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The influence of Chinese tallow (*Triadica sebifera*) leaf litter on water quality and microbial community composition

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Abstract Previous studies have shown that moderate concentrations of Chinese tallow leaf litter can quickly reduce dissolved oxygen and pH in the aquatic environment. While these studies mostly focus on its effects on the performance of amphibians, this study focuses on determining the causes of deoxygenation and acid water. We also examined the effects of Chinese tallow litter on other water quality parameters and how changes may influence microbial communities in aquatic environments. We used laboratory and outdoor experiments to demonstrate the effects of Chinese tallow litter on aquatic chemistry. Additional laboratory studies investigated litter quality and soluble nutrients. We tested the effects of an antimicrobial agent on microbial activity in Chinese tallow litter treatments. Outdoor mesocosms were used to assess the impact of Chinese tallow and native litter monocultures on aquatic chemistry and microbial community composition. We measured water chemistry and sampled mesocosms for microbial rRNA genes. We found evidence that biological mechanisms are causing deoxygenation, while chemical mechanisms may be influencing acid water. Chinese tallow litter was of different quality, decomposed faster and leached more soluble nutrients than native species. Chinese tallow litter traits appear to have different effects on microbial activity and community composition than native litter. Our results suggest that Chinese tallow litter can have an impact on aquatic chemistry and the composition of aquatic microbial communities as it replaces native species in southern forests. The implications of our results are potential shifts in aquatic ecosystem processes.

Keywords Invasive plant litter · Chinese tallow · Litter quality · Microbial community composition · Aquatic chemistry · Invasive plant nutrients

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Introduction

Several non-native plant species have invaded southern forests of the USA (Miller 1995, 2003; Webster et al. 2007). Many of these non-native plants have spread throughout forested landscapes, degrading forest habitats and reducing native species at an alarming rate (Miller et al. 2015). In some regions, the invasion process has changed forest composition from a mixed, native community to single, non-native tree species (Leonard 2008). Shifts in the quality and quantity of litter inputs are expected to have effects on ecosystem processes and community structure (Rubbo and Kiesecker 2004). Non-native plants have altered nutrient cycling rates (Ehrenfeld 2003) and contributed to changes in native soil microbial communities (Mummey and Rillig 2006; Yannarell et al. 2011).

Leaf litter inputs to aquatic systems have influenced variations in water chemistry and community composition in streams (Abelho 2001; Canhoto and Laranjeira 2007), ponds (Leonard 2008; Stoler and Relyea 2015) and marshes (Farrer and Goldberg 2009). Changes in water quality and community composition are largely driven by species-specific differences in litter quality (Canhoto and Graca 1996; Stoler and Relyea 2011, 2015) and litter leachate (Fanin et al. 2014; Wymore et al. 2017), suggesting that any changes in forest composition may have an effect on proximate aquatic systems (Yavitt and Williams 2015). Wetland habitats across southern forests appear to be especially vulnerable to non-native plant invasions (Zedler and Kercher 2004).

A non-native tree species of particular concern within the southern forests of the USA is the Chinese tallow tree (*Triadica sebifera*). Chinese tallow has invaded the southeastern coastal plains from North Carolina to Florida and into Texas where it can be found throughout inland forests, wetlands, and coastal prairies (Miller 1995; Bruce and Cameron 1997; Renne 2001; Zedler and Kercher 2004; Wang et al. 2011). The abundance of Chinese tallow has rapidly increased across the landscapes of Louisiana and eastern Texas, where it is now the fifth most common tree species (Oswalt 2010) and the most prevalent invasive tree in eastern Texas (Herbert 2005; Gan et al. 2009; Wang et al. 2011, 2014). Chinese tallow has reduced native tree species in bottomland hardwood forests (Camarillo et al. 2015), converted coastal grasslands into single-species woodlands (Bruce et al. 1995), and has contributed to the degradation of wetlands throughout the Gulf Coast (Herbert 2005).

Several attributes contribute to the Chinese tallow's success in wetland habitats. For instance, although the Chinese tallow can be found in dry, upland areas, the invasive tree thrives in mesic to wet soils (Jubinsky and Anderson 1996; Barrilleaux and Grace 2000; Fan et al. 2012). Chinese tallow can tolerate flooding (Jones and Sharitz 1990), shade (Jones and McLeod 1989), and can prosper in both fresh and saline soils (Conner 1994). Seeds are dispersed by birds (Renne et al. 2000) and flooding (Jubinsky and Anderson 1996). Once established, seedlings can form dense monospecific stands, often outgrowing native species within the first year (Bruce et al. 1995). Abscised leaf litter has a rapid decomposition rate relative to native species, quickly releasing nutrients (Cameron and Spencer 1989) and tannins (Cameron and LaPoint 1978; Cameron and Spencer 1989), self-facilitating its own growth.

Chinese tallow leaf litter can have a deoxygenating effect and can reduce pH in the aquatic environment, negatively affecting the performance of aquatic species (Leonard 2008). Deoxygenation and pH reduction occur shortly after Chinese tallow litter is immersed into water, and the effects are directly related to litter concentration (Adams and Saenz 2012). Even modest amounts of Chinese tallow litter can negatively influence amphibian hatching success (Adams and Saenz 2012), larvae survival (Cotten et al. 2012; Saenz et al. 2013) and behavior (Saenz and Adams 2017). We suspect that microbiological and/or chemical (polyphenolics) mechanisms are involved in reducing dissolved oxygen and pH in the water column (Tremolieres 1988; Chergui 1997; Gulis and Suberkropp 2003; Canhoto and Laranjeira 2007).

We propose that the introduction of Chinese tallow litter is stimulating microbial activity, thus altering aquatic chemistry and potentially influencing shifts in microbial community composition (Gulis and Suberkropp 2003; Yavitt and Williams 2015; Findlay 2010). We performed a series of laboratory and outdoor experiments to better understand how biological mechanisms may be playing a role in the reduction of dissolved oxygen and pH after Chinese tallow litter enters the aquatic environment and to understand how single-species litter can affect water chemistry, microbial activity and microbial (bacterial and fungi) community composition. We hypothesized that dissolved oxygen and pH are reduced by stimulated microbial activity (aerobic respiration) from the introduction of Chinese tallow litter and its leachates. We further hypothesized that Chinese tallow litter would differentially alter the composition of aquatic microbial communities in comparison with native litter.

Methods

Leaf collection

Leaf litter from the non-native Chinese tallow (*Triadica sebifera*), the native water oak (*Quercus nigra*), and native loblolly pine (*Pinus taeda*) were collected and used in separate laboratory and outdoor studies to assess the comparative impacts of single-species litter on aquatic chemistry and microbial community composition. Water oak and loblolly pine tree species are native throughout east Texas, commonly found in forested wetland systems, and abundant throughout southern forests of the USA (USDA 2020). We hand-collected fallen leaves from eastern Texas (Nacogdoches County) during November–December 2014. Recently senesced leaves that looked fresh were selected over those that looked too damaged or weathered. Litter samples (separated by species) were air-dried to constant weight in plastic buckets (30 cm diameter × 28 cm depth) and kept in a climate-controlled room for 60 days before being used for laboratory and outdoor experiments. Previous studies have found that storing Chinese tallow leaves for 12 months had no effect on measured chemical changes when compared to freshly fallen Chinese tallow leaves that had been submerged in water; therefore, short-term storage should not influence results (Saenz et al. 2013).

All laboratory experiments were conducted at the US Forest Service Southern Research Station Laboratory between March and June 2015. Analysis of samples took place at the Soil, Plant and Water Analysis Laboratory, Stephen F. Austin State University, Nacogdoches, Texas, USA, between March and June 2015.

