a risk to the transfer of energy to terrestrial ecosystems (Twining et al. 2018; Lewis-Phillips et al. 2020).

Introduction of non-native floating macrophytes threaten the structure of aquatic ecosystems. Giant salvinia, *Salvinia molesta* Mitchell (Salviniaceae) (hereafter referred to as salvinia), is a free-floating fern native to Brazil, and considered highly invasive in tropical and subtropical regions (Luque et al. 2014; CABI 2019). It typically invades still and slow moving waterbodies and forms a mat of vegetation on the water surface, completely covering the surface, acting as a barrier between the terrestrial and aquatic environments (Rommens et al. 2003). The mat limits light entering the water, reducing phytoplankton, periphyton, and submerged macrophyte abundances (Oliver 1993; Pinto and O'Farrell 2014; Motitsoe et al. 2020). The decreased phytoplankton and periphyton could limit the presence of consumers of those resources, and the loss of submerged macrophytes reduces insect habitat, creating a homogeneous habitat structure, resulting in decreased biodiversity (Thomaz and Cunha 2010; Coetzee et al. 2014). Furthermore, salvinia will decrease dissolved oxygen, through submerged macrophyte and phytoplankton loss and decomposition, stressing invertebrates, fish and other aquatic organisms (Marshall and Junor 1981; Flores and Carlson 2006; Coetzee and Hill 2020). Environmental filtering, the selecting of a subset of species from a regional species pool (Lebrija-Trejos et al. 2010), due to reduction in primary producers, habitat structure, and dissolved oxygen, could alter species occurrence and aquatic insect community structure.

The presence of a salvinia mat on the water surface may prevent aquatic insects from completing their life cycle by impeding emergence or colonization. If individuals were able to emerge from under the mat or arrive from surrounding habitats, they may not be able to recolonize or lay eggs in locations where salvinia is present, leading to communities that are different from uninvaded locations (De Szalay and Resh 2000). Limited studies have been conducted examining salvinia effects on aquatic insect communities (Motitsoe et al. 2020; Wahl et al. 2021), and to our knowledge no studies exist examining the effect of this invasive macrophyte on colonization of adult aquatic insects. We designed a mesocosm study

to examine the effect of salvinia on aerial colonization and community structure of aquatic insects. The objectives were to: 1) determine how salvinia affected aquatic insect aerial colonization, and 2) how salvinia cover affected insect community structure. It is hypothesized that the mat would impede aerial colonization of aquatic insects, and abundance and richness would decrease with increasing salvinia coverage, resulting in unique assemblage structure when salvinia covered 100% of the water surface.

Methods

Mesocosm Design

The study was conducted at the Louisiana State University (LSU) AgCenter Aquaculture Research Station in Baton Rouge, Louisiana, USA (30.368336, -91.183706). The research station has over 60 ponds, ~22 ha water surface, and is directly adjacent to the Mississippi River where wooded wetlands and natural ponds on the floodplain and in the river batters, provide sources of aquatic insect colonists. Mesocosms consisted of 568 L ($1.47 \times 0.99 \times 0.61$ m, $l \times w \times h$; surface area = 1.16 m²) tanks filled with pond (pH = 7.0) and rainwater. The study was conducted from 27 July through 14 November 2018. Monthly average temperature and precipitation in Baton Rouge during this period was 22.78 °C and 145 mm (National Oceanic Atmospheric Administration). To provide habitat for aquatic insects, two 3.8 L planting pots (0.08×0.16 m; $r \times h$), filled with 13 cm top soil (Organic Valley®, Garick LLC, Cleveland, OH, USA) covered with 3 cm sand, and ten shoots (0.3 m) of *Ceratophyllum demersum* L., were placed in each mesocosm. The macrophyte was collected from Blind River in Ascension Parish, Louisiana (52 km from mesocosm site; 30.103231, -90.727329). Following planting, *C. demersum* grew undisturbed for 21 d then salvinia coverage treatments were implemented. Salvinia was collected from outdoor ponds at the LSU AgCenter Reproductive Biology Center in St. Gabriel, Louisiana (13.1 km from mesocosm site). Once salvinia was added, an insecticide (22.8% lambda-cyhalothrin; half-life of ~7 days in water) was added to each tank, ensuring invertebrates had been removed. One mL of the insecticide was diluted in 1 L of water, and 25 mL of this solution was combined with ~250 ml of tank water then poured into the tank and mixed throughout. Routine visual inspection for insect mortality and removing of dead individuals confirmed the tanks were toxic. After ~30 days, insects were observed colonizing mesocosms without mortality and the study was initiated. Mesocosms were fertilized monthly with ammonium sulfate to a concentration of 3 mg L⁻¹ nitrogen. Mean water depth over the duration of the study was 0.44 m (± 0.04 ; $n = 160$).

