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# Juvenile Amphibian Response to Oak and Maple Leaf Litter

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## Abstract

The composition of tree species within New England forests has changed significantly in recent decades, with an increase in maple (*Acer* spp.) abundance and a decrease in oak (*Quercus* spp.) abundance. Changing forest structure results in changing leaf litter composition of the forest floor, which influences the ground-dwelling amphibians that live in the litter. To better understand how changes to forest composition alters amphibian habitat quality, we recorded the growth and survival of 27 juvenile wood frogs (*Lithobates sylvaticus* or *Rana sylvatica*) and 27 juvenile American toads (*Anaxyrus americanus*) in response to leaf litter type. Between early August and late October 2017, half of the individuals of each species were raised in terrestrial enclosures with maple litter, and the other half were raised in terrestrial enclosures with oak litter. We used Kaplan-Meier survival estimates to find that frogs and toads raised in maple leaf litter had higher survival rates than those raised in oak leaf litter. Additionally, we created a mixed-effects model with individual as the random effect to quantify the effect of leaf litter type on growth. In both amphibian species, mass of individuals raised in maple litter was greater than mass of individuals raised in oak litter. Increased survival and enhanced growth in maple litter suggests that juvenile amphibians benefit from the changing forest composition. Our results are in contrast with research in aquatic systems research, which found negative effects of maple litter decomposition on amphibian larvae. Future research should take our results and larval results to model population level effects of forest change on amphibian growth and survival. Furthermore, our research can help inform future soil quality and leaf litter community studies by accounting for a potential increase in amphibian populations as maple forest expands.

## Introduction

New England's forest composition has been drastically altered over the past four centuries, and this habitat modification has strong impacts on the region's wildlife. Since European settlement, oak (*Quercus spp.*) trees declined from composing 18% of trees in the forest to only 11% of the trees. In contrast, maple trees (*Acer spp.*) have increased from 11% of tree composition to 31% (Thompson et al. 2013). The change in forest composition has been traced to a variety of factors. Red maple (*Acer rubrum*), for example, is becoming widespread as a result of fire suppression, frequent disturbance, and the decline of competitors such as ash (*Fraxinus spp.*) and American chestnut (*Castanea dentata*). The expanding deer population favors the growth of maple trees in the forest understory, because deer preferentially browse on oak saplings and high deer density prevents oak regeneration. These ecological factors have allowed red maple to become more abundant in their lowland wetland habitat and even spread into upland forests where they were previously rare (Abrams 1998).

Changing forest species composition has major effects on forest floor dynamics. Forest floor dynamics refers to the many processes of change in the leaf litter and soil. These changes come about through processes such as ecological succession, chemical cycling, and decomposition. Ecological succession, such as the shift from oak dominance to maple dominance in the canopy, leads to different levels of carbon, mineral (e.g. calcium), and nutrient (e.g. nitrate) deposition on the forest floor, and changing chemistry affect decomposition rate in the leaf litter (Alexander and Arthur 2014). Decomposition is a dominant process that occurs within the forest floor, in which invertebrates, fungi, and bacteria consume and break down organic matter, including leaves, dead plants and animals, and excrement. The decomposition process affects carbon cycling within forested systems and thus has implication for climate change, as

carbon is either sequestered into the soil or, often upon decomposition, released back into the atmosphere. Amphibian biomass is a large component for forest floor systems because their life history in both aquatic to terrestrial environments allows for nutrient transfer between the two ecosystems (Grieg et al. 2012). Amphibians both consume invertebrates as prey and serve as prey to other forest floor-dwelling animals, and thus potentially affect the abundance of herbivores, detritivores, and nutrients within the system. If the amphibian population declines, then the invertebrate populations and the associated decomposition rates and carbon dioxide release would increase as well. Alternatively, an expanding amphibian population could reduce invertebrate populations and slow decomposition rates. A larger terrestrial amphibian population will also enhance the cycling of nutrients between terrestrial and aquatic habitats. Here we focus on two pond-breeding amphibian species that are likely to be abundant within the forest floor surrounding wetlands.