Laboratory antimicrobial experiment

To help determine whether biological activity is causing dissolved oxygen and pH changes associated with the introduction and decomposition of Chinese tallow litter, we employed a benchtop laboratory study using plastic buckets (18 cm diameter × 18 cm depth) filled with 2 L of de-chlorinated tap water. We then used four treatments to test the hypothesis that microbiological activity is the cause of changes in dissolved oxygen and pH when Chinese tallow is introduced into the aquatic environment. We used 10% formalin as an antimicrobial agent to prevent microbial respiration from consuming dissolved oxygen and creating carbonic acid in the water column. The following four treatments were used: treatment 1-de-chlorinated tap water only (2 L), treatment 2- de-chlorinated tap water (2 L), air-dried Chinese tallow litter (4 g), treatment 3-de-chlorinated tap water (2 L), air-dried Chinese tallow litter (4 g), formalin (15 mL); treatment 4- de-chlorinated tap water (2 L), formalin (15 mL). We replicated each treatment ten times for a total of 40 experimental units. All experimental units were set up at the same time for a period of 48 h. Dissolved oxygen (mg/L) and pH were measured and recorded after 48 h using a portable Quanta© Hydrolab water monitoring meter.

Mesocosms experiment

To assess the effects of Chinese tallow and native litter on aquatic chemistry and microbial community composition, we employed a mesocosm study to simulate a wetland/aquatic habitat. Prior experiments demonstrated that mesocosms can be helpful in determining the effects of Chinese tallow leaf litter on aquatic species (Cotten et al. 2012; Saenz et al. 2013). A similar approach was used for this study. Our mesocosm experiment was conducted at the Stephen F. Austin Experimental Forest, part of the Angelina National Forest, in eastern Texas (Nacogdoches County), USA, between March 2, 2015, and June 22, 2015 (16 weeks in total). We used a completely randomized design with four treatments that were replicated 10 times for a total of 40 experimental mesocosms. For our mesocosms, we used 100-L plastic pools (1.2 m diameter × 0.3 m height). Four 9-mm holes were drilled near the top in each pool to prevent the overflow of leaves during precipitation events. All pools were exposed to the same temperature, light cycles and weather conditions. We filled each pool with 80 L of local well water on February 27, 2015, and added 160 g (for a final concentration of 2 g/L) of single-species leaf litter to each of the pools on March 2, 2015. Our experimental mesocosms included single leaf litter monocultures of Chinese tallow (*Triadica sebifera*), water oak (*Quercus nigra*), loblolly pine (*Pinus taeda*) and control (water only) treatments. We based our litter concentration on Leonard (2008), who found a mean standing stock of 1.27 g Chinese tallow leaf litter/L of water in a natural pond, and on Adams and Saenz (2012), who found that 1–2 g/L Chinese tallow litter can reduce dissolved oxygen and influence acidic conditions within a 48-h period.

We measured water quality parameters: temperature (°C), dissolved oxygen (mg/L), pH, turbidity (NTU), salinity (PSS), oxidation–reduction potential (mv) and collected water samples for DNA analysis of microbial communities for a total of 16 weeks. Water quality parameters were measured with a Hach Hydrolab Quanta© hydrometer. Water samples were collected by drawing 30 mL of mesocosm water into sterile syringes and pushing the water samples through sterile cellulose acetate syringe filters (0.45 µm, VWR). We began measuring water quality parameters and collected water samples for microorganism identification on March 2, 2015, and continued measuring and sampling mesocosm water every 24 h, for 3 days (March 2, 3, 4). We then reduced the collection of water quality parameters and water samples to once weekly, for 16 weeks, beginning on March 10, 2015, and ending on June 22, 2015. All mesocosms were covered with 30% knitted shade cloth to exclude wildlife disturbances and/or debris and litter input from surrounding forest trees. Temporary removal of shade cloth occurred during water parameter measurements and the collection of water samples.

Water samples collected from our mesocosms were sent to the Research and Testing Laboratory (Lubbock, Texas, USA) for high-throughput sequencing (Illumina MiSeq) of rRNA genes for microorganism (16S for bacteria and 18S for fungi) identification. Only samples collected from the initial (March 2, 2019), 48-h (March 5, 2015), and 16-week (June 22, 2019) periods were used in this study due to funding limitations. Two operational taxonomic unit (OTU) matrices (bacteria and fungi) were delivered as the product, listing bacterial and fungi operational taxonomic units that were found in each sample, for each of the three time periods.

Decomposition comparison

An in situ litterbag approach was used to compare how quickly Chinese tallow can decompose in a wetland compared to native litter species. Our decomposition comparison of mean mass loss of native and non-native litter species was conducted between March 2, 2015, and June 22, 2015, in a forested wetland located within the Stephen F. Austin Experimental Forest, part of the Angelina National Forest, in eastern Texas (Nacogdoches County), USA. We secured 60 nylon litterbags (20 cm × 25 cm with 2-mm^2 mesh) with 5 g of air-dried, single-species litter (20 litterbags × 3 species). All bags were simultaneously deployed in the forested wetland habitat and secured with stakes. Ten litter bags of each species (30 litter bags total) were retrieved after 1 and 16 weeks of in situ decomposition in the wetland. Litter bag samples retrieved from the wetland were air-dried and re-weighed to determine mass lost after each decomposition period.

Litter quality comparison

We compared carbon, along with macro- (N, P, K, Ca, Mg, S) and micro- (Ca, Mg, S, Fe, Mn, Cu, B) nutrients contained in Chinese tallow and native species leaf litter. We ground five grams of air-dried litter from each litter species, digested in a nitric acid solution (EPA Method 200.7) and analyzed with an inductively coupled plasma optical emission spectrometer (ICP-OES-7400 Thermo Scientific, Dual View, Nacogdoches, Texas, USA). Carbon and nitrogen were determined with a C/N analyzer (Leo C/N model 628, Nacogdoches, Texas, USA). Five grams of litter samples were replicated ten times for each litter species.

Soluble element comparison

We compared soluble nutrients released from three litter treatments (Chinese tallow, water oak, loblolly pine) submerged in de-chlorinated water for a 48-h period. We used plastic buckets (18 cm diameter × 18 cm depth) filled with 2 L of de-chlorinated tap water and 4 g of either Chinese tallow, water oak, or loblolly pine leaf litter. We replicated each treatment 10 times for a total of 30 buckets. After 48 h, we collected 250 mL of water from each bucket with prewashed, plastic bottles. We observed and recorded Munsell color of water samples. Water samples were then analyzed for sodium, along with macro- (N, P, K, Ca, Mg, S) and micro- (Fe, Mn, Cu,

B) nutrients using nitric digestion (SPC Scientific; EPA Method 200.7) followed by analysis using an ICP-OES 7400 (Thermo Scientific, Dual View analyzer, Nacogdoches, Texas, USA).

Statistical analysis

An analysis of variance of the treatment means (aquatic chemistry parameters) was determined at the initial (March 2, 2015), 48-h (March 4, 2015) and 16-week (22 June 2015) periods with the PROC GLM program of SAS 9.2 (SAS Institute, Inc., 2002). We determine differences in microbial community composition associated with time and litter type, using R-3.2.3 (R Core Team, 2015) statistical software along with the VEGAN package and its allies. We used a Bray–Curtis distance matrix to determine the dissimilarity of microbial communities between samples and a permutation multivariate analysis (PERMANOVA) of aquatic chemical parameters. A stress plot function in R was used to determine non-metric or linear fit. Non-metric multidimensional scaling ordinations based on the Bray–Curtis distance matrix were used to visualize dissimilarities of microbial composition. Richness, evenness and the Shannon–Weiner diversity Index were used to evaluate microbial community assembly. Microbial richness, evenness and diversity means were compared at the $\alpha = 0.05$ level using Tukey's studentized range test. An ANOVA was used to compare the treatment means in the antimicrobial experiment, litter quality comparison, soluble nutrients comparison and decomposition comparison at the 0.05 level using Tukey's studentized range test (SAS 9.2, SAS Institute, Inc., 2002).

Results

Laboratory antimicrobial activity experiment

Dissolved oxygen and pH differed significantly among treatments ($F_{[3, 36]} = 22{,}887$, $P < 0.05$; $F_{[3, 36]} = 1480$, $P < 0.005$, respectively) after a 48-h decomposition period. Chinese tallow + de-chlorinated water treatments had the lowest mean dissolved oxygen (DO = 1.28 mg/L) and lowest mean pH (pH = 5.39) (Table 1). Chinese tallow litter + formalin + de-chlorinated water treatments prevented a significant reduction of dissolved oxygen (DO = 7.88 mg/L), but did not prevent a reduction in pH (pH = 5.37), suggesting that biological activity may not be the cause of pH reduction. Formalin + de-chlorinated water treatments had no effect on dissolved oxygen (DO = 8.61 mg/L) or pH (pH = 7.77) and were no different than results from de-chlorinated water only treatments. These results suggest that formalin has no influence on dissolved oxygen or pH and supports our hypothesis that dissolved oxygen is reduced by microbiological activity. Results fail to support the hypothesis that microbial activity reduces pH.