Fish were excluded from the mesocosms, and fishless condition was maintained through the experiment.

Three salvinia cover treatments, 25%, 50% and 100%, and a reference *C. demersum* treatment, 0% cover, were used to test the effect of salvinia on aquatic insect colonization (40 mesocosms = 4 coverages × 10 replicates). Mature tertiary stage salvinia was used for all the three salvinia treatments, and a complete single plant layer mat was established in 100% coverage. Cover treatments were maintained for the duration of the study using a gridded frame. Once a week a frame with 56 equal sized squares was placed over each mesocosm and percent cover was calculated as the (number of squares containing at least half salvinia) / (total number of squares) × 100. Excess plant matter over the desired percent cover was rinsed in the tank to remove insects then discarded.

Environmental Conditions

Environmental conditions, water quality and light availability, were sampled monthly and coincided with aquatic insect assemblage sampling. Dissolved oxygen (DO), specific conductance, pH, and temperature were collected with a handheld multiprobe (Pro-DS5, YSI Incorporated, Yellow Springs, OH, USA). Light transmission through the water column was measured with a handheld light meter (MW700, Milwaukee Instruments, Rocky Mount, NC, USA). Light intensity was measured directly above and below (1 cm) the water surface, then at 10 cm increments until the bottom. Additionally, water temperature was recorded every 30 min using HOBO® pendant temperature loggers (accuracy ±0.53 °C; Onsite Computer Corporation, Bourne, MA 02532) and measured at 0.2 m depth. Ambient air temperature was recorded ~0.4 m above the ground, in the middle of the mesocosm array, and the logger was placed inside a Solar Radiation Shield (Onsite Computer Corporation, Bourne, MA 02532).

Aquatic Insects

Aquatic insect assemblages were sampled monthly, over four months, for a total of 160 community samples during the study (160 samples = 4 covers × 10 replicates × 4 months). Aquatic insects were sampled using a suitcase sampler, consisting of 0.31 × 0.31 m panels covered with 0.400 mm mesh. The panels were attached using a hinge and a chain, which standardized the trap to opening at 0.31 m. The sampling area was triangular prism shaped (0.31 × 0.31 × 0.31 × 0.31 m) that enclosed a volume of 0.009 m³ (Colon-Gaud and Kelso 2003). Sampling was done by lowering the sampler into *C. demersum* plants, once in place, the trap was closed, and vegetation sticking out of the edges of the sampler was trimmed away. If salvinia was present in the sampler with *C. demersum*, both plants were processed. Although it was

not possible to directly observe *C. demersum* in the 100% salvinia coverage, the sampler was deployed in the same way to sample salvinia and any *C. demersum* present.

Material from the sampler was processed immediately following collection. Samples were processed by flushing and rinsing plant material in 75 L plastic bin filled with water. Plant material removed from the bin was processed to determine dry biomass. If both vegetation types were collected, then biomass was processed separately. Plant material was dried in an oven for 72 h at 65 °C to measure dry mass. Aquatic insects rinsed from plant material and captured on a 0.500 mm sieve were then enumerated and identified to lowest practical taxonomic level, usually genus (Merritt and Cummins 1996, 2008).

Statistical Analysis

Analyses first examined differences among water quality and light availability between salvinia cover treatments over time. Next, multivariate and community analyses examined invertebrate response among salvinia cover and months. Analyses were conducted using R statistical software version 3.4.4 (R Core Team 2019).