Within wetlands, previous experiments have found that larvae of two common amphibian species, the wood frog (*Rana sylvatica* or *Lithobates sylvaticus*), and the American toad (*Anaxyrus americanus*) have reduced mass and survival rates when raised in ponds with red maple litter when compared to oak litter (Rubbo and Kiesecker 2004, Cohen, Rainford and Blossey 2014, Stephens, Berven, and Tiegs 2013). This reduced performance is partly due to the fact that red maple litter is nutrient-poor and phenolic-rich (Abrams 1998). For wood frogs, higher phenolics lead to decreased larval survival, delayed tadpole development, and increased exposure rate to the parasite *Ribeiroia ondatrae*. This trematode parasite can cause limb deformities in metamorphs, which in turn contribute to early mortality (Stephens et al. 2016). Furthermore, oak litter in ponds is more beneficial for amphibian larvae because oak litter favors phytoplankton communities whereas maple litter favors bacterial communities, and

phytoplankton communities provide food for tadpoles (Rubbo and Kiesecker 2004). Conversely, ponds with white oak and sugar maple litter both have high tannin concentrations, and high tannin concentrations lead to low primary production (Earl et al. 2014). Meanwhile, other studies suggest that toads exhibit lower sensitivity to litter type than wood frogs as toad tadpoles are unaffected by tannin concentrations (Earl and Semlitsch 2015a). While many studies have investigated the effect of maple litter on larval growth and survival, few researchers have studied these same effects on juvenile amphibians.

Our goal was to understand how changes to the tree species composition within New England hardwood forests alters the habitat quality for juvenile amphibians. Wood frogs and American toads are less abundant in upland maple litter than in other hardwood litter (DeGraaf and Rudis 1989), which suggests that this habitat is less suitable for amphibians than other habitats. Maple litter on the forest floor decomposes more rapidly than oak litter (Cote and Fyles 1994), and thus maple litter may have fewer large leaves available to juvenile amphibians seeking shelter under the structure provided by leaf litter.

We hypothesized that both juvenile wood frogs and American toads would exhibit a similar trend to larval wood frogs and American toads, and have higher survival and growth when raised in terrestrial enclosures with litter composed predominantly of oak leaves as opposed to litter composed of predominantly maple leaves. We also expected that the negative effects caused by maple litter would be more negative for wood frogs than American toads. American toads are habitat generalists and tolerant of tannins, and thus expected to perform well in both litter types. Our experiment tested this hypothesis by raising both species in oak and maple leaf litter to determine survival and growth.

## Methods

### *Life History of Wood Frogs and American Toads*

The American toad and the wood frog both begin life as larvae that hatch in aquatic environments. They live in water for less than two months, metamorphose into juveniles, and then spend the majority of their life on land (Rittenhouse and Semlitsch 2007). The American toad is a habitat generalist with a large geographic range that includes both forests and grasslands (Lannoo 2005). By contrast, while the wood frog has the largest geographic range of any amphibian in North America, it is more of a habitat specialist. Wood frogs breed in forested wetlands with high canopy cover, and use forest ravines and drainage areas with high moisture during terrestrial life stages (Rittenhouse and Semlitsch 2007, Pitt et al. 2017). This species shifts between moist places within the forest during the summer and upland hardwood stands in the winter (Baldwin et al 2006). Wood frogs and American toads are both listed as Least Concern throughout their ranges (IUCN).

### *Experimental Design*

We created four treatments for our experiment so that each amphibian species was raised in both types of litter:

- 1) American toads in maple litter
- 2) American toads in oak litter
- 3) Wood frogs in maple litter
- 4) Wood frogs in oak litter

We randomly assigned treatments to enclosures using a random number generator (Figure 1).