Mesocosm water chemistry

Mesocosm water chemistry trends over the 16-week period were similar across treatments. Mesocosm

Table 1 Results of one-way ANOVA and summary of post hoc Tukey–Kramer test comparing treatment means in our experimental, antimicrobial benchtop laboratory study, using plastic buckets (30 cm × 30 cm), de-chlorinated water (4 L), Chinese tallow litter (2 g), and 10% formalin (15 mL) as the antimicrobial agent. Means in the same row with different letters are significantly different ($P < 0.05$)

	One-way ANOVA results			Post hoc Tukey–Kramer results mean (SE)			
Parameter	df	F	p-value	De-chlorinated tap water	De-chlorinated tap water + Chinese tallow litter	De-chlorinated tap water + Chinese tallow litter + formalin	De-chlorinated tap water + formalin
Dissolved oxygen (mg/L)	3, 36	22,887	< 0.05	8.70 (0.07) a	1.28 (0.07) c	7.88 (0.09) b	8.61 (0.07) b
pH	3, 36	1480	< 0.05	7.80 (0.02) a	5.39 (0.14) b	5.37 (0.18) b	7.77 (0.01) a

water temperature varied consistently with ambient air temperature over time. Dissolved oxygen varied with ambient air temperature over time but differed between litter types. Water pH varied with time but differed between litter types. Turbidity generally increased with time and differed between litter types. Salinity decreased with time. Oxidation–reduction varied over time and differed between Chinese tallow and litter treatments.

At the initial period, mean water temperature was 7.8–7.9 °C, dissolved oxygen from 12.2 to 12.4 mg/L, pH from 8.9 to 8.9, turbidity from 9.1 to 11.7 NTU, salinity from 17 to 18 PSS, and oxidation–reduction was a mean 55 mv in Chinese tallow treatments and ranged from 83 to 89 in native and control treatments (Table 2). Water chemistry differed between litter treatments 48 h after litter immersion. Dissolved oxygen, pH and turbidity differed significantly ($F_{[3,\ 35]} = 651$, $P < 0.005$; $F_{[3,\ 35]} = 128$, $P < 0.05$, and $F_{[3,\ 35]} = 6.9$, $P < 0.005$, respectively) between litter treatments at the 48-h time period (Fig. 1). Mean dissolved oxygen concentrations in control treatments were 10.2 mg/L and lowest in Chinese tallow litter treatments (DO = 3.5 mg/L), followed by water oak litter treatments (DO = 6.0 mg/L), then loblolly pine litter treatments (DO = 8.7 mg/L) after a 48-h period. Acidic conditions did not develop in any of the mesocosms after a 48-h period; however, mean pH was lowest in Chinese tallow litter treatments (pH = 8.0), followed by water oak litter treatments (pH =

Table 2 Results of one-way ANOVA and summary of post hoc Tukey–Kramer test comparing the means of temperature (°C), dissolved oxygen (mg/L), pH, turbidity (NTU), oxidation–reduction potential (mv), salinity (PSS), from control, loblolly pine, water oak and Chinese tallow treatments the initial, 48-h and 16-week time periods. Means in the same row with different letters are significantly different ($P < 0.05$)

Parameter	One-way ANOVA results			Post hoc Tukey–Kramer results mean (SE)			
	df	F	*p*-value	control	loblolly pine	water oak	Chinese tallow
Initial time period							
Temp (°C)	3, 35	0.21	0.89	7.8 (0.4) a	7.8 (0.4) a	7.9 (0.4) a	7.9 (0.4) a
DO (mg/)	3, 35	0.28	0.84	12.3 (0.4) a	12.2 (0.4) a	12.4 (0.3) a	12.3(0.4) a
pH	3, 35	0.10	0.96	8.9 (0.2) a	8.9 (0.2) a	8.9 (0.2) a	8.9 (0.1) a
Turbidity (NTU)	3, 35	1.45	0.24	9.1 (2.2) a	11.7 (3.1) a	9.7 (2.2) a	10.2 (4.0) a
ORP (mv)	3, 35	3.04	0.04	89 (26) a	85 (22) a	83 (27) a	55 (32) a
Salinity (PSS)	3, 35	0.55	0.65	0.18 (0.01) a	0.17 (0.01) a	0.17 (0.01) a	0.17 (0.01) a
48 h time period							
Temp (°C)	3, 35	0.59	0.63	15.9 (0.7) a	16.0 (0.9) a	16.0 (0.9) a	16.4 (1.1) a
DO (mg/)	3, 35	651	< 0.05	10.2 (0.2) a	8.7 (0.3) b	6.0 (0.4) c	3.4 (0.7) d
pH	3, 35	128	< 0.05	8.9 (0.1) a	8.6 (0.1) b	8.4 (0.1) c	8.0 (0.1) d
Turbidity (NTU)	3, 35	6.89	< 0.05	4.8 (0.8) a	4.9 (0.6) a	5.5 (1.4) a	7.6 (2.5) b
ORP (mv)	3, 35	0.49	0.74	20 (11) a	24 (8) a	31 (7) a	29 (6) a
Salinity (PSS)	3, 35	8.94	< 0.05	0.18 (0.01) a	0.17 (0.01) b	0.18 (0.01) a	0.19 (0.01) a
16 week time period							
Temp (°C)	3, 35	0.24	0.86	35.1 (1.9) a	35.2 (2.2) a	35.8 (2.0) a	35.5 (2.4)
DO (mg/)	3, 35	8.19	< 0.05	7.4 (0.2) a	7.3 (0.3) a	7.2 (0.4) a	7.8 (0.3) b
pH	3, 35	28.49	< 0.05	9.5 (0.2) a	9.3 (0.3) a	9.3 (0.4) a	10.4 (0.2) b
Turbidity (NTU)	3, 35	34.47	< 0.05	14.1 (2.6) a	21.3 (6.1) b	21.2 (6.8) b	38.5 (5.) c
ORP (mv)	3, 35	2.12	0.11	−7.5 (18) a	−1.4 (19) a	−5.0 (23) a	−26 (31) a
Salinity (PSS)	3, 35	65,535	–	0.02 (0.00) a	0.02 (0.00) a	0.02 (0.00) a	0.02 (0.00) a

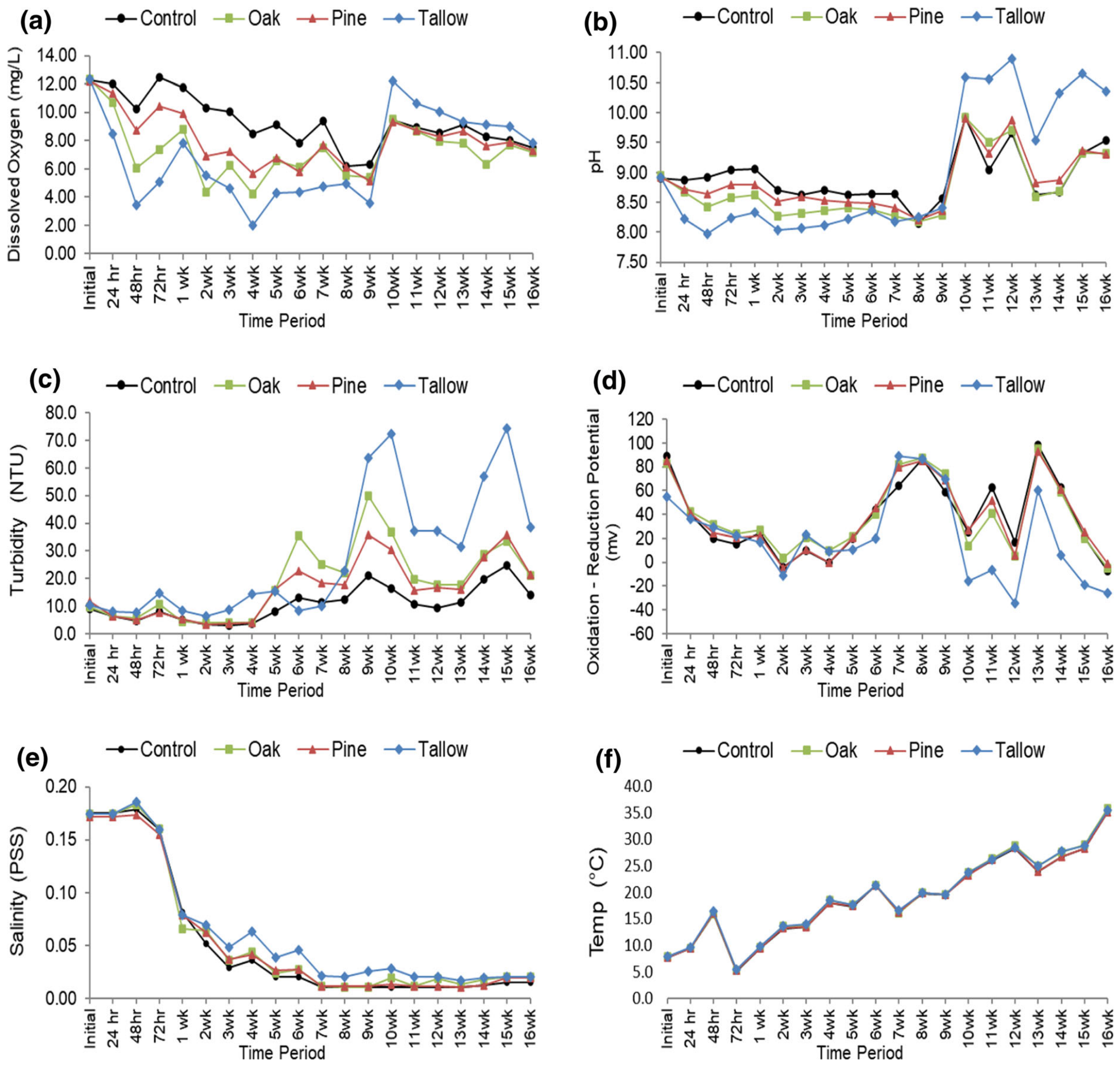


Fig. 1 Mean **a** dissolved oxygen (mg/L), **b** pH, **c** turbidity (NTU), **d** oxidation–reduction potential (mv), **e** salinity (PSS) and **f** temperature (°C) over the 16 week experiment in Chinese tallow, water oak, loblolly pine and control treatments

8.4), then by loblolly pine litter treatments (pH = 8.6). Mean pH (pH = 8.9), while control treatments remained unchanged after a 48-h period. Turbidity decreased in all mesocosm after 48 h and was highest in Chinese tallow litter treatments (7.6 NTU), followed by water oak litter treatments (5.5 NTU), then loblolly pine litter treatments (4.9 NTU). Turbidity in control treatments after a 48-h period was 9.1 NTU. Oxidation–reduction and salinity decreased after a 48-h period and was similar among litter treatments.

After the 48-h period, water parameter trends varied throughout the remainder of the study, but trends remained similar across treatments. Mean water temperature generally increased, while mean salinity decreased throughout the 16-week study. There were no differences in salinity or temperature between treatments at any period of the 16-week study. Mean water temperature generally increased, while mean salinity continued to decrease with time. Chinese tallow litter reduced dissolved oxygen concentrations after a 48-h period and continued to influence on dissolved oxygen for several weeks. Dissolved oxygen concentrations were reduced to as little as 2 mg/L after 4 weeks of litter treatment. Several storm events temporarily reversed the effects of Chinese tallow litter on dissolved oxygen, pH and turbidity.

Water oak litter reduced dissolved oxygen to as little as 4.4 mg/L after 2 weeks. Loblolly pine litter reduced dissolved oxygen to as little as 5.1 mg/L after nine weeks. Mean dissolved oxygen in control treatments remained above 6.1 mg/L. Water chemistry remained stable and consistent for a duration of 8 weeks. After this period, water chemistry changed rapidly. After 9 weeks, dissolved oxygen, turbidity and alkalinity increased in all mesocosms. By the end of the 16-week period, Chinese tallow litter treatments had significantly higher mean pH (pH = 10.4), higher mean dissolved oxygen (DO = 7.85 mg/L) and higher mean turbidity (38.5 NTU) than native litter treatments ($F_{[3,\ 35]} = 28$, $P < 0.005$; $F_{[3,\ 35]} = 8.2$, $P < 0.05$, and $F_{[3,\ 35]} = 34$, $P < 0.005$, respectively). Results from our water chemistry analysis over a 16-week period support our hypothesis that the introduction of Chinese tallow litter can alter aquatic chemistry. Furthermore, the effects on aquatic chemistry were more significant than the effects of native litter.

Microbial community analysis

Bacteria

Eleven of the 120 water samples contained insufficient bacterial rRNA for high-throughput sequencing analysis, reducing sequenced bacterial rRNA samples to 109. Metagenomic analysis identified 510 bacterial Operational Taxonomic Units (OTU) among the 109 samples. Results show that time period, more than litter type, influenced bacterial community composition differences. Non-multidimensional scaling ordination of Bray–Curtis dissimilarities results placed the 109 bacterial samples in three distinct clusters that are associated with time period (Fig. 2). Bacterial community richness, evenness and diversity also varied more by time period than by leaf type and were lowest at the 48-h time period and the highest at the 16-week period (Table 3).

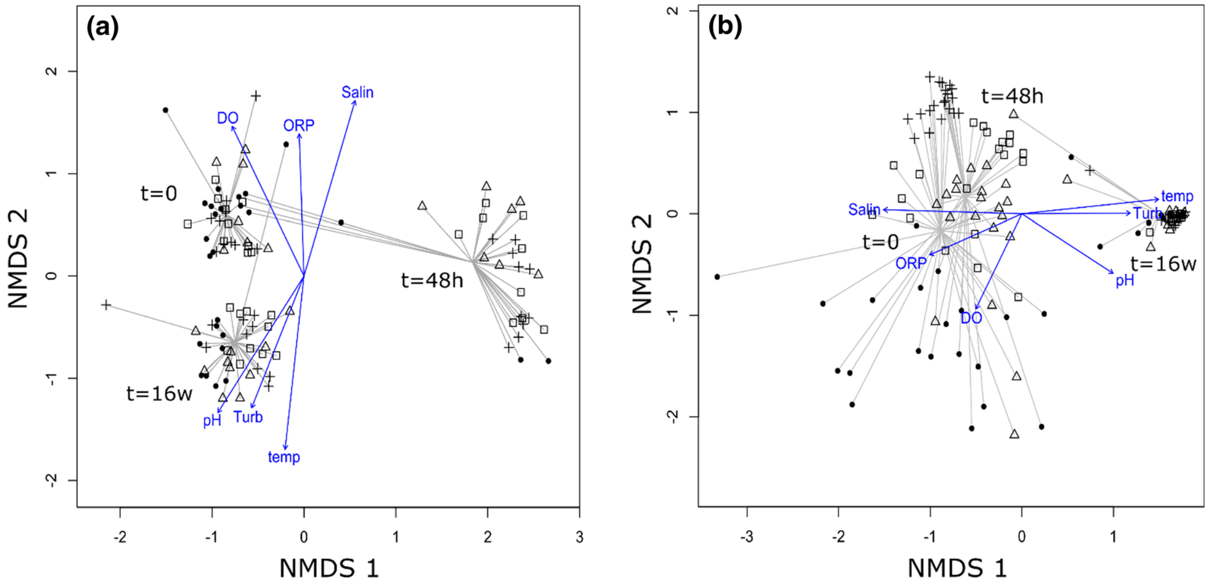


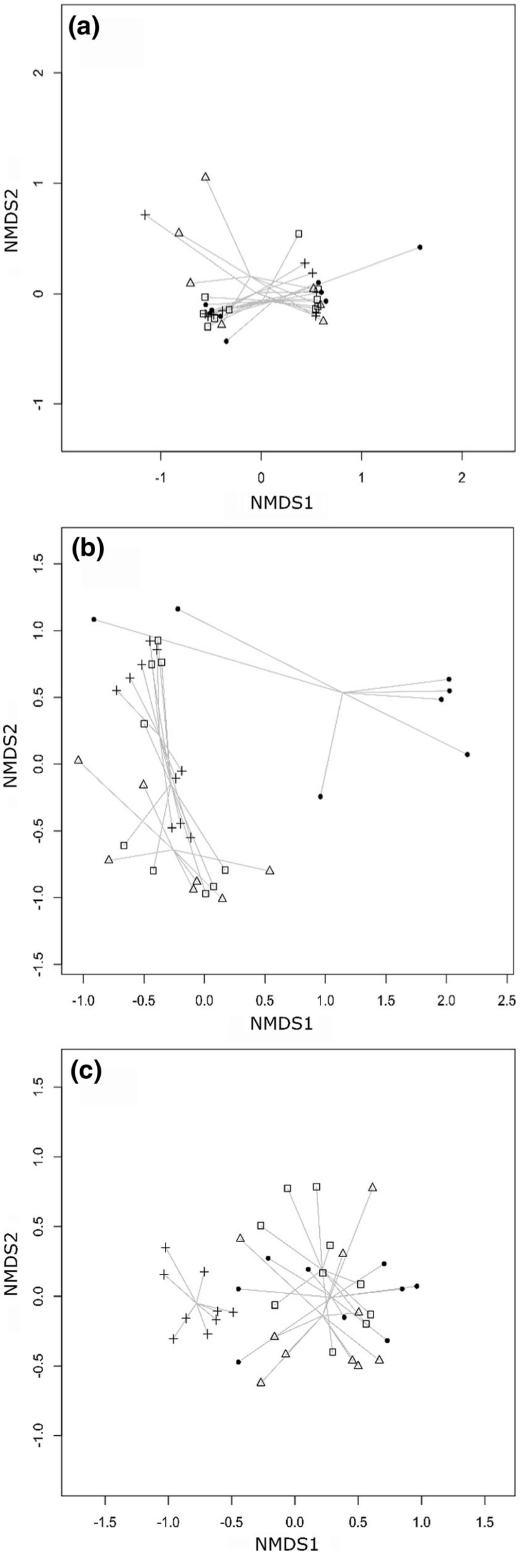
Fig. 2 Non-metric multidimensional scaling (NMDS) plots based on Bray–Curtis dissimilarity of **a** 109 bacteria and **b** 120 fungi communities from Chinese tallow (plus), water oak (square), loblolly pine (triangle) litter and control (filled circle) samples from the initial (*t* = 0), 48-h (*t* = 48 h) and 16-week (*t* = 16 w) time periods. Radial lines connect communities to their respective time periods. Lines with arrows specify water chemistry, and the direction of arrow indicates gradient of higher concentration or value of dissolved oxygen, mg/L (DO), pH (pH), turbidity, NTU (turb), salinity, PSS (Salin), oxidation–reduction potential, mv (ORP), temperature, °C (temp)

Table 3 Results of one-way ANOVA and summary of post hoc Tukey–Kramer test comparing the control, water oak, loblolly pine and Chinese tallow treatment means of the bacteria (top) and fungi (bottom). Richness (S), evenness (E) and Shannon–Wiener Diversity Index (H′) at the initial, 48-h and 16-week time periods. Means in the same row with different letters are significantly different ($P < 0.05$)

Parameter	One-way ANOVA results			Post hoc Tukey–Kramer results mean (SE)			
	df	F	p-value	Control	Loblolly pine	water oak	Chinese tallow
Initial time period							
Richness (S)	3, 32	1.96	0.140	49 (17) a	65 (22) a	62 (21) a	76 (90 a
	3, 36	4.42	0.0096	50 (21) a	76 (26) b	67 (12) b	52 (12) a
Evenness (E)	3, 32	0.22	0.883	0.61 (0.12) a	0.60 (0.12) a	0.063 (0.12) a	0.58 (0.16) a
	3, 36	14.6	< 0.05	0.41 (0.16) a	0.44 (0.12) a	0.47 (0.06) a	0.17 (0.08) b
Shannon–Wiener diversity (H′)	3, 32	0.22	0.883	2.33 (0.53) a	2.48 (0.062) a	2.54 (0.54) a	2.46 (0.67) a
	3, 36	14.4	< 0.05	1.59 (0.66) a	1.92 (0.54) a	1.97 (0.23) a	0.69 (0.31) b
48-h time period							
Richness (S)	3, 29	3.42	0.30	44 (10) a	41 (17) a	50 (13) a	58 (9) a
	3, 36	15.7	< 0.05	40 (17) a	69 (12) b	60 (7) b	41 (6) a
Evenness (E)	3, 29	1.29	0.296	0.49 (0.12) a	0.39 (0.12) a	0.46 (0.08) a	0.45 (0.06) a
	3, 36	38.0	< 0.05	0.43 (0.13) b	0.50 (0.06) c	0.35 (0.05) b	0.15 (0.05) a
Shannon–Wiener diversity (H′)	3, 29	2.72	0.062	1.86 (0.46) a	1.41 (0.35) a	1.80 (0.32) a	1.82 (0.23) a
	3, 36	43.3	< 0.05	1.55 (0.50) b	2.12 (0.21) c	1.44 (0.21) b	0.56 (0.22) a
16-week time period							
Richness (S)	3, 36	2.04	0.125	74 (11) a	74 (11) a	85 (8) a	78 (18) a
	3, 36	0.87	0.464	20 (7) a	20 (13) a	16 (7) a	16 (5) a
Evenness (E)	3, 36	3.58	0.231	0.54 (0.08) a	0.51 (0.08) a	0.60 (0.02) a	0.53 (0.06) a
	3, 36	1.44	0.247	0.11 (0.09) a	0.11 (0.11) a	0.04 (0.05) a	0.08 (0.07) a
Shannon–Wiener diversity (H′)	3, 36	4.80	0.006	2.31 (0.31) a	2.17 (0.37) a 0.36 (0.42) a	2.65 (0.12) b	2.29 (0.32) a
	3, 36	1.41	0.256	0.34 (0.31) a		0.13 (0.18) a	0.23 (0.19) a

We separated bacteria samples by time period to determine community composition differences between litter treatments. Although we found major differences between time periods, we found minor differences between litter types supporting our hypothesis that Chinese tallow litter can influence shifts in bacterial community composition. NMDS ordination arranged bacterial sequences from the initial time period in two main clusters (Fig. 3.) There was no litter association with cluster arrangement. We identified similar taxa between both clusters, including *Gamaproteobacteria*, *Oxalobateraceae, Propionibacterium, Spirochaetia*, *Desulfovibrio*, *Geobacter*, *Gallionella*, *Nitrospira*, *Chryseobacterium, Desulfovibria*, *Hymenobacter, Sphingomonas*, *Firmicutes*, *Rhodocyclales* and several other taxa. However, slight compositional differences were observed between the two clusters. The left cluster was dominated by *Deltaproteobacteria* and followed by taxa such as *Gamaproteobacteria*, *Pedobacter*, *Escherichia coli*, *Roseococcus*, *Acidobacterium*, *Aquabacterium*, *Chloroflexi*. The right cluster was dominated by *Betaproteobacteria* followed by taxa such as *Clostridia*, *Desulfovibria*, *Burkolderia*, *Hymenobactor*, *Oxalobacteracea*, *Citrobacter*, *Novosphingobacter*. There were no differences in bacteria diversity, richness or evenness between litter treatments within the initial time period.

NMDS ordinations arranged bacterial sequences from the 48-h period by litter and control treatments.



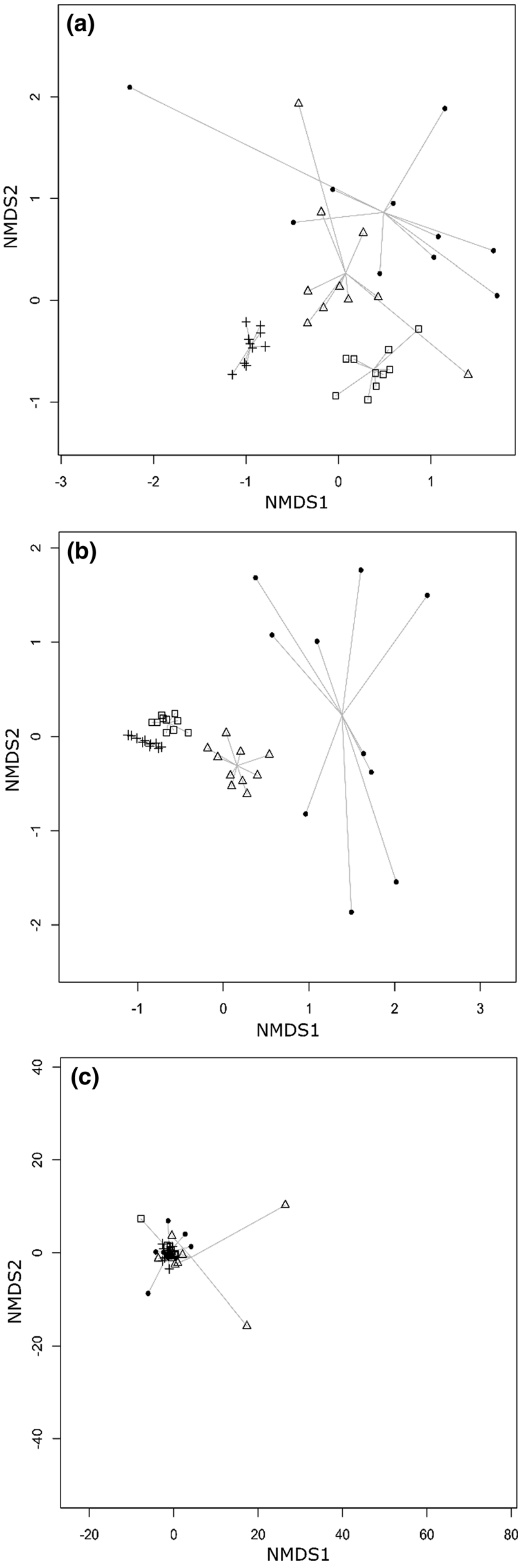
◀**Fig. 3** Non-metric multidimensional scaling (NMDS) plots based on Bray–Curtis dissimilarity of bacterial community composition from Chinese tallow (plus), water oak (square), loblolly pine (triangle) litter and control (filled circle) treatments at the **a** initial, **b** 48-h and **c** 16-week periods

Chinese tallow, loblolly pine and water oak litter treatments had similar bacterial community composition among each other, with Chinese tallow having more bacterial community composition similarities with water oak litter treatments than with loblolly pine litter treatments. These bacterial communities were dominated by *Hymenobacter*, *Sphingomonas*, *Oxalobateraceae and Chryseobacterium* taxa. All other taxa identified represented less than 10% of the community and include *Alphaproteobacterial*, *Roseococcus*, *Massillia sp*, *Legionella* and *Acetobacter*. There were no differences in bacteria diversity, richness or evenness between litter treatments within the 48-h time period.

NMDS ordinations arranged the bacterial sequences from the 16-week period in two separate clusters. Sequences from Chinese tallow treatments formed a distinct cluster separate from native litter and control treatments. *Alphaproteobacteria*, *Betaproteobacterium*, *Detaproteobacterium*, *Candidatus Haliscomenonobacter calcifugiens, Synechococcus and Rhodospirillales* taxa were identified in native and control treatments. Chinese tallow litter treatments contained many of the same taxa of native and control litter treatments; however, Chinese tallow litter treatments were dominated by *Rosoecoccus*, *Hymenobacter*, *Desulfuromonas sp*, *Chryseobacterium* and *Novosphingobium* taxa at the 16-week time period. There were no differences in bacteria, richness or evenness between litter treatments within the 16-week time period. Bacterial diversity significantly differed ($F_{[3, 36]} = 4.8, P < 0.005$) among litter treatments at the 16-week period. Water oak litter treatments had significantly higher bacterial diversity than Chinese tallow and loblolly pine species litter.

Fungi

All 120 water samples contained amplifiable and readable fungi rRNA. Metagenomic analysis identified 185 operational taxonomic units (OTUs) of fungi among the 120 samples. Non-multidimensional scaling ordination of Bray–Curtis dissimilarities placed



◀**Fig. 4** Non-metric multidimensional scaling (NMDS) plots based on Bray–Curtis dissimilarity of fungal community composition from Chinese tallow (plus), water oak (square), loblolly pine (triangle) litter and control (filled circle) treatments at the **a** initial, **b** 48-h and **c** 16-week periods

the 120 fungi samples in distinct clusters based on litter treatments and the 16-week time period (Fig. 2). Results show that litter type and time had influence on the composition of fungi communities. Fungi community composition at the initial and 48-h periods were separated and grouped by litter treatment. There were no community composition differences between litter treatments at the 16-week period, as they were all grouped together. We hypothesized that alterations in aquatic chemistry from the introduction of Chinese tallow litter would influence the composition of fungi communities. However, our results suggest that fungi community composition may be directly related to litter type.

Fungi community richness, evenness and diversity were highest at the initial time period and generally declined in all treatments over the 16-week study. Chinese tallow litter treatments had a significantly lower fungi richness and diversity at the 48-h periods. Community dissimilarity analysis of the three time periods period separately again reveals distinct clusters based on litter treatments at the initial and 48-h periods (Fig. 4). Several fungi sequences were identified, but we found that only few species dominated each community. Chinese tallow litter treatments had the lowest fungi richness ($F_{[3,\ 36]} = 4.42$, $P < 0.005$), evenness ($F_{[3,\ 36]} = 14.6$, $P < 0.005$) and diversity ($F_{[3,\ 36]} = 14.6$, $P < 0.005$) at the initial time period. Fungi communities in Chinese tallow litter treatments were dominated by *Aureobasidium pullulans* and *Alternaria* species. Fungi communities in water oak litter treatments were dominated by fungal species such as *Alternaria, Dicarpella*, *Polysctalum algarvense*, *Gnomoniaceae*and *Aureobasidium pullulans.* Fungi communities from loblolly pine litter treatments also contained *Aureobasidium pullulans* but shared dominance with different fungal species such as *Cladosporium cladosporioides*, *Alternaria*, *Pleosporales*, *Curreya*, and *Fusarium*. Control treatments were more variable in composition, and the following fungal species were identified and abundant; *Cladosporium cladosporioides*, *Cryptococcus mangus*, *Amphisphaeriacea*, *Leucosporidium, Udeniomyces* and *Aureobasidium pullulans* and many more.

At the 48-h period, Chinese tallow treatments were mainly dominated by *Aureobasidium pullulans.* The relative abundance of *Aureobasidium pullulans* sequences increased to approximately 95–98% of the community in Chinese tallow treatments. *Aureobasidium pullulans* sequences were also found in native litter and control treatments. However, the composition of these communities was different. Fungi communities in water oak litter treatments contained *Aureobasidium pullulans* but continued to share community dominance with other species such as *Rhodosporidium, Pseudeurotium*, *Cystofilobasidium capitatum* and *Pleosporales.* Loblolly pine litter treatments contained *Aureobasidium pullulans* but shared dominance with different fungal species such as *Bulleromyces albus*, Microbotryomycetes (family), *Cryptococcus mangus*, *Fusarium*, *Microstromatales* and *Pseudeurotium.* Control treatments were variable in composition. Control treatments continued to vary widely in composition and contained taxa such as *Cladosporium cladosporioides*, *Bulleromyces albus*, *Leucosporidium*, *Sproidiobolus pararoseus* and *Cryptococcus mangus.* Pine litter treatments had the highest community richness ($F_{[3,\ 36]} = 15.7, P < 0.005$, evenness ($F_{[3,\ 36]} = 38.0$, $P < 0.005$) and diversity ($F_{[3,\ 36]} = 43.3$, $P < 0.005$) at the 48-h period. Chinese tallow litter treatments had significantly lower fungi richness and diversity than native litter treatments at the 48-h period.

There were no differences in fungi community composition between litter types at the 16-week period. All litter treatments were dominated by *Sporidiobolus pararoseus*, Aureobasidium pullulans, *Cryptococcus mangus*, *Ascomycota*, *Amanita muscaria* and *Pleosporal*es. There were no significant differences in fugal richness, evenness or diversity among litter treatments at the 16-week period. Fungi community richness, evenness and diversity were lowest at the 16-week period.

Litter quality

The amount of carbon and nutrients differed between litter types (C; $F_{[2,\ 27]} = 91.3$, $P < 0.05$), (Ca; $F_{[2,\ 27]} = 76.1$, $P < 0.05$), (N; $F_{[2,\ 27]} = 5.9$, $P < 0.05$), (K; $F_{[2,\ 27]} = 16.2$, $P < 0.05$), (Mg; $F_{[2,\ 27]} = 11.1$, $P < 0.05$), (P; $F_{[2,\ 27]} = 18.9$, $P < 0.05$), (S; $F_{[2,\ 27]} = 9.1$, $\mathrm{P} < 0.05$), (B; $F_{[2,\ 27]} = 18.9$, $P < 0.05$), (Cu; $F_{[2,\ 27]} = 9.4$, $P < 0.05$). Chinese tallow litter had less carbon (438.71 g/kg) but more calcium (21.46 g/kg) than both the native water oak (475.22 g/kg, 12.84 g/kg, respectively) and native loblolly pine litter (497.69 g/kg, 5.10 g/kg, respectively). Other than carbon and calcium, only copper and boron differed between Chinese tallow and water oak litter. Chinese tallow litter contained more nitrogen (9.54 g/kg), potassium (4.14 g/kg), magnesium (2.61 g/kg), phosphorous (0.970 g/kg), sulfur (0.766 g/kg), boron (0.041 g/kg) and copper (0.003 g/kg) than loblolly pine litter.

Soluble nutrients

The amount of soluble nutrients leached differed between litter types. There were significant differences in the concentration of K ($F_{[2,\ 27]} = 171.7$, $P < 0.05$), P ($F_{[2,\ 27]} = 387.3$, $P < 0.05$), Mn ($F_{[2,\ 27]} = 196.2$, $P < 0.05$), B ($F_{[2,\ 27]} = 37.5$, $P < 0.05$), Zn ($F_{[2,\ 27]} = 15.6$, $P < 0.05$), Cu ($F_{[2,\ 27]} = 15.2$, $P < 0.05$), between litter treatments. Chinese tallow litter leached significantly more soluble nutrients than native litter. A sum of 10.1 mg/L of soluble nutrients was leached from Chinese tallow litter, 5.5 mg/L from water oak and 0.086 mg/L from loblolly pine litter after a 48-h period. Leached nutrients from Chinese tallow litter followed this order: potassium (8.52 mg/L, 84%), followed by phosphorous (1.10 mg/L, 11%), with the remaining being manganese > sulfur > boron > zinc > iron > copper (5% total). Soluble nutrients leached from native litter followed the same respective order but in slightly different percentages. Calcium and magnesium were not detected in Chinese tallow or native litter leachates. We note that water collected from Chinese tallow treatments was yellowish-brown in color (Munsell color range of 10YR 5/8 to 10YR 6/8). Water collected from native water oak and loblolly pine litter treatments was absent of color.

Decomposition comparison

Mean mass loss differed significantly between litter treatments after one ($F_{[2,\ 27]} = 288.6$, $P < 0.05$) and 16 weeks ($F_{[2,\ 27]} = 42.8$, $P < 0.05$) of being immersed in a forested wetland. Chinese tallow litter lost significantly more mass (29%) than the native water oak (13.0%) and native litter after the first week of decomposition. By the end of the sixteen-week study, Chinese tallow litter nearly entirely decomposed. Only the petiole and midrib portions of Chinese tallow leaves remained. On average, Chinese tallow litter lost approximately 72% of its original biomass, while the native water oak and loblolly pine litter only lost approximately 20 and 14%, respectively, of their original biomass in the same 16-week period. Native litter was still structurally intact and resembled identifiable forms of each species.

Discussion

Laboratory antimicrobial activity experiment

Prior studies have established the negative effects of Chinese tallow litter on amphibians due to changes in water quality (Leonard 2008; Adams and Saenz 2012; Cotten et al. 2012; Saenz et al. 2013; Saenz and Adams 2017). Here we address the proximate causes of water quality changes driven by the introduction of Chinese tallow litter, particularly on dissolved oxygen and pH. We assume that adding formalin as an antimicrobial agent to Chinese tallow treatments in our laboratory experiments hindered biological activity, thus preventing aerobic respiration from reducing dissolved oxygen in the water column.

Based on these assumptions, our results support our hypothesis that biological mechanisms (microbial respiration) are reducing dissolved oxygen concentrations in the water column after Chinese tallow litter enters the aquatic environment. Our results also suggest that chemical oxidation may be partially involved in the reduction of dissolved oxygen, perhaps by the oxidation of polyphenolics that leach from Chinese tallow litter (Cameron and LaPoint 1978; Cameron and Spencer 1989). The dark brown/yellow color of water after Chinese tallow immersion suggests that these polyphenolic substances are leached within a 48-h period and may contribute to partial deoxygenation of the water column (Boto and Bunt 1981; Tremolieres 1988).

Our results fail to support the hypothesis that biological mechanisms are the cause of pH changes when Chinese tallow litter enters the aquatic environment. The addition of formalin to Chinese tallow litter treatments did not prevent acidic conditions from developing. Results suggest that formalin had no effect on pH. Carbonic acid production, a by-product of respiration, is likely not the primary source in which acidic conditions develop. Rather, we suggest that polyphenolic substances from Chinese tallow litter are responsible for reducing pH in the water column (Boto and Bunt 1981; Canhoto and Laranjeira 2007).

Cameron and LaPoint (1978), and Cameron and Spencer (1989) concluded that Chinese tallow litter readily leaches polyphenolics. Conway and Smith (2002) later identified inositol in Chinese tallow extracts. Perhaps other polyphenolic compounds such as tannins and tannic acids that leach from Chinese tallow litter are responsible for acid water in our laboratory experiment. Additional studies are needed to find the cause of pH reduction when Chinese tallow litter is introduced into the aquatic environment.

Mesocosm water chemistry, litter quality, soluble nutrients, decomposition

The results of this study indicate that Chinese tallow litter can have an influence on aquatic chemistry. The immersion of Chinese tallow litter in our outdoor mesocosms deoxygenated the water column, reduced pH and increased turbidity significantly more than native litter within a 48-h period. Intermittent storm events reversed the effects of Chinese tallow litter, suggesting that rainfall may mitigate the effects of Chinese tallow litter in natural aquatic systems. Saenz et al. (2013) found similar results.

Species-specific differences in litter quality may explain changes in water quality after litter immersion (Stoler and Relyea 2011). While broadleaf litter species contained more nutrients than loblolly pine litter, Chinese tallow leaves seem to be more susceptible to decomposition and leaching once immersed in water. We found that Chinese tallow litter decays faster and starts breaking down immediately, losing 3 to 4 times more mass and releasing more soluble nutrients than native water oak and loblolly pine litter. We suggest that these soluble nutrients and secondary compounds that are leached from Chinese tallow litter are essentially responsible for driving changes in water quality. Soluble nutrients leached from Chinese tallow litter are likely stimulating microbial activity (Gulis and Suberkropp 2003), reducing dissolved oxygen via respiration after litter immersion. The native water oak and loblolly pine litter species provided a much slower release of solutes after immersion into the water column, leaching relatively little nutrients, and having relatively little effect on water quality.

Sudden changes in water quality at later stages of our study are difficult to explain. Dissolved oxygen and pH suddenly increased in all litter-treated mesocosms. While we largely attribute these rapid changes to intermittent rainfall, algal blooms may have played a role (Stoler and Relyea 2011). Alternatively, or perhaps additively, calcium and magnesium released at later stages of decomposition may partially explain why water pH increased more in Chinese tallow litter treatments than in native litter treatments after nine weeks of litter saturation. Elevated calcium and magnesium coupled with later stages of decomposition and algal growth may have shifted the water column to more alkaline-, turbid- and oxygen-rich levels.

We used mesocosms to help determine how Chinese tallow litter would affect a body of water that was pooled or lentic in nature. We used single-species litter since it is common for Chinese tallow to form dense monocultures around wetland systems. We found that Chinese tallow liter can influence aquatic chemistry. We attribute these influences in water chemistry to litter composition and quality. Preceding studies have determined that Chinese tallow litter is physically and chemically different from other native deciduous trees. In addition to nutrient differences, Cameron and Spencer (1989) concluded that Chinese tallow litter is high in polyphenolics and low in lignin, resulting in a faster decomposition rate than several deciduous tree species in temperate forests.

Litter characteristics such as low lignin and high nutrient content found in Chinese tallow litter explain its fast decomposition rate and rapid nutrient release in comparison with native litter in our study. As in laboratory experiments, Chinese tallow litter treatments produced dark, tannic colored water in mesocosm experiments, suggesting leached polyphenolics. We observed little to no change in the color of water in native litter treatments during our study, suggesting a lack of leached polyphenolics. We consider this relevant because leached dissolved organic carbon (DOC) may be an important co-component in the stimulation of microbial organisms (Stoler and Relyea 2015; Wymore et al. 2017).

We suggest that rapid changes in aquatic chemistry are driven by species-specific differences in litter quality. However, Marks (2019) argues that, rather than litter quality, the rates and pathways of element loss from leaf litter should be considered, since carbon is either respired, transformed to higher trophic levels, or transported downstream. A substantial amount of Chinese tallow litter mass was lost to leaching during the initial stages of decomposition. As a result, we conclude that Chinese tallow litter is more labile than native litter. Therefore, the rates and pathways of element loss in water are likely different from native litter species. Chinese tallow litter leachate DOC is expected to be quickly respired by microbes and lost to the atmosphere as carbon dioxide rather than providing refractory carbon sources for macroscopic food webs (Marks 2019).

Based on our results, we predict ecosystem-level changes in aquatic systems from shifts in surrounding forest composition, specifically from the invasion of Chinese tallow tree. Dense monoculture stands of Chinese tallow tress can produce copious amounts of single-species litter (Leonard 2008). There is evidence that nutrient enrichment can increase the decomposition of native litter species (Gulis and Suberkropp 2003; Li et al. 2017), suggesting that Chinese tallow litter may influence decomposition processes of native litter in aquatic systems, since litter fall occurs in autumn with other native deciduous trees. We suggest that the effects of Chinese tallow litter on aquatic chemistry may be limited to lentic or low flow aquatic systems, rather than flowing streams. Forested wetlands throughout the Gulf Coast appear to be especially vulnerable to the effects of Chinese tallow litter because monocultures are typical in these habitats (Zedler and Kercher 2004; Herbert 2005).

The connection between terrestrial and aquatic habitats in wetland systems makes litter input unavoidable. Consequentially, ecosystem processes may be affected by the introduction of Chinese tallow litter. Keddy (2000) suggests that nutrient enrichment in wetland habitats can influence all trophic levels, including changes in species abundance, displacement of species, reduced species diversity and shifts in community structure and composition. Of course, the volume of water may play a role, with small bodies of water incurring a greater risk, simply due to a potently higher concentration of litter in relatively lower volumes of water (Saenz et al. 2013). Finally, wetlands and other water bodies have a photic zone that varies in depth. We argue that vertical patterns of microbial distribution may be disrupted by an increase in turbidity, thus causing the natural balance between respiration and photosynthesis to be altered, potentially shifting microbial driven processes in wetland systems.

Microbial community composition

We found evidence that Chinese tallow litter can differentially affect the composition of aquatic microbial communities in comparison with native litter. Although we consider microbial diversity, richness and community composition found at the initial period as the ambient community, bacteria and fungi likely had different sources. Nonetheless, our results suggest that Chinese tallow can have a differential influence on the composition bacteria and fungi communities.

Since we collected water samples after litter immersion, we suspect that bacteria came from either groundwater sources, were ubiquitous across litter types, or both. Based on our results, we conclude that bacteria found from samples taken at the initial period reflect the two-separate occasions of groundwater draw and that groundwater, rather than litter, is the primary source of initial bacteria found. Litter did not appear to have an effect on bacterial richness or diversity in our study. However, leaf litter, regardless of species, shifted bacterial community composition. Specifically, the abundance of certain bacterial taxa increased with exposure to both native and non-native litter.

Longer exposures to Chinese tallow litter influenced changes in dominant taxa that were quite different from those found in native litter treatments. It is unknown whether water quality or polyphenolics leached from Chinese tallow litter played a role. Research by other authors suggest that leachates may have had an influence (Wymore et al. 2017). Others have found that high phenolic and tannic contents can inhibit microbial activity (Canhoto and Graca 1996). Despite these findings, we found that bacterial richness, diversity and major compositional shifts were due to temporal changes between the three time periods. Perhaps changes in temperature, pH and turbidity had more significant influences on the richness, diversity and composition of bacterial communities than did liter type.

Unlike bacteria, we suspect that the primary source of fungi was leaf litter rather than groundwater. Fungi diversity and composition were dependent on leaf litter treatments. This leads us to believe that fungi found at the initial period may have come directly from the leaf surface. What is not clear is whether the identified fungi were colonized on the leaf surface before, or after leaf abscission. Given that fungi diversity and community composition were strongly linked to litter type, fungi were likely dispersed into water column immediately upon litter immersion. Other researchers demonstrate that the living leaf surface can support a variety of microorganisms (Lindow and Brandl 2003). Based on our results, it is reasonable to suggest that fungal community composition is linked to the leaf surface of individual plant species. Our results also suggest that fungi may be intolerable of Chinese tallow leaf litter. Chinese tallow litter treatments were considerably less diverse in fungi than those found in native litter treatments.

Litter quality differences and/or litter leachates may have contributed to the differences found in fungi community composition between litter types. Perhaps other invasive plant species contain fungi communities that are different in composition from those found on native litter. Our results suggest that variation in plant composition may play a role in the composition and structure of fungi communities and that Chinese tallow invasions may reduce fungi richness, diversity and composition. Our results also suggest that fluctuations in water chemistry such as increases in alkalinity, turbidity and temperature and/or decreasing salinity appeared to negatively influence fungi richness, diversity and community composition.

Our results support our hypothesis that aquatic microbial community composition can be differentially altered by Chinese tallow litter when compared to native litter. We found that Chinese tallow has differences in plant traits such as litter quality, decomposition ability, soluble nutrient content and leachates (DOC), which had a large influence on microbial activity, diversity and community composition. Since microorganisms are responsible for many processes in aquatic environments (Findlay 2010; Leff and Lemke 1998), it is important to understand how they will respond to non-native plant invasions such as the Chinese tallow tree. Allochthonous litter inputs following Chinese tallow invasions are likely to alter resource diversity, carbon cycles and microbial activity. Temporary forest ponds, forested wetlands, seasonally flooded riparian wetlands and coastal wetlands alike are all vulnerable to the effects as this invasive tree species continues to replace native tree species throughout southeastern US forests.

Conclusion

The invasion of Chinese tallow tree is considered a threat to southern forests. Based on our study, Chinese tallow invasions throughout southern forests will potentially alter resource diversity, nutrient dynamics, water chemistry and microbial communities in aquatic systems through the input of leaf litter. We suggest that the quick release of soluble nutrients from the decomposition of Chinese tallow litter is stimulating microbial respiration, thus causing an increase in biological oxygen demand and a reduction in dissolved oxygen. Other factors such as secondary chemicals are likely the driving force behind pH alterations. Temporal factors were likely the main driver of large shifts in bacterial community composition between time periods. However, our results indicate that Chinese tallow can differentially alter the composition of bacterial communities over longer periods of time when compared to native litter species.

Our results also suggest that fungi community composition was directly linked to litter type and that Chinese tallow litter contained fungal communities that were distinguishable from the fungi communities found from native litter. Given the results of this study, it is likely that the invasive Chinese tallow tree will continue to alter many components of the ecosystems it invades; from forest tree composition, to soil and aquatic chemistry, to shifts in microbial communities. Our study adds to the growing list of consequences that invasive plant species present as they migrate into native ecosystems.

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Compliance with ethical standards

Conflict of interests All authors declare no conflict of interest.

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