Generalized linear models (GLM) compared water quality and light availability among fixed effects of salvinia cover and months. For all variables, the selected combination of link and distribution was determined by comparing candidate models and their fit statistics (\hat{c} and AIC). Log link, Gaussian distribution GLMs were used for DO, specific conductance, pH, and dry biomass. GLMs with log link, gamma distribution were used for temperature and light intensity.

For aquatic insect analysis, we removed taxa that had a total abundance of less than four individuals collected during the study. For comparability, we standardized species richness and abundance by per gram of dry plant biomass. GLMs with log link and gamma distributions were used to examine abundance per gram and richness per gram among salvinia cover and months. A multivariate generalized linear model (MGLM), with a negative binomial distribution and log link, was used to test for differences in aquatic insect community between habitats and among months (package mvabund; Warton et al. 2012). The model was adjusted for multiple comparisons using a step-down resampling procedure.

To visualize the assemblage level similarity between salvinia cover and among months, ordination of taxa was produced using nonmetric multidimensional scaling (NMDS) of a Bray-Curtis similarity matrix (k = 4) (Clarke 1993). Comparisons of exploratory ordinations (e.g., principal component analysis and detrended correspondence analysis) indicated that NMDS would be the appropriate analysis (package vegan, Oksanen et al. 2019). Analysis of variance using distance matrices (ADONIS) was used to test the solution from NMDS analysis (package Vegan, Oksanen et al. 2019).

Multivariate dispersion test showed that salvinia cover treatments, 0% ($\delta^2 = 0.080$), 25% ($\delta^2 = 0.087$), 50% ($\delta^2 = 0.089$) and 100% ($\delta^2 = 0.072$), were similar in multivariate distance within treatment, and appropriate for the analysis (Anderson and Walsh 2013). Association with salvinia cover (Ordiselect, package Vegan, Oksanen et al. 2019) and community dissimilarity between coverages (similarity percentage, SIMPER, package Vegan, Oksanen et al. 2019) also were examined.

Results

Environmental Conditions

Water quality variables varied between salvinia cover (Table 1). Salvinia cover, month, and the interaction of salvinia cover with month affected DO ($\chi^2 = 32.36$, $p < 0.01$). Dissolved oxygen was the greatest in the 0% cover treatment and decreased with increasing salvinia coverage. Variation in pH was explained by salvinia cover, month, and the interaction of salvinia cover with month ($\chi^2 = 36.04$, $p < 0.01$). As salvinia coverage increased, pH decreased, and the 100% coverage treatment had the lowest values. Specific conductance was affected by salvinia cover, month, and the interaction of salvinia cover with month ($\chi^2 = 46.63$, $p < 0.01$), with the 100% coverage treatment having decreased conductance. Water temperature was affected by salvinia cover, month and the interaction of salvinia cover with month

($\chi^2 = 75$, $p < 0.01$). Although not statistically analyzed, ambient air temperature decreased over the study duration, ranging from mean high of 29.20 °C in August to 13.83 °C in November, with mean temperature during the study being 23.66 °C (± 7.02). Mean water temperature over the study duration, regardless of salvinia cover, was 25.45 °C (± 5.85).

Light availability and dry biomass varied with salvinia cover. Unsurprisingly, light availability decreased with increased salvinia cover. The reduction in light availability increased with salvinia cover (Table 2). Variation in light availability was explained by salvinia cover, month, and the interaction of salvinia cover with month ($\chi^2 = 90.28$, $p < 0.01$). Light availability at 10 cm decreased as salvinia coverage increased and light under 1000% cover treatment was 766-times lower than 0% coverage treatment (39.7 ± 3.65 lx, t-value = -28.44 , $p < 0.01$).

Salvinia cover, month, and the interaction of salvinia cover with month affect total dry biomass collected from the suitcase sampler ($\chi^2 = 21.87$, $p = 0.01$). Total dry biomass increased with increasing salvinia cover, and 100% cover samples (23.03 ± 1.05 g (mean \pm SE)) were higher than 0% (2.58 ± 0.22 g, t-value = -10.30 , $p < 0.01$), 25% (4.47 ± 0.27 g, t-value = -11.00 , $p < 0.01$), and 50% (5.83 ± 0.34 g, t-value = -11.38 , $p < 0.01$) coverage treatments. Additionally, total dry biomass from the 50% salvinia cover was higher than 0% cover (t-value = -2.27 , $p = 0.02$). Dry biomass of *C. demersum* was highest in 25 (3.35 ± 0.22 g) and 50% (3.81 ± 0.24 g), followed by 0% (2.58 ± 0.22 g) then

Table 1 Mean values (\pm SE) of dissolved oxygen (DO), pH, specific conductance (Sp. Cond), and temperature (Temp) in 0%, 25%, 50%, or 100% salvinia cover in field mesocosms located in Baton Rouge, LA

Month	Salvinia Cover	DO (mg L ⁻¹)	pH	Sp. Cond. (μ S)	Temp. (°C)
August	0%	7.59 (± 0.48)a	9.56 (± 0.07)a	256.26 (± 8.10)a	28.66 (± 0.17)a
	25%	6.27 (± 0.11)b	9.00 (± 0.09)b	253.05 (± 5.65)a	27.70 (± 0.07)b
	50%	5.68 (± 0.32)b	8.30 (± 0.09)c	245.41 (± 12.12)a	27.90 (± 0.06)b
	100%	5.59 (± 0.17)b	7.94 (± 0.05)c	220.15 (± 12.48)a	28.64 (± 0.15)a
September	0%	7.98 (± 0.56)a	9.46 (± 0.15)a	266.14 (± 10.99)a	28.96 (± 0.33)a
	25%	5.06 (± 0.29)b	9.07 (± 0.15)ab	252.14 (± 7.26)a	27.77 (± 0.10)b
	50%	5.72 (± 0.28)b	8.58 (± 0.12)b	239.92 (± 13.49)a	28.05 (± 0.13)b
	100%	5.67 (± 0.09)b	7.97 (± 0.04)c	171.43 (± 13.77)b	29.07 (± 0.17)a
October	0%	7.00 (± 0.28)a	8.42 (± 0.13)a	188.05 (± 10.72)a	21.11 (± 0.07)a
	25%	4.91 (± 0.19)b	7.33 (± 0.05)b	157.73 (± 7.18)a	21.22 (± 0.02)a
	50%	5.45 (± 0.16)b	7.12 (± 0.06)b	138.54 (± 11.18)a	21.37 (± 0.05)a
	100%	6.43 (± 0.09)a	6.52 (± 0.13)c	83.43 (± 9.02)b	22.55 (± 0.06)b
November	0%	10.95 (± 0.20)a	8.56 (± 0.10)a	169.01 (± 9.40)a	13.36 (± 0.03)a
	25%	9.56 (± 0.10)b	7.66 (± 0.06)b	140.91 (± 6.15)a	13.13 (± 0.02)a
	50%	9.46 (± 0.09)b	7.45 (± 0.07)b	120.30 (± 10.99)a	13.11 (± 0.04)a
	100%	9.21 (± 0.06)b	6.54 (± 0.11)c	65.35 (± 7.19)b	13.81 (± 0.05)b

Letters indicate statistically significant differences for a variable within a sampling month

Table 2 Mean light intensity (lux) (\pm SE) measured in 0%, 25%, 50% or 100% salvinia coverages at different depths from field mesocosms located in Baton Rouge, LA

Depth	0%	25%	50%	100%
Above	59,390 (\pm 5269)	57,823 (\pm 4837)	60,400 (\pm 5443)	58,708 (\pm 5327)
1 cm	40,858 (\pm 3523)	39,543 (\pm 3310)	40,153 (\pm 3857)	4655 (\pm 828)
10 cm	30,415 (\pm 3098) ^a	17,658 (\pm 2362) ^b	8023 (\pm 1397) ^c	40 (\pm 3.65) ^d
20 cm	24,465 (\pm 2673)	11,528 (\pm 1860)	3743 (\pm 573)	20 (\pm 1.1)
30 cm	18,801 (\pm 2430)	4788 (\pm 963)	2867 (\pm 576)	17 (\pm 1.1)
Bottom	13,224 (\pm 2133)	259 (\pm 433)	1824 (\pm 345)	16 (\pm 1.2)

Light availability was measured at above the water surface, below (1 cm), and at 10 cm intervals until mesocosm bottom. Letters indicate statistical differences in light availability at 10 cm depth among salvinia coverages, based on generalized linear model (glm) output ($\chi^2 = 90.28$, $p < 0.01$)

100% (0.18 ± 0.05 g). Dry mass of salvinia was highest in 100% (22.85 ± 1.06 g) followed by 50% (2.01 ± 0.18) and 25% (0.94 ± 0.13).

Aquatic Insects

A total of 8383 aquatic insect specimens (2157 from 0%, 2246 from 25%, 2329 from 50% and 1651 from 100%) in 40 lowest practical taxonomic units (LPTs) in 28 families within 6 orders, were identified (Table S1). Eighteen of the 40 LPTs occurred less than four times, thus were removed prior to analysis. This was done because of the sensitivity of the multivariate analyses to associating rare taxa with a treatment. Standardized aquatic insect abundance per gram total dry biomass was highest in 0% cover and decreased as salvinia coverage increased (Fig. 1). Standardized aquatic insect richness per gram dry biomass was the lowest in 100% cover and increased with decreasing salvinia coverage (Fig. 1). Shannon-Weiner index identified 25% salvinia coverage (6.24) as the highest diversity, followed by 50% (5.13), 0% (3.78), then 100% (0.95), additionally, Pielou's evenness was the highest in 25% cover (0.54), followed by 50% (0.49), 0% (0.43), then 100% (0.33).

Relative insect abundance of standardized per gram of dry biomass varied with salvinia cover. Assemblages in 0% and 25% salvinia cover were Chironomidae (Diptera) dominant

with 66% and 45% relative abundance, respectively. In 0% salvinia cover, other LPTs $\geq 5\%$ relative abundance were *Berosus* sp. (Coleoptera; 14%), *Buenoa* sp. (Hemiptera; 6%), and *Sympetrum* sp. (Odonata; 7%), and in 25% cover *Berosus* sp. (Coleoptera; 5%), *Anax* sp. (5%; Odonata), *Erythemis* sp. (Odonata; 24%), *Sympetrum* sp. (Odonata; 9%). In the 50% and 100% salvinia cover treatments however, *Erythemis* sp. (Odonata; 53%) and *Scirtes* sp. (Coleoptera; 67%) were the dominant taxon, respectively. Other taxon above 5% relative abundance in the 50% salvinia cover were Chironomidae (Diptera; 23%) and *Sympetrum* sp. (Odonata; 9%), and in the 100% cover Chironomidae (Diptera; 17%) and *Erythemis* sp. (Odonata; 13%). Salvinia cover and month described aquatic insect LPT abundance. Significant differences in abundance were most explained by salvinia cover (16 of 22 LPTs; Deviance = 884.9, $p < 0.01$) followed by month (7 of 22 LPTs; Deviance = 313.3, $p < 0.01$; Table 3). Examination of associations of LPT with salvinia cover revealed that taxa responded differently to coverage treatments, however, most taxa abundances were lower in 100% cover, with the lone exception of *Scirtes* sp. (Table S2).

Overall, aquatic insect assemblage structure showed variation among salvinia coverages. Ordination of aquatic insect community (22 LPTs with ≥ 4 individuals) compositions found three distinct groups (Fig. 2 and Table S3), with 25% and 50% salvinia cover treatments being one similar group.

Fig. 1 Bar graphs of aquatic insect abundance per gram of total dry biomass (left) and richness per gram (right) (\pm SE) in 0, 25, 50, and 100% salvinia coverage treatments

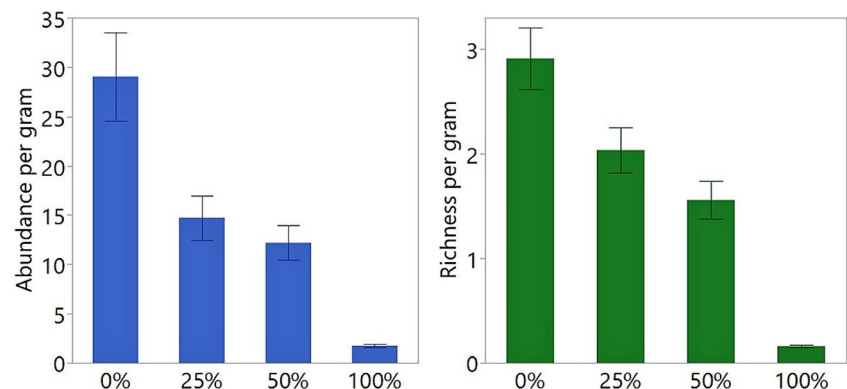


Table 3 Multivariate generalized linear model results (deviation test statistic, *p* value) of insect abundance examining taxa response to salvinia cover and month

Order	Family	Taxon	Salvinia Cover		Month	
			Dev.	p value	Dev.	p value
Coleoptera	Dytiscidae	<i>Brachyvatus</i> sp.	14.52	0.035	21.29	0.002
		<i>Dytiscus</i> sp.	3.43	0.473	5.91	0.556
		<i>Eretes</i> sp.	29.34	0.001	13.06	0.089
		<i>Laccophilus</i> sp.	26.78	0.001	10.97	0.157
Coleoptera	Halplidae	<i>Peltodytes</i> sp.	7.20	0.220	0.36	0.964
Coleoptera	Hydrophilidae	<i>Berosus</i> sp.	60.57	0.001	15.42	0.036
		<i>Helocombus</i> sp.	12.40	0.050	20.50	0.003
		<i>Laccobius</i> sp.	42.04	0.001	24.55	0.001
		<i>Tropisternus</i> sp.	41.59	0.001	11.99	0.123
Coleoptera	Noteridae	<i>Hydrocanthus</i> sp.	13.98	0.035	7.59	0.348
Coleoptera	Scirtidae	<i>Scirtes</i> sp.	175.89	0.001	30.45	0.001
Diptera	Ceratopogonidae	<i>Probezzia</i> sp.	4.82	0.473	2.17	0.964
Diptera	Chironomidae	–	46.98	0.001	12.01	0.123
Diptera	Culicidae	–	29.85	0.001	14.08	0.072
Ephemeroptera	Baetidae	<i>Fallceon</i> sp.	14.39	0.032	4.49	0.738
Hemiptera	Hebridae	<i>Hebrus</i> sp.	10.56	0.074	9.32	0.241
Hemiptera	Notonectidae	<i>Buenoa</i> sp.	68.37	0.001	1.93	0.964
Odonata	Aeshnidae	<i>Anax</i> sp.	54.73	0.001	24.05	0.001
Odonata	Coenagrionidae	<i>Coenagrion</i> sp.	26.22	0.001	9.02	0.241
Odonata	Corduliidae	<i>Cordulia</i> sp.	11.74	0.065	51.59	0.001
Odonata	Libellulidae	<i>Erythemis</i> sp.	76.40	0.001	10.13	0.199
		<i>Sympetrum</i> sp.	113.11	0.001	12.44	0.110

Taxon names are italicized for proper nomenclature

Residual STRESS was 0.111, which is within ranges for interpretability (Clarke 1993). The first axis presumably explained community differences between 100% salvinia cover and the other cover treatments. The second axis likely explained community differences between 0% salvinia cover and the two-remaining salvinia cover treatments, 25% and 50%. Salvinia cover, month, and the interaction of cover with month (ADONIS $F = 3.48$, $R^2 = 0.11$, $p < 0.01$), explained variation in aquatic insect communities. Habitat association analyses identified *Buenoa* sp. (Hemiptera) and *Eretes* sp. (Coleoptera) as associated with 0% salvinia cover; *Laccophilus* sp. (Coleoptera), *Laccobius* sp. (Coleoptera), *Hydrocanthus* sp. (Coleoptera), and *Erythemis* sp. (Odonata) with the 25% or 50% cover treatments, and *Scirtes* sp. (Coleoptera) with 100% salvinia cover (Table S3). Similarity percentages (SIMPER) identified 73.3% dissimilarity between 0% and 100% cover groups, 71.2% dissimilarity between 0% and 25% cover groups, and 71.8% dissimilarity between 0% and 50% cover groups. Additionally, SIMPER identified 64.4% dissimilarity between 25% and 50% cover groups, 66.7% dissimilarity between 25% and 100% cover groups, and 67.2% dissimilarity between 50% and 100% cover groups.

Discussion

We found evidence that salvinia changed environmental conditions, including available habitat, and limited aerial colonization when a full mat was present, resulting in assemblages containing fewer individuals and lower richness of aquatic insects. A decrease in aquatic insect abundance and richness, with increased salvinia cover, supported our hypothesis, but aerial colonization was impeded only when salvinia covered 100% of the water surface. 0% and 100% salvinia coverages contained unique aquatic insect assemblages, while 25% and 50% coverages yielded communities there were similar to one another but different from the previous treatments.

Individual taxa responded to salvinia cover treatments differently. Chironomidae (Diptera) is an abundant and common aquatic insect in freshwater wetlands (Kang and King 2013; Mercer et al. 2017; Weller and Bossart 2017) and had the highest abundance in the 0% salvinia cover, however, their abundance decreased when salvinia was introduced. This decline may have been due to changes in environmental conditions, or to increased predation on Chironomidae, which could be supported by the observed increased abundance of predators, *Erythemis* sp., *Sympetrum* sp., and *Anax* sp., (Odonata) in

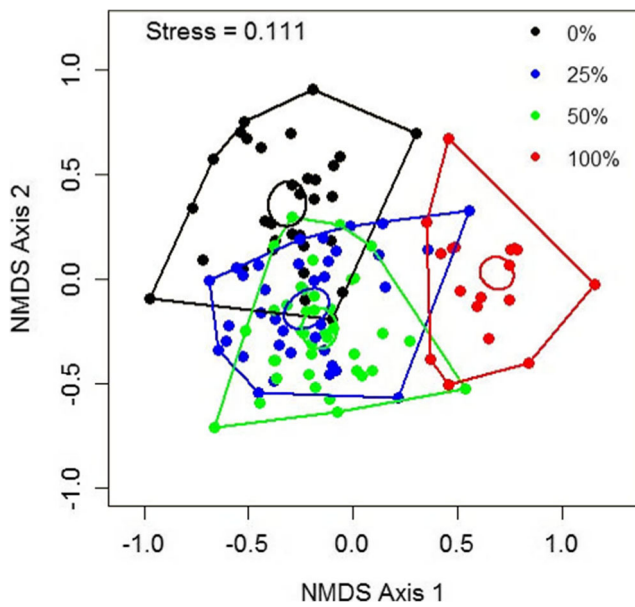


Fig. 2 Nonmetric multidimensional scaling (NMDS) ordination plot of aquatic insect assemblage similarity collected from mesocosms differing in salvinia coverages located in Baton Rouge, Louisiana. Points are individual samples and distance between points represents assemblage similarity, with most similar samples being located closest together. Colors reflect percent salvinia cover treatments 0%, black, 25%, blue, 50%, green, and 100%, red. Circles represent 95% confidence interval around the centroid for salvinia cover groups, and a line connects sites furthest from the centroid within a group. Analysis of deviance (ADONIS) identified significant differences in community similarity (ADONIS $F = 3.48$, $R^2 = 0.11$, $p < 0.01$), identifying three different communities, 0%, 25–50%, and 100% community groups

the 25%–50% coverage group. The increase in predator abundance in both 25% and 50% coverage treatments could have been made possible by an increase in habitat complexity (Huikkonen et al. 2019). The only taxon to be positively associated with salvinia, specifically 100% cover, was *Scirtes* sp. (Scirtidae: Coleoptera), which has been found in *Salvinia minima* Baker in southern Louisiana (Parys et al. 2013). Individuals in the Scirtidae family feed on fine particulate organic matter and decaying plant material, such as herbaceous and wood detritus; additionally, larvae breath atmospheric air and have terrestrial life phases (Ruta et al. 2018; Watts and Zwick 2019). Thus, salvinia could be a food source and provide access to atmospheric air for *Scirtes* sp.

Salvinia mats reduce horizontal light reflection, thus adults may not recognize the aquatic environment leading to fewer number of taxa colonizing the habitat. Most aquatic insects are polarotactic, attracted to reflected light, and adults detect water surface through horizontal polarization of light reflected from the water surface (Schwind 1995; Horváth and Csabai 2014; Heinloth et al. 2018). Light reflecting horizontally off the water has a high degree of linear polarization giving it a dark appearance, which attracts adult aquatic insects (Horváth 1995; May 2019). The detection of water varies with aquatic insects, with some species of dragonflies (Odonata) being able

to detect open water at lower degrees of linear polarization than species of Ephemeroptera and Diptera (Kriska et al. 2009).

Habitat complexity differences among cover treatments may also explain variation in aquatic insect community structure. Ordination analysis identified three different aquatic insect groupings, which relate to habitat complexity. The 0% and 100% salvinia covers contain one habitat type, *C. demersum* or salvinia, while 25%–50% coverages had both habitat types present. Increased habitat complexity, due to the addition of salvinia with *C. demersum*, offers additional niches, promoting species coexistence through reduced competition (Huston and DeAngelis 1994; Smith et al. 2014; Casartelli and Ferragut 2018), and increased refuge from predation (Diehl and Kornijów 1998; Wolters et al. 2018). At moderate densities, the invasive floating plant *Pontederia crassipes* Martius has shown to increased abundance and diversity of aquatic invertebrates within the root of the macrophyte, due to increased habitat heterogeneity and complexity provided by the plant (Masifwa et al. 2001; Villamagna and Murphy 2010).

The flow of energy through the aquatic and adjacent terrestrial ecosystems could be impaired due to salvinia. The change in aquatic insect community structure, due to environmental filtering, has been observed in salvinia (Motitsoe et al. 2020), and other floating invasive macrophytes, such as *Lemna minuta* Kunth (Ceschin et al. 2020), *Pistia stratiotes* L. (Coetzee et al. 2020), and *P. crassipes* (Coetzee et al. 2014). Invasion of *P. crassipes* has shown to impact food web structure through bottom-up processes because of alterations to phytoplankton, macrophyte, and macroinvertebrate communities (Schultz and Dibble 2012; Wang and Yan 2017). Fish and waterfowl select habitat based on aquatic insect abundance (Little and Budd 1992; Diehl and Kornijów 1998; Schummer et al. 2008; Tománková et al. 2013), and wading birds select foraging locations based on fish abundance (Gawlik 2002; Kloskowski et al. 2010), thus, alterations to aquatic insect community structure could change habitat use and decrease ecosystem productivity. Reduction in aerial colonization could also result in a decreased ecosystem productivity as the insect community would not be replenished and further change community structure from uninvaded locations.

Salvinia is a fast growing macrophyte that forms expansive mats and rapidly changes local environmental conditions. In favorable lake conditions, salvinia can double its biomass and surface coverage in 2–4 days (Finlayson 1984; Room and Thomas 1986), with mats covering hundreds of square meters of water within a couple months following introduction (Mitchell 1969; Mitchell and Tur 1975). Aquatic insects must cope with the sudden changes in water quality and habitat. This would presumably change environmental filtering and species interactions, leading to a change in aquatic insect

community structure (Fisher and Kelso 2007; Thomaz et al. 2008; Calizza et al. 2017). Given the growth rate in unmanaged field conditions, invaded locations could quickly become 100% covered in salvinia, therefore, results from our 25–50% treatments represent ephemeral, transitional communities, which would ultimately result in a mat covering the waterbody completely.

This study highlights impacts from salvinia that have not been previously examined. The presence of a full salvinia mat limited aquatic insect aerial colonization, resulting in structure that was different from assemblages in the native submerged macrophyte. This change to the structure of this lower trophic level could have implications to energy flow in aquatic and adjacent terrestrial ecosystems, indicating larger implications from salvinia than previously understood. Our results currently represent a local phenomenon, but the results should be explored further with additional research examining if similar results occur in other regions, or in a field setting, and how energy transferred to higher trophic levels is impacted by changes in community structure of aquatic insects. Evidence from this study, and invasive plant studies (e.g., Watkins II et al. 1983; Villamagna and Murphy 2010), suggest that management to suppresses and maintain low to moderate levels of salvinia may conserve biodiversity and ecosystem services. Where applicable, biological control of floating invasive plants has been successful restoring aquatic habitat (Coetzee et al. 2020, Motitsoe et al. 2020).

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Data Availability Data will be available on the Dryad Digital Repository.

Code Availability Not applicable.

Declarations

Ethics Approval Not applicable.

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