To create the treatments, we collected leaf litter from the UConn Forest Fenton Tract and placed approximately two kilograms of leaf litter into each enclosure in late July 2017. The leaf litter covered the entire enclosure soil surface, providing shelter for the amphibians as well as invertebrate food sources. The oak litter was collected from a stand that was predominately white oak (*Quercus alba*), and also contained other oak species: red oak (*Q. rubra*), scarlet oak (*Q. coccinea*), and black oak (*Q. velutina*). The litter also contained leaves from big tooth aspen (*Populus grandidentata*), birch (*Betula*) species, and hickory (*Carya*) species. The maple litter was collected from a stand of sugar maple trees (*Acer saccharum*) tapped for making maple syrup. This stand is predominately sugar maple, but also contains red maple (*A. rubrum*), birch (*Betula*) species, and American beech (*Fagus grandifolia*). We collected litter in fall of 2016, the time of year when litter was most abundant on the forest floor, and stored the litter in bags for the winter. We supplemented this litter with additional litter collected in spring 2017. In late July we spread the leaf litter into enclosures according to the predetermined treatment arrangement.

#### *Enclosure Construction*

Students from the Rittenhouse Lab constructed 18 terrestrial enclosures in spring 2017 (Figure 2). The enclosure walls were constructed of wildlife exclusion mesh from ERTEC Environmental Systems. ERTEC is a manufacturer of non-toxic, polymer matrix fences for wildlife and sediment control. Each enclosure had an area of one by two meters. Enclosure walls were approximately one meter high above the ground, with fifteen centimeters of connected mesh folded inward above the wall to create a barrier. Additionally, approximately fifteen centimeters of mesh wall were buried below the ground to secure the structures. Enclosures were constructed in pairs such that one wall is in common between two enclosures. We constructed lids for each enclosure pair out of high density polyethylene PAK knit shade cloth that provides



52% shade from Hummert International, with PVC attached to the north and south ends.

Uniform shading controls the light exposure and, presumably, the soil moisture evaporation for all enclosures. Lids also prevented predation from birds.

In mid-summer 2017 we spread the leaf litter into enclosures according to the predetermined treatment arrangement. Each enclosure received approximately two kilograms of leaf litter, enough to cover the entire enclosure floor and provide shelter for the amphibians as well as their invertebrate food sources.

### *Raising Amphibian Larvae*

Larvae were raised as part of another experiment that manipulated water temperature (Cordero, Jacobson, and Rittenhouse, In prep). We collected American toad and wood frog egg masses in spring 2017 and held them in the laboratory through hatching. When tadpoles reached the free-swimming stage (approximately Gosner Stage 21), we placed tadpoles in aquatic mesocosms created from 1,000L tanks of water with 52% shade cloth lids, phytoplankton, zooplankton, and leaf litter. Leaf litter originated from the same source and composition as that in the terrestrial enclosures. The amphibians remained in the mesocosms from hatching until metamorphosis. We inspected the mesocosms every day in summer 2017. When a frog or toad showed at least one front leg (Gosner Stage 37), we collected them with dip nets and housed them in small containers until they completed metamorphosis. For the first few days following tail absorption, we fed recent metamorphs flightless fruit flies from another UConn lab. As quickly as possible, we transitioned to feeding the recent metamorphs live house crickets (*Acheta domestica*) from Fluker's Cricket Farms, and provided crickets *ad libitum* each week until the recent metamorphs were feeding readily and actively moving within the containers.

### *Data Collection*

On 9 August 2017 we released all amphibians into their enclosures according to the predetermined, randomized treatment layout. Before release, we weighed and tagged all individuals with visible implant elastomer (VIE) tags from Northwest Marine Technology, Inc. for individual recognition. Each individual received a tag on the left, right, or both hind limbs. Individuals in even-numbered enclosures received a yellow-colored tag and individuals in odd-numbered enclosures received a red-colored tag. Our marking strategy allowed for six uniquely marked individuals in every linked enclosure pair. Within species-specific litter treatments, each frog or toad was randomly assigned to an enclosure using a random number generator. We released three amphibians of the same species into each enclosure. Every enclosure received ten two-week-old crickets weekly from 9 August to 21 October. These crickets served as supplemental food to the invertebrates naturally occurring within the leaf litter.

Data collection took place between August and October 2017. We sampled weekly from 9 August until 23 September, then every other week through 21 October. This sampling design resulted in 8 sampling occasions. In each sampling session, we searched each enclosure for approximately twenty minutes or until we found all three individuals. We padded each individual to remove excess moisture, then recorded mass, snout-vent length (SVL), and the VIE mark, then released the amphibians back into the enclosure.

### *Analysis Methods*

We determined our survival data using minimum number known alive (MNKA) in each week. For example, when we did not observe an individual in a week but observed that individual in following weeks, we listed these individuals as surviving even in weeks they were not detected. We calculated both weekly and experiment-long survival rates using Kaplan-Meier

estimates (Kaplan and Meier 1958). Kaplan-Meier survival estimates account for the number of individuals at risk of death during each time interval. We were able to extract survival estimates for survival probability within each given week, as well as cumulative Kaplan-Meier survival to each week. We also modeled growth based on weekly measurements of individuals' weight using the lmer function in Program R (R Core Team 2017). We used an information theoretic approach and AIC model ranking to determine whether enclosure needed to be accounted for within the model of growth. We expressed three candidate models as mixed-effects models. All models included fixed effects of an interaction between amphibian species and leaf litter type, an interaction between leaf litter type and week number, an interaction of amphibian species and week. All models also included individual as a random effect. The second candidate model included enclosure as a fixed effect, and the third candidate model included enclosure as a random effect. By including individual as a random effect in all models, we were using individual as the unit of analysis and assuming that the grouping of individuals within enclosures has no measurable effect on survival and growth. We used model ranking procedure to test this assumption. Enclosures could conceivably explain variation in the data as differences could occur between enclosures at the edge versus center of the array, proximity to different habitat types, and slight elevation difference across the enclosure array. We ranked models according to the AIC value of each model and the model complexity. For each model, we tested assumptions of normality and equal variance using a normal q-q plot and a residual plot (Figure 3 and 4). We tested for model fit by calculating the marginal r-squared and the conditional r-squared values. Marginal r-squared value describes the proportion of variance due to fixed effects, while conditional r-squared value describes the proportion of variance due to both fixed and random effects. The best model had a marginal r-squared value of 0.545 and a conditional r-squared

value of 0.801. Using the top ranked model, we estimated the difference in mass between leaf litter type and between species.

## Results

### *General Information*

We initially released 54 amphibians: 27 of each species. While we sampled 8 times, the recapture rate in the final sampling session dropped sharply from 21 individuals to 11 individuals. The weather was cooling at this time, so we interpreted the low recapture rate as a result of the amphibians beginning their hibernation period rather than reduced survival rate. We therefore did not include Week 8 in our analysis for either growth or survival. Total recapture rate dropped from 40 individuals per week in Week 1 to 21 individuals per week in Week 7, with a mean recapture rate of 24 individuals each week. Weekly recapture rate was relatively constant from Week 2 onward (Table 1). American toad mean mass for all individuals was 0.566g upon release. Similarly, mean mass upon release for only the toads who survived the entire experiment was 0.594g. Mean toad mass in Week 7 was 1.441g. Mean wood frog mass for all individuals was initially 0.805g, and mean mass for survivors of the entire experiment was 0.884g. Mean wood frog mass was 2.096g in Week 7.

### *Survival*

We estimated that Kaplan-Meier survival was higher for frogs raised in maple litter than for frogs raised in oak litter (Figure 5, Table 2). Survival rate using MNKA steadily declined over time, while the weekly probability of survival showed no clear trend among the four treatments (Table 1, Figure 6).

### *Growth*

After ranking several models, we discovered that regardless of complexity, all models had AIC values that were within 2 AIC units of each other and thus are competing models. When models are competing, the model deviance is not reduced by an amount greater than the penalty for adding the additional parameter (i.e., enclosure) to the model and thus this parameter is uninformative (Arnold 2010). We therefore selected the model without enclosure as a parameter as the best model (Table 3). Using this model we determined that leaf litter type had a significant impact on mass (Table 4), and that amphibians in maple litter had higher masses than amphibians in oak litter (Figure 7). SVL showed no clear trend and was therefore not included as a measure of amphibian growth.

### Discussion

Our experiment simulated the shift in forest floor litter composition to reflect the effect of the expansion of maple and the reduction of oak on juvenile amphibians. We conclude that wood frogs and American toads living in maple-dominant litter experienced higher growth and survival rates than those living in oak-dominant litter. The high r-squared values, especially for the conditional r-squared value ( $r^2=0.801$ ), demonstrate that this model is a good fit and explains the data well. Additionally, neither species exhibited a significantly higher growth or survival rate than the other in response to leaf litter type. These results contradict our hypotheses, as we expected both species to have greater growth and survival rates in oak litter. We also expected wood frogs to have lower survival rates than American toads due to toads' niche as habitat generalists.

Our results also seem to contradict several other areas of research into the impacts of leaf litter on amphibian development. The misconceptions may have arisen in part because the

ecology of leaf litter in aquatic environments with larvae is very different from the ecology of leaf litter in terrestrial environments with juvenile amphibians. For example, while maple litter in ponds contains highly concentrated tannins, sugar maple leaf litter in terrestrial environments loses 70% of its tannins to the soil in the first month after leaf drop in the fall (Baldwin and Schultz 1984). The loss of tannins to the soil may prevent juvenile amphibians from being exposed to the tannins. Sugar maple litter also shows higher levels of nitrate production and loss than red oak litter (Lovett et al. 2004). Additionally, sugar maple litter has higher levels of carbon, organic matter, and moisture than oak litter (Templer, Findlay, and Lovett 2003). Moisture is especially important as amphibian presence in forests is positively associated with habitats of high soil moisture, suggesting that the habitat is more suitable for them (Rittenhouse et al. 2008, Wyman 1988). Furthermore, microbial respiration is higher in sugar maple litter tannins than in red oak litter tannins, implying a more productive community (Talbot and Finzi 2008). Finally, while high nutrient levels in detritus resulted in lower wood frog survival, these nutrient levels also contribute to greater mass of individual juveniles (Milanovich, Barrett and Crawford 2016). While further study is needed, the microbial productivity of maple leaf litter could support a more diverse and productive invertebrate community than oak litter, which in turn could provide additional food for the amphibians.

The results of our study have important implications for the life history and ecology of American toads and wood frogs. The initial mean mass of survivors of the entire experiment was very similar to mean mass of all individuals for both amphibian species. This suggests that initial mass of individuals did not affect their likelihood of survival. Additionally, both species appear to be more strongly fit to changing forest composition than we predicted. Juvenile amphibians therefore are not greatly threatened by the continued expansion of maples. While tadpoles are

still negatively affected by maple litter, we found that terrestrial juveniles were very successful in the maple litter, creating the potential for success in the juvenile life stage balancing out losses in the larval life stage. Higher juvenile fitness in maple litter could result in more individuals that survive to breed, which could lead to future population-wide adaptation to changing forest structure.

One important note in this study was the presence of predators and competitors. We chose to use mesh-walled enclosures so that invertebrates could enter freely. The mesh walls kept out many large animals, but at least one juvenile garter snake (*Thamnophis sirtalis*) was observed inside some of the enclosures multiple times. It is possible that this snake preyed on some amphibians or their invertebrate food. Some other animals, such as white-footed mice (*Peromyscus leucopus*), praying mantises (*Mantis religiosa*), wolf spiders (family Lycosidae), and other small animals were also able to enter the enclosures. These other species may have competed with the amphibians for space and food. While these complications may have affected individuals, our information theoretic approach allowed us to account for their effects on enclosure-level data. By ranking models with AIC values and observing that AIC value did not significantly differ between models (Table 3), we determined that enclosure is insignificant as either a fixed and random effect.

Our procedure allowed us to eliminate the possibility of other potential causes of death and errors in the study. We calculated weekly probability of survival, which showed no clear trend between all four treatments in either short term or long term (Figure 6). There is no particular week in which all treatment survival rates decrease together. Each of the four treatments also does not show a trend in weekly survival probability over the course of the study. If a severe storm or a particularly dry week affected juveniles, then weekly probability of

survival should have dropped for all treatments. Furthermore, weekly recapture rate was relatively consistent while weekly survival rate (MNKA) