# Leaf litter mediates the negative effect of road salt on forested wetland communities

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**Abstract:** Human modification of landscapes has substantially altered the quality and quantity of terrestrial subsidies to freshwater ecosystems. The same modifications frequently lead to addition of chemical contaminants to freshwater environments. Both types of environmental change can alter the abundance of species and can lead to ecological interactions that affect entire communities. We examined how variation of tree litter inputs interacts with inputs of road salt deicers, which are an increasingly common contaminant in northern latitudes. Based on studies of the effects of each factor in isolation, we hypothesized that elevated $Cl^-$ levels would reduce copepod densities, increase algal abundance, and subsequently increase salt-tolerant consumer densities and biomass. We also hypothesized that these effects would be most pronounced in the presence of highly soluble leaf litter (e.g., *Acer rubrum*). We constructed experimental freshwater ponds containing assemblages of phytoplankton, periphyton, zooplankton, *Physa acuta* snails, and 2 species of tadpoles (*Lithobates sylvaticus* and *Anaxyrus americanus*). We used a fully factorial design, manipulating leaf litter (none, *A. rubrum*, or *Quercus velutina*) and $Cl^-$ concentration (114, 220, 314, and 867 mg Cl/L). Road salt at the 3 lower concentrations had few significant effects. The highest $Cl^-$ concentration reduced copepod densities and increased phytoplankton concentrations, but only in the presence of maple litter. We also observed increased rotifer densities in the highest $Cl^-$ concentration, but only in the presence of either litter species. Our results indicate that road salt contamination can have significant effects on wetland community composition at relatively high concentrations, but these effects depend on the chemistry of allochthonous inputs.

**Key words:** American toads, amphibians, deforestation, deicer, sodium chloride, salinization, tadpoles, temperate forest, wood frogs

The productivity of freshwater food webs often depends on nutrient and energy subsidies from the surrounding terrestrial landscape (e.g., insects, woody debris; Polis et al. 1997, Rubbo et al. 2006). The quantity and quality of these resource subsidies are determined largely by environmental conditions in the terrestrial environment, such as tree species composition (Earl et al. 2014). Landuse change can alter the composition of resource inputs to freshwater food webs and is associated with numerous chemical contaminants (e.g., pesticides, fertilizers) that can enter freshwater systems and can strongly affect community composition and ecosystem function (Gilliom 2007). Chemical contamination and rapid changes in terrestrial conditions are environmental changes that can stress organisms and severely alter the functionality and stability of freshwater ecosystems. Given that chemicals often interact in ecologically important ways (Côte et al. 2016), there is immediate need to understand how the combination of these environmental changes alter freshwater communities.

Terrestrial leaf-litter inputs are an important trophic subsidy in freshwater ecosystems, particularly in temperate forests where up to 99% of all terrestrial primary production can enter the aquatic detrital cycle (Petersen and Cummins 1974). Microbial communities mineralize litter inputs and provide the energetic and nutrient resources for primary production (Rubbo et al. 2006). Zooplankton subsequently consume pelagic phytoplankton, and generalist consumers (e.g., tadpoles, snails) consume benthic microbes, algae (i.e., periphyton), and fragments of litter (Altig et al. 2007, Stoler et al. 2016). In experimental wetlands, loss of leaf-litter inputs from anthropogenic development has resulted in acute reductions of consumer biomass (i.e., Rubbo et al. 2006, Stoler and Relyea 2016). In addition, turnover in terrestrial vegetative composition through natural succession and human

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activities (e.g., introduction of nonindigenous species) can alter the physical and chemical properties of freshwater environments because of intraspecific differences in leaf chemistry (Stephens et al. 2013, Stoler and Relyea 2016). For example, the high soluble C content of red maple (*Acer rubrum*) leaf litter in wetlands can darken the water column, reduce photosynthesis, and decrease concentrations of dissolved $O_2$ (DO), but also provides a valuable resource for benthic detritivores (Stoler et al. 2016). In contrast, recalcitrant litter species, such as black oak (*Quercus velutina*), are a less labile resource for detritivores, but can lead to higher water clarity, increased rates of photosynthesis in wetlands, and higher densities of primary consumers (Stoler and Relyea 2016). Litter remains in wetlands for long periods of time, so the ecological effects of autumn-shed litter can persist into the spring and summer (Stephens et al. 2013).

Anthropogenic development that causes deforestation and turnover in forest composition also is associated with the growing use of road salt as a deicing agent to maintain roadways in winter, particularly in northern latitudes. In the USA, >22 million metric tons of road salt is applied on roadways annually, primarily during winter months (Findlay and Kelly 2011). Spring snowmelt and stormwater runoff can lead to accumulation of $Cl^-$ in ponds and wetlands throughout the growing season (Environment Canada 2001). $Cl^-$ concentrations in wetlands can be as high as 500 mg/L by the end of the growing season (Sriyaraj and Shutes 2001, Sadowski 2002). Severe runoff events can lead to temporary $Cl^-$ concentrations up to 5000 mg/L, which are then diluted by rainwater and groundwater outflow (Environment Canada 2001). Survival of many aquatic consumers (e.g., tadpoles, snails) is substantially reduced at such high levels of $Cl^-$ contamination (Collins and Russel 2009, Langhans et al. 2009). Chronically elevated, but lower $Cl^-$ concentrations also are harmful to freshwater organisms (Kaushal et al. 2005). For example, $Cl^-$ concentrations that result in electrical conductivities as low as 100 μS/cm can reduce microbial functionality in streams and lead to slower leaf-litter decay (Schäfer et al. 2012, Cook and Francoeur 2013).

Most investigations of the effects of salinity have been done through laboratory-based toxicity trials on single species or groups of functionally related organisms (e.g., bacteria), but the effects of salt in nature are expressed via complex community interactions. For example, Van Meter et al. (2011) and Dananay et al. (2015) found that copepod and cladoceran abundance declined with increasing salinity across a range of 0 to 900 mg $Cl^-$/L, whereas tadpole mass was positively associated with salinity. In both studies, investigators attributed these effects to an increase in periphytic algal abundance, which increased with salinity. The expectation that the effects of contaminants on temperate wetland community dynamics will be mediated by leaf litter inputs is reasonable because leaf-litter quantity and quality can strongly alter the abundance of microbial and algal abundance (Stoler and Relyea 2016). Given evidence that salt reduces the decay rate of C compounds (Schäfer et al. 2012, Swan and DePalma 2012), freshwater systems with fast-decaying litter inputs are likely to be affected far more than systems with recalcitrant, slow-decaying inputs. Such interactions must be explored to understand fully the effects of salt in natural ecosystems and to improve management of salt application.

We examined the interactive effects of road salt and leaf-litter quality on forested freshwater wetland communities. We manipulated salt concentrations and the type of leaf litter present (none, red maple, or black oak) in outdoor wetland mesocosms containing communities with microbes, algae, zooplankton, snails, and tadpoles. Based on the leaf-litter studies by Stoler and Relyea (2016) and Stephens et al. (2013), we hypothesized that an absence of litter would be associated with lower consumer density or biomass and a subsequent increase in algal and microbial biomass. We further hypothesized that consumer biomass would be lower with the addition of litter containing high amounts of toxins and soluble C (e.g., maple) than with slow-decaying litter (e.g., oak). Based on the road salt studies by Van Meter et al. (2012) and Dananay et al. (2015), we hypothesized that elevated salinity would reduce copepod density, increase algal biomass, and increase consumer mass. However, because salinity is inversely correlated with the breakdown of allochthonous C (Schäfer et al. 2012, Swan and DePalma 2012, Van Meter et al. 2012), we hypothesized that the effects of salt would be modified by the type of leaf-litter input. Specifically, we predicted that the effects of salt would be more pronounced in mesocosms containing a fast-decaying litter species than in mesocosms containing a slow-decaying species.

## METHODS

We conducted our experiment at the Rensselaer Aquatic Lab (Troy, New York) in summer 2015. We used a full-factorial, randomized experimental design with 3 leaf litter treatments (red maple, black oak, and no litter) and 4 salt treatments (0, 100, 200, and 800 mg Cl/L; see below for actual $Cl^-$ concentrations) for a total of 12 treatments. We replicated each treatment 4 times for a total of 48 experimental units. Both litter species used in our study are common and dominant throughout our study region and much of temperate North America. The 3 lower $Cl^-$ concentrations are representative of chronic salt levels typical of ponds within a km of treated roadways (Karraker et al. 2008, Van Meter et al. 2012), whereas the highest salt concentration is representative of chronic salt levels in wetlands immediately adjacent to a treated roadway and stormwater retention ponds (Van Meter et al. 2012).

Experimental units were 750-L plastic mesocosms. We filled all mesocosms with 500 L of well water on 13 May. We placed a 60% shade-cloth cover on each mesocosm to simulate moderate canopy cover and to prevent entry or emergence of any organisms. On 14 May, we added 20 g of rabbit chow (Blue Bunny 16; Kent Nutrition Group, Muscatine, Iowa) to each mesocosm to simulate an initial nutrient and energy supply that would be present in natural systems after spring thaw (Stoler and Relyea 2016). On 15 May, we added 250 g of dried leaf litter to all mesocosms except those assigned to the no-litter treatment. This amount of litter mimics natural litter densities in forest ponds, which can vary from 0.5 g/L to 5 g/L (Rubbo et al. 2008, ABS, unpublished data). We collected the litter from local forests in spring 2015 and allowed it to air-dry for 1 wk before adding it to mesocosms. Thus, litter used in our experiment represents terrestrial subsidies that have been naturally degraded and leached throughout autumn and winter and is representative of litter that would be present in a vernal wetland. On the same day as litter addition, we placed two 15-cm$^2$ clay tiles on the east-facing side of each mesocosm to provide a standardized substrate for sampling periphyton biomass. We added 0.5 L of homogenized pond water collected from 4 local, canopy-covered vernal pools to each mesocosm. The pond water served as a natural source of bacteria, fungi, algae, and zooplankton. On 18 May, we added 2 coarse-mesh litter bags (10-mm mesh size) to each mesocosm to measure litter decomposition rate. Each bag contained 3 g of maple or oak litter for the maple or oak treatments, respectively. We did not add empty bags to no-litter treatments. The mesh size of the bags was sufficiently large to allow entry by all consumers in the experiment, except some wood frogs during their later developmental stages.

In each mesocosm, we established identical macroconsumer communities comprising wood frog (*Lithobates sylvaticus*) and American toad (*Anaxyrus americanus*) tadpoles and pouch snails (*Physa acuta*). In spring, we collected 10 newly laid egg masses of each species from two wetlands (i.e., one wetland for each species) and reared the tadpoles that hatched under common garden conditions in outdoor culture pools. We maintained all tadpoles at similar densities and fed them rabbit chow ad libitum. On 28 May, tadpoles of both species reached a safe handling stage (stage 25; Gosner 1960) and we added 20 individuals of each species to each mesocosm for a total of 40 tadpoles/mesocosm. Mean initial masses were 122 ± 7 mg (SE) and 40 ± 3 mg for wood frogs and American toads, respectively. We set aside 20 tadpoles of each species to assess 24-h survival after handling stress. Survival of these tadpoles was 100%. On the same day, we added 9 adult snails collected from a single wetland to each mesocosm.

We added road salt to the mesocosms on 30 May. We used 100% sodium chloride (NaCl) rock salt (Ice-a-Away Rock Salt Ice Melter; Compass Minerals, Overland Park, Kansas). Use of salt alternatives (e.g., $MgCl_2$) is increasing, but NaCl is the dominant de-icing agent used in the USA and Canada (Environment Canada 2001, National Research Transportation Board 2007). We calculated the amount of NaCl needed to achieve our nominal $Cl^-$ concentrations. We added salt by removing 20 L of water from each mesocosm, dissolving the salt in it, and then slowly pouring it back into the mesocosm. To ensure that the salt dispersed evenly throughout the mesocosms, we distributed the water across the surface and gently stirred the mesocosm for ~10 s without disturbing the leaf litter. To equalize the disturbance across all treatments, we repeated this process for the treatment without salt addition. We designated the day of salt addition as day 0 of the experiment.

The ambient $Cl^-$ concentration in our water supply was 60 mg/L, and our target salt concentrations were 60, 160, 260, or 860 mg/L among treatments. We verified $Cl^-$ levels in our mesocosms on day 25 by taking measurements with a solid-state membrane $Cl^-$ probe (6882 Chloride ISE Sensor attached to a ProPlus multimeter; Yellow Springs Instruments [YSI], Yellow Springs, Ohio) just below the water surface and just above the leaf litter. Before taking measurements, we calibrated the $Cl^-$ probe based on solutions of known $Cl^-$ concentration. We did not find any $Cl^-$ stratification. On average, actual concentrations among salt treatments were 114, 220, 314, and 867 mg/L. We report all results as actual concentrations because the first 3 values were >10% different from nominal concentrations.

### Light attenuation, DO, temperature, and pH

We measured several abiotic variables throughout the experiment (Appendix S1). We measured pH, DO (mg/L), and water temperature (°C) of each mesocosm on days 1 and 25 with a calibrated multimeter (ProPlus; YSI). We measured light attenuation on days 4 and 25 with a submersible quantum sensor (Li-Cor Instruments, Lincoln, Nebraska). We conducted all measurements at approximately midday.

### Litter decay rate

We assessed litter decay rate by measuring litter mass loss at 2 time points during the experiment. On days 17 and 32, we collected a single litter bag from each mesocosm, rinsed all leaves, and oven-dried remaining material at 60°C for 24 h. To calculate litter decay rate, we fit our data to an assumed exponential model of decay (sensu Petersen and Cummins 1974). We $\ln(x)$-transformed values of % mass remaining (3 data points, including the initial mass) and then calculated the least-squares slope of these values vs time.

### Community response variables

We measured phytoplankton density, periphyton biomass, zooplankton density, and snail abundance via a variety of methods (Appendix S1). On days 5 and 28, we measured phytoplankton density as fluorescence of chlorophyll *a* in a sample of the water column based on the fluorometric method of Arar and Collins (1997) without acid correction. On days 12 and 31, we measured periphyton biomass as the oven-dried mass of attached material brushed from a single clay tile. On days 2 and 25, we collected zooplankton samples and counted copepods, cladocerans, and rotifers after preservation in 30% ethanol. This sampling frequency might have caused us to miss subtle fluctuations in zooplankton population sizes, but previous work suggests that it is sufficient to detect major changes (Stoler and Relyea 2016). We estimated snail abundance on day 43 by scraping a net across a standardized section of bottom and side surface in each mesocosm. After preserving snails, we sorted them as hatchlings and adults. We then combined snails from both groups, dried them at 60°C for 24 h, and recorded total biomass. On day 18, we also recorded the density of snail egg masses found on the wall (area = 1.7 $m^2$) of each mesocosm.

### Amphibian response variables

We assessed amphibian survival to metamorphosis, time to metamorphosis, and mass at metamorphosis. American toads began emerging on day 16, and wood frogs began emerging on day 17. After day 17, we checked mesocosms daily for new metamorphs until the end of the study (day 44). After tadpoles had completed metamorphosis (Appendix S1), we anesthetized all individuals in 2% MS-222 solution, preserved them in 10% formalin, and calculated time to metamorphosis as the time between day 0 and the date of preservation. We assessed mass at metamorphosis (metamorph mass) of preserved individuals and calculated time to metamorphosis and mass at metamorphosis as means of measurements from each mesocosm. We estimated % survival of individuals as the number of individuals that we brought into the laboratory. Throughout the study, we adhered to all applicable institutional guidelines for the care and use of animals.

### Statistical analyses

We first assessed the effects of salt and litter species on all abiotic responses. We analyzed $Cl^-$ (measured once) with a 2-way analysis of variance (ANOVA) and a model that included both main effects and their interaction. We analyzed water temperature, pH, DO, and light attenuation (measured repeatedly) based on a protected analysis of variance (ANOVA) technique (Scheiner and Gurevitch 2001). We first conducted a repeated-measures multivariate ANOVA (rmMANOVA). After finding a significant multivariate effect, we conducted univariate repeated-measures ANOVAs on each response variable. When we found a significant effect of time, we conducted analyses within sampling dates. We could measure litter decay rate only for treatments that included leaf litter, so we analyzed these data with a separate 2-way ANOVA. We conducted Tukey's post hoc comparisons to identify significant differences among treatments.

We also assessed the effects of salt and litter treatments on all community responses. We conducted 2 rmMANOVAs, one for consumer resources (phytoplankton concentration, periphyton biomass) and one for zooplankton (densities of rotifers, copepods, and cladocerans). We conducted 2 additional MANOVAs for all snail responses (snail abundance in both size fractions, snail biomass, and snail egg mass abundance) and for all amphibian responses (survival to collection, metamorph mass, time to metamorphosis).

When necessary, we $\log(x)$-transformed data to fit parametric assumptions of normality and homogeneity of variance. We $\arcsin\sqrt{(x)}$-transformed amphibian survival data. We analyzed all data in R (version 3.1.2; R Project for Statistical Computing, Vienna, Austria) with packages *vegan* and *car* (Fox and Weisberg 2010) for conducting ANOVAs and the package *agricolae* for conducting post hoc comparisons.

## RESULTS

### $Cl^-$

$Cl^-$ concentration was affected by salt ($F_{3,36} = 54.5$, $p < 0.001$) but not by litter ($F_{2,36} = 1.0$, $p = 0.392$) or a salt × litter interaction ($F_{6,36} = 1.0$, $p = 0.419$).

### Light attenuation, DO, temperature, and pH

Light attenuation, DO, temperature, and pH were influenced by multivariate effects of litter and time, but not salt or interactions (Table 1). Light attenuation was affected by litter but not salt and tended to be influenced by time (Table S1; Fig. 1A, B). Light attenuation was 2.48 and 5.20× higher in maple than in oak and no-litter treatments, respectively ($p < 0.001$), 2.09× higher in oak than in no-litter treatments ($p < 0.001$), and 0.95× greater on day 25 than on day 4. DO was affected by litter and time (Table S1). DO was 1.23× higher in no-litter than in oak treatments ($p < 0.001$), 1.13× higher in oak than in maple treatments ($p < 0.001$), and increased by 1.27× between days 1 and 25. Temperature and pH were affected only by time (Table S1), with increases of 10.2°C and 0.8 pH units, respectively, from day 1 to day 25.

### Litter decay rate

Litter decay rate was affected by litter ($F_{1,24} = 132.6$, $p < 0.001$) but not salt ($F_{3,24} = 0.2$, $p = 0.890$) or a salt × litter interaction ($F_{3,24} = 1.1$, $p = 0.367$). Litter decay rate of red maple was 1.74× greater than that of oak litter ($p < 0.001$).

### Community response variables

***Phytoplankton and periphyton*** Phytoplankton concentration and periphyton biomass were influenced by multivariate effects of salt, litter, time, and all 2-way interactions (Table 1). Therefore, we examined the phytoplankton and periphyton data on each sampling date.

Phytoplankton concentrations were affected by salt, litter, time, and all 2-way interactions (Table S2, Fig. 2A–F). We did not detect salt, litter, or salt × litter effects on day 5

Table 1. Results of repeated-measures multivariate analysis of variance (rmMANOVA) for abiotic, phytoplankton, periphyton, and zooplankton responses and results of MANOVA for snail and amphibian responses. Subscripts of *F*-values refer to treatment and error degrees of freedom. Bold indicates $p \leq 0.05$, * indicates $p \leq 0.09$.

| | Abiotic | | Phytoplankton and periphyton | | Zooplankton | | Snails | | Amphibians | |
|---|---|---|---|---|---|---|---|---|---|---|
| Factor | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* |
| Salt | $0.5_{3,36}$ | 0.675 | **$3.0_{3,36}$** | **0.044** | $0.6_{3,36}$ | 0.639 | $1.3_{12,88}$ | 0.261 | $1.5_{18,99}$ | 0.128 |
| Litter | **$7.5_{2,36}$** | **0.002** | **$5.9_{2,36}$** | **0.006** | **$63.8_{2,36}$** | **<0.001** | **$12.1_{8,66}$** | **<0.001** | **$9.5_{12,64}$** | **<0.001** |
| Salt × litter | $0.9_{6,36}$ | 0.510 | $1.9_{6,36}$ | 0.106 | $1.5_{6,36}$ | 0.220 | $1.3_{24,116}$ | 0.185 | $0.7_{36,216}$ | 0.876 |
| Time | **$17631.7_{1,36}$** | **<0.001** | **$142.4_{1,36}$** | **<0.001** | $0.1_{1,36}$ | 0.766 | | | | |
| Salt × time | $0.8_{3,36}$ | 0.526 | **$3.7_{3,36}$** | **0.012** | **$3.5_{3,36}$** | **0.026** | | | | |
| Litter × time | $<0.1_{2,36}$ | 0.975 | **$6.2_{2,36}$** | **0.005** | **$5.6_{2,36}$** | **0.007** | | | | |
| Salt × litter × time | $0.8_{6,36}$ | 0.571 | $2.3_{6,36}$ | 0.058* | $2.1_{6,36}$ | 0.072* | | | | |

(Fig. 2A–C), whereas all terms were significant on day 28 (Table S2). Among red maple litter treatments, phytoplankton concentrations were 1.33 to 1.39× higher in the 867 mg $Cl^-$/L treatment relative to the other 3 salt treatments ($p \leq 0.006$; Fig. 2F). Among 220 mg $Cl^-$/L treatments, phytoplankton concentrations were 1.33 to 1.48× higher in the no-litter than in maple and oak treatments, respectively ($p \leq 0.021$; Fig. 2D–F).

Periphyton biomass was affected by a litter × time interaction (Table S2). Periphyton biomass differed among litter treatments on day 12 but not on day 31 (Table S2). On day 12, periphyton biomass was 1.46 to 1.64× higher in no-litter than in maple or oak treatments, respectively ($p \leq 0.018$).

***Zooplankton*** Zooplankton densities were influenced by multivariate effects of litter and salt × time and litter × time interactions (Table 1). Cladoceran density was affected only by litter (Table S3). Averaged across salt treatments and sampling dates, cladoceran density was 2.46 to 2.86× higher in the oak and maple than in the no-litter treatments. Copepod densities tended to be affected by a salt × litter × time interaction and rotifer densities were affected by this 3-way interaction (Table S3). Therefore, we examined copepod and rotifer densities on each sampling date.

On day 2, copepod densities were affected by litter and salt (Table S3, Fig. 3A–C). Post hoc pairwise comparisons did not reveal a difference among salt treatments ($p \geq 0.168$), but copepod densities were 1.61 to 1.98× higher in oak and red maple, respectively, than in no-litter treatments ($p \leq 0.030$). On day 25, copepod densities were affected by litter, salt, and a salt × litter interaction (Table S3, Fig. 3D–F). Copepod densities were 0.37 to 0.45× lower in the 867 mg $Cl^-$/L than in all other salt treatments, but only in the presence of red maple ($p < 0.001$; Fig. 3F). In addition, copepod densities were 0.11 to 0.25× lower in no-litter than in red maple and oak litter treatments, respectively, but only in the 3 lowest salt treatments ($p \leq 0.046$). In the highest salt treatment, densities in the no-litter treatment were similar to those in the red maple ($p = 0.240$) but 0.22× lower than in the oak treatment ($p = 0.030$).

On day 2, rotifer density was not affected by litter, salt, or a salt × litter interaction (Fig. 4A–C), but on day 25, all terms were significant (Table S3; Fig. 4D–F). In treatments with maple litter, densities were 2.80× higher in the 867 than in the 220 mg $Cl^-$/L salt treatment ($p = 0.010$; Fig. 4F). In oak treatments, densities were 1.94 to 2.85× higher in the 867 mg $Cl^-$/L treatment than in all other salt treatments ($p \leq 0.008$; Fig. 4E). In addition, densities were 1.34 and 1.62× higher in treatments with oak than with maple or no litter, respectively, but only when salt was 867 mg $Cl^-$/L ($p = 0.002$).

***Snails*** Snail responses were influenced by multivariate effects of litter, but not by salt or a salt × litter interaction (Table 1). Litter affected snail egg mass abundance and hatchling abundance, tended to affect adult abundance,

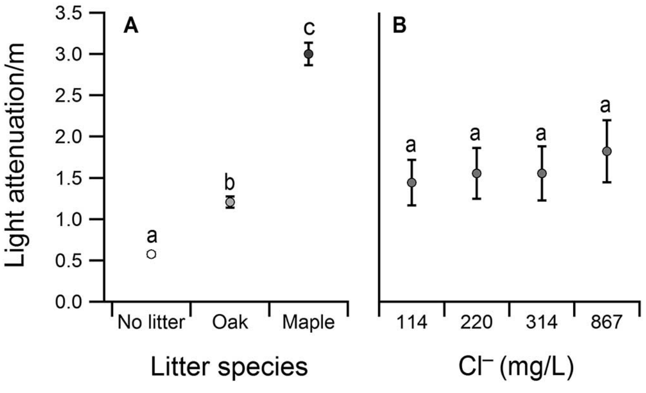

Figure 1. Mean (±SE) light attenuation in the water column of mesocosms in leaf-litter (A) and salt (B) treatments. Points with the same letter are not significantly different within panels ($p > 0.05$). Maple = red maple, Oak = black oak.

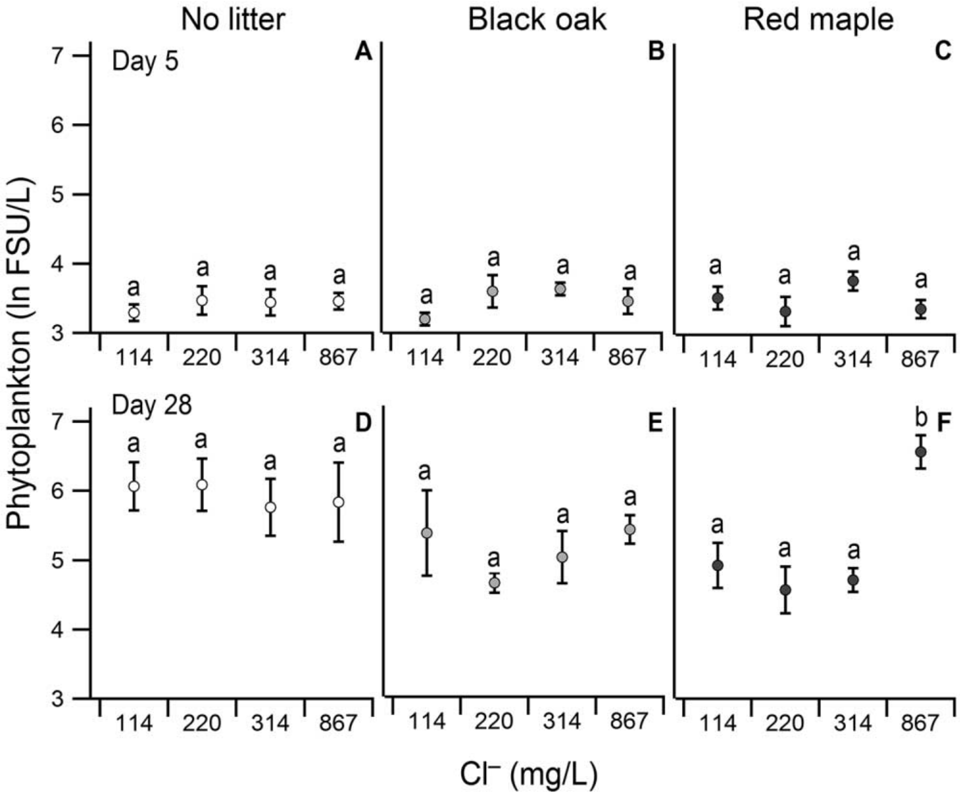

Figure 2. Mean (±SE) phytoplankton densities in salt treatments within no-litter (A, D), black oak (B, E), and red maple (C, F) treatments on days 5 (A–C) and 28 (D–F). Points with the same letter are not significantly different within panels ($p > 0.05$). FSU = fluorescence standard units.

but did not affect snail biomass (Table S4). Hatchling abundances were 3.58 and 3.74× higher in red maple and oak, respectively, than in no-litter treatments ($p \leq 0.036$; Fig. 5A). Adult abundances were 0.58 and 0.62× lower in red maple and oak, respectively, than in no-litter treatments ($p \leq 0.076$; Fig. 5B). Egg mass abundances were 0.45× lower in red maple and oak than in no-litter treatments ($p \leq 0.003$; Fig. 5C).

### Amphibian responses

Amphibian responses were influenced by multivariate effects of litter but not salt or a salt × litter interaction (Table 1). Litter species influenced all American toad response variables (Table S5). American toad survival was 1.07 to 1.14× higher in the no-litter than in the oak and red maple treatments, respectively ($p \leq 0.015$; Fig. 6A). However, metamorph mass was 0.87× lower in red maple than in both oak and no-litter treatments ($p \leq 0.001$; Fig. 6C). In addition, toads required an average of 1 d more to metamorphose in red maple than oak or no-litter treatments ($p \leq 0.009$; Fig. 6E). Litter species influenced wood frog metamorph mass and time to metamorphosis, but not survival (Table S5; Fig. 6B, D, F). Wood frog metamorph mass was 1.15× greater in red maple than oak treatments ($p < 0.001$), and 1.79× greater in oak than no-litter treatments ($p < 0.001$; Fig. 6D). Wood frogs tended to require an average of 1 d more to metamorphose in no-litter and red maple than in oak litter treatments ($p \leq 0.074$; Fig. 6F).

## DISCUSSION

Our study adds to the growing body of literature concerning the effects of road salt in aquatic systems (e.g., Swan and DePalma 2012, Van Meter et al. 2012). By adding the interacting factor of litter-resource chemistry, we have provided an additional mechanism that might alter the effects of salt in natural environments. As expected from prior studies of leaf-litter chemistry in wetlands (e.g., Rubbo and Kiesecker 2004, Stephens et al. 2013, Earl et al. 2014, Stoler and Relyea 2016), wetland communities were altered by the presence and species of leaf litter. The effects of salt inputs were less ubiquitous, but salt at the highest concentration induced significant changes in zooplankton densities and phytoplankton concentration. However, these changes depended on the type leaf litter present. As hypothesized, the effects of salt were more pronounced in the presence of a fast-decaying litter species (i.e., red maple) than in a slow-decaying species (i.e., oak). However, salt did not affect macroconsumers (i.e., snails and tadpoles), which suggests that many components of wetland communities might be tolerant of direct or indirect effects of environmentally relevant $Cl^-$ concentrations.

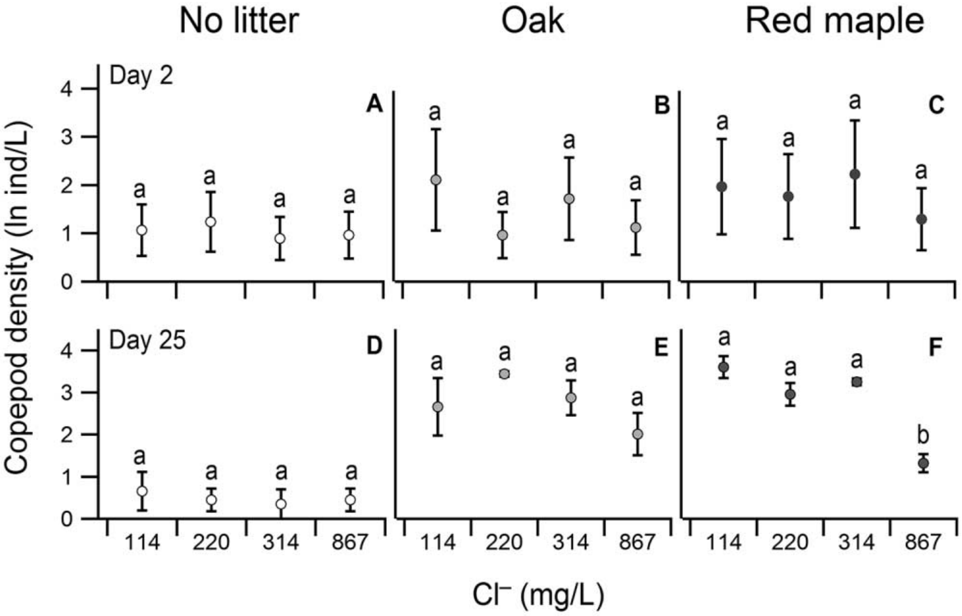

Figure 3. Mean (±SE) copepod densities in salt treatments within no-litter (A, D), black oak (B, E), and red maple (C, F) treatments on days 2 (A–C) and 25 (D–F). Points with the same letter are not significantly different within panels ($p > 0.05$). Ind = individuals, Oak = black oak.

### Effects of leaf litter

We found mixed evidence in support of our first hypothesis that the absence of litter would be associated with declines in consumer density and biomass. In support of our hypothesis, an absence of litter induced a decline in the density of large-bodied zooplankton (copepods and cladocerans) and led to lower wood frog mass at metamorphosis. In addition, periphyton biomass increased in the absence of litter, a result suggesting growth of inedible periphytic algal species after initially strong grazing pressure. Without sufficient energy and nutrients to sustain productivity, consumers can rapidly deplete standing crops of periphyton. Periphyton

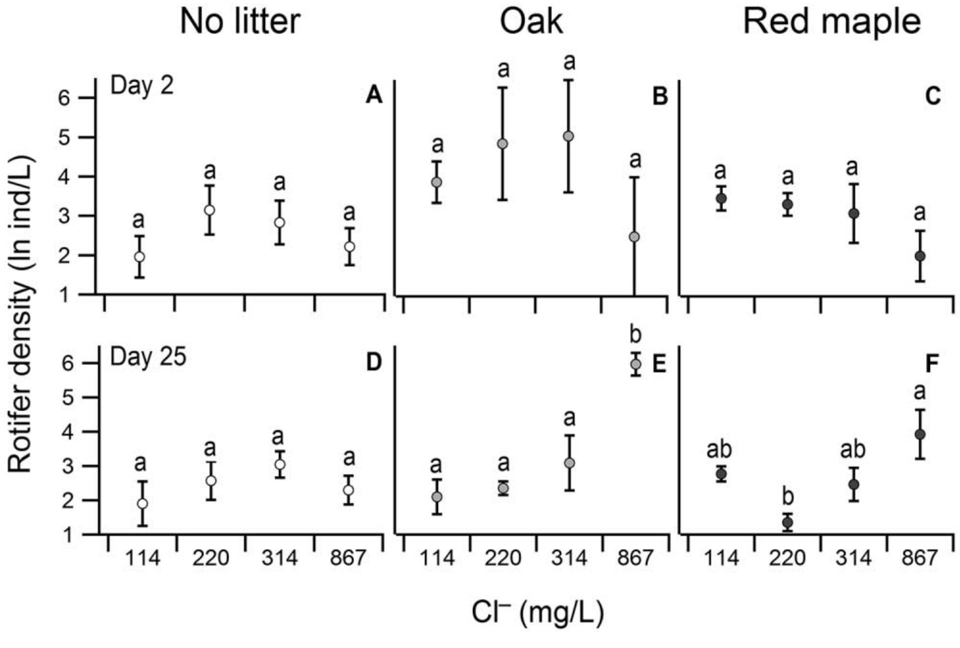

Figure 4. Mean (±SE) rotifer densities in salt treatments within no-litter (A, D), black oak (B, E), and red maple (C, F) treatments on days 2 (A–C) and 25 (D–F). Points with the same letter are not significantly different within panels ($p > 0.05$). Ind = individuals, Oak = black oak.

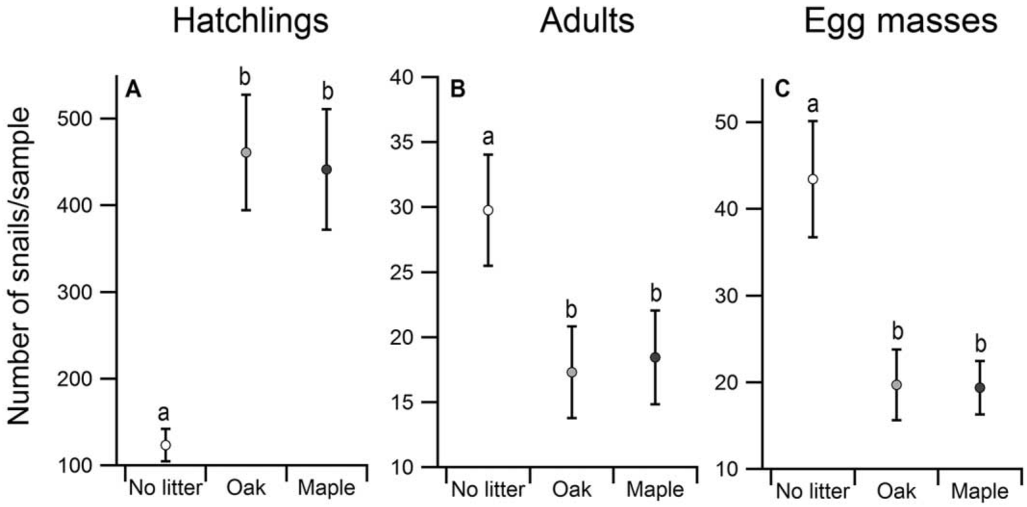

Figure 5. Mean (±SE) snail hatchling (A), adult (B), and egg mass (C) abundance in leaf litter treatments (hatchling and adult abundances measured on day 43; egg mass abundance measured on day 18). Points with the same letter are not significantly different within panels ($p > 0.05$). Maple = red maple, Oak = black oak.

depletion is followed by declines in consumer growth and establishment of inedible periphytic algae species (Steiner 2003). Stephens et al. (2013) also found greater periphyton biomass in mesocosms without leaf litter than with red maple litter. Combined, these results provide further support for the conclusion that the loss of leaf litter has adverse indirect effects on many consumers, but these effects must be understood in the context of the chemistry of available litter inputs (Stoler and Relyea 2016).

In contrast to our hypothesis, we found higher survival of American toads in no-litter treatments. This result was not entirely unexpected because the species is highly sensitive to litter leachates (Stoler and Relyea 2016). We found more snail egg masses and more adult snails in no-litter than in oak or red maple treatments. These results suggest that these snails underwent earlier reproduction in no-litter relative to oak or red maple treatments. Auld and Henkel (2014) found that a nutrient-poor diet delayed reproduction by *P. acuta*, but Auld (2010) demonstrated that predation risk accelerated time to first reproduction, with an associated decrease in the survival of hatchlings. We did not add predators of adult snails to our mesocosms, but tadpoles prey on snail eggs and hatchlings (Petranka and Kennedy 1999), and predation might increase in absence of other resources. If predation risk decreases hatchling survival (Auld 2010), the absence of litter might have negative long-term effects on *P. acuta* populations. This question could be addressed with a study focused on *P. acuta* and litter resources in isolation from the rest of the aquatic community.

Red maple litter had stronger effects than oak litter on the abiotic characteristics of the mesocosms and had more effects on tadpole consumers. Red maple induced lower DO, higher light attenuation, longer time to toad and wood frog metamorphosis, and greater wood frog and smaller toad metamorph mass. Our findings for toads agree with those of Stoler and Relyea (2016), who reared toad tadpoles in an assemblage with 4 other competing anuran species. However, our findings differ from those of Earl and Semlitsch (2015), who reported no change in toad biomass across treatments with different concentrations of phenols, although they did not include consumers that compete with toads. Thus, effects of competition might influence the effects of litter leachate on toads. Also in contrast to our results, other investigators have observed lower growth and survival of wood frogs in the presence of red maple litter than oak litter (Rubbo and Kiesecker 2004, Stephens et al. 2013). These investigators used freshly abscised leaf litter collected in autumn, whereas we used partially leached and decayed spring-collected litter, which typically contains fewer phenolic acids and other soluble C compounds and might be a more nutritious resource than autumn-collected litter. Stoler and Relyea (2011) found no difference in gray tree (*Hyla versicolor*) tadpole growth between spring-collected maple and oak litter. Such comparisons among studies bolster the conclusion that the effects of leaf litter in wetlands depend strongly on interspecific differences in litter chemistry (Stoler and Relyea 2016).

### Interactive effects of leaf litter and road salt

The effects of salt in our study were largely attributable to an interaction with litter treatments and generally were apparent only at the highest salt concentration. Among the most pronounced effects was a decline of copepods at the highest salt concentration, but only in the presence of red maple litter. This effect probably was a consequence of synergistic toxicity from maple chemistry and road salt. Addition of soluble C can benefit some zooplankton (Fey et al.

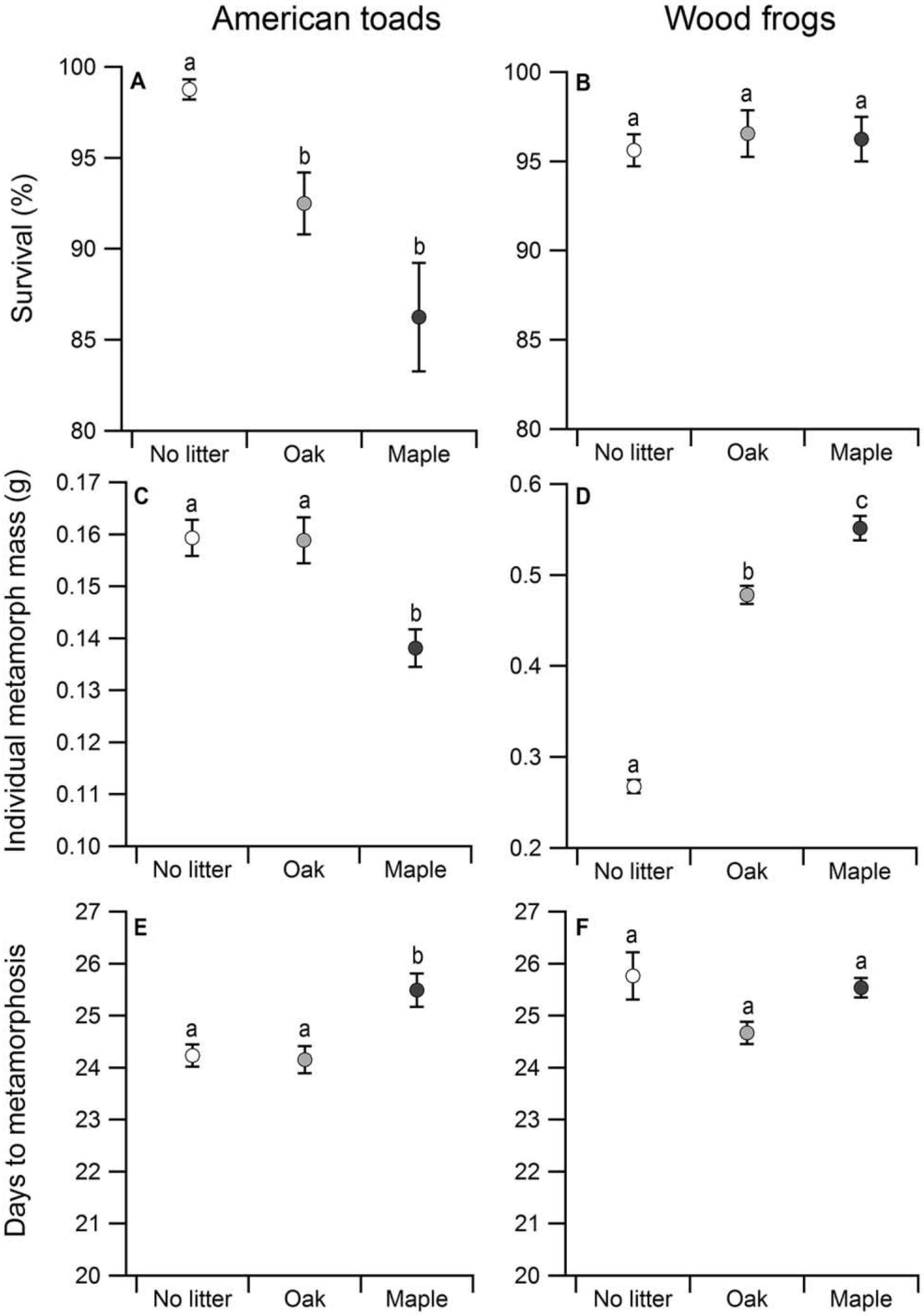

Figure 6. Mean (±SE) % survival (A, D), mass at metamorphosis (C, D), and days to metamorphosis (E, F) of American toads (A, C, E) and wood frogs (B, D, F) in leaf litter treatments (pooled across salt treatments). Points with the same letter are not significantly different within panels ($p > 0.05$). Maple = red maple, Oak = black oak.

2015) and can ameliorate the effects of elevated salinity (Suhett et al. 2011), but red maple litter contains numerous phenolic compounds that can reduce the survival or performance of some consumers (e.g., tadpoles; Stoler and Relyea 2016). The salt tolerance of most zooplankton varies greatly across genera and families (James et al. 2003, Sarma et al. 2006), but the maximum tolerance of one common copepod group (*Microcyclops* sp.) is 670 mg total dissolved solids/L (mostly NaCl; James et al. 2003). Results of manipulative studies in freshwater mesocosms confirm that copepod densities are significantly reduced at similar salinities (Van Meter et al. 2011). Hence, our results indicate that low levels of salt contamination might not affect copepods, but a combination of elevated salinity and maple leachate might have synergistic effects. Research is needed to elucidate the chemical mechanism underlying this synergy and to examine effects at higher concentrations of both $Cl^-$ and maple litter inputs.

The decline in copepod densities with oak and red maple litter was associated with a concurrent increase in rotifer densities at the highest salt concentration. In contrast to copepods, several common rotifer species can tolerate salt up to 1.5 g NaCl/L (~0.9 g $Cl^-$/L; Sarma et al. 2006) and appear to benefit from small amounts of soluble C (Suhett et al. 2011). Cladocerans exhibit similar or higher tolerance to $Cl^-$ levels (Sarma et al. 2006). Rotifers generally are considered important prey resources for copepods (Diéguez and Gilbert 2002). In addition, the population growth rate of most rotifers is substantially higher than that of copepods (Allan 1976), so it seems reasonable to expect a relatively rapid and large increase in rotifer densities with even minor reductions in copepods.

We found no effects of elevated $Cl^-$ on amphibians or snails. Given the high tolerance of wood frogs (Langhans et al. 2009), American toads (Dougherty and Smith 2006), and *Physa* (Williams et al. 1999) to elevated $Cl^-$ levels, we did not expect direct toxicity. However, Karraker et al. (2008) found reductions in larval salamander and wood frog survival at conductivities of 3000 μS/cm (~1000 mg $Cl^-$/L), results suggesting that our highest $Cl^-$ concentration might be nearing the tolerance of wood frog tadpoles. Regardless, we expected to see effects of salt on tadpoles and snails through indirect foodweb pathways. In response to salt additions, Van Meter et al. (2011) found an increase in gray tree frog biomass and a decrease in time to metamorphosis. They speculated that these effects were caused by an increase in algal resources following a decrease in copepod densities, but they did not detect any actual change in phytoplankton or periphyton responses. In contrast, we found an increase in phytoplankton at higher $Cl^-$ concentrations. We think it unlikely that this response would directly affect snails or tadpoles, which are grazers of periphyton (Altig et al. 2007, Brady and Turner 2010). Instead, an increase in phytoplankton is more likely to have a negative indirect effect on consumer mass because of shading-induced reduction of periphyton biomass (Sand-Jensen and Borum 1991, Relyea and Diecks 2008). We detected changes in zooplankton and phytoplankton only at the end of the experiment, so a longer experimental duration might reveal more effects on consumers.

Despite evidence that elevated $Cl^-$ reduces microbially driven rates of litter decay (Cook and Francoeur 2013), we did not observe an effect of salt on litter decay rate. This result contrasts with those of Van Meter et al. (2012), who found a 9.7% reduction in breakdown rate of oak litter under elevated $Cl^-$ conditions (645 mg/L) and in the presence of gray tree frog tadpoles. Van Meter et al. (2012) attributed the slower breakdown rate to a reduction in microbial respiration in the elevated-$Cl^-$ treatment, and a consequent reduction in decomposition activity. One possible reason for the contrast between our results and those of Van Meter et al (2012) is the potential turnover of microbial communities in favor of salt-tolerant organisms. Langenheder et al. (2003) found that such turnover can restore the functionality of microbial communities. However, we see no reason to think that such turnover would occur in one study but not another. A 2nd possible explanation is that 32 d was an insufficient length of time in which to observe changes in mass loss, whereas Van Meter et al. (2012) recorded mass loss over 75 d. However, Schäfer et al. (2012) found that elevated $Cl^-$ concentrations in streams led to a 2-fold reduction in mass loss of *Eucalyptus* litter in 35 d, and Swan and DePalma (2012) found a 44% reduction in mass loss of *Fagus grandifolia* litter incubated for 16 d in chambers with 5000 mg $Cl^-$/L. A 3rd possible explanation is that we used wood frog tadpoles and pouch snails as consumers instead of gray tree frog tadpoles. Both wood frogs and pouch snails are generalist grazers that typically inhabit closed-canopy ponds and can ingest fragments of litter directly (Schiesari 2006, Altig et al. 2007, Turner and Montgomery 2009, Brady and Turner 2010). Such grazing activity might mask variation in litter decomposition rate. In contrast, gray tree frog tadpoles are more limited to open-canopy ponds and might be more adapted to an autochthonous diet. Functional feeding differences among wetland consumers are likely to generate different responses to salt inputs, and the role of these functional differences should be explored in future work.

## Conclusion

Our results suggest that changes in forest composition are likely to interact with ongoing anthropogenic stressors to freshwater ecosystems. Over the past century, oak has gradually declined in abundance throughout North American temperate forests because of over-browsing by white-tailed deer (*Odocoileus virginianus*), fire suppression, logging, and climate change (Abrams 1998), whereas maple stands have increased in abundance because of avoidance by browsers. Such turnover in species composition represents a major shift in the chemistry of litter inputs to both terrestrial and aquatic systems. Similarly dramatic shifts in litter chemistry are also occurring subsequent to declines in nutrient-rich species, such as elms (*Ulnus* sp.) and ashes (*Fraxinus* sp.), and the near extinction of American chestnut (*Castanea dentate*; Moser et al. 2009). Ongoing changes in forest composition might make wetlands more vulnerable to road salt pollution. Moreover, we examined only concentrations of $Cl^-$ in the lower range of observed values for wetlands in North America. Our results indicate that wetland communities might be resilient to road salt pollution at these low levels. The effects of road salt runoff will be more substantial as $Cl^-$ concentrations approach lethal levels for consumers (Kaushal et al. 2005). We observed interactions of salt inputs with leaf litter only at the highest salt level, so the interaction of salt and litter chemistry is likely to be exacerbated at higher $Cl^{-}$ concentrations.

Comparisons among studies suggest several potential mechanisms underlying the consequences of salt contamination, including functional feeding differences among consumers, species-specific toxicity of elevated $Cl^{-}$ to zooplankton, and synergistic effects of road salt and litter inputs. These potential mechanisms warrant further laboratory studies to understand the effects of human activity on wetland ecosystems. Moreover, salt pollution probably has sublethal effects on consumer populations. For example, Lambert et al. (2017) found that exposure of wood frogs to oak litter feminized sex ratios, whereas contamination by 800 mg $Cl^{-}$/L masculinized populations. In addition, the effects of highly-concentrated, short-duration pulses of road salt that are typical of many stormwater drainage wetlands are worth exploring (Silver et al. 2009). Last, surveys of natural systems that vary in $Cl^{-}$ concentration and litter inputs should be conducted to assess whether our findings in mesocosms are representative of the effects of salt on natural aquatic communities.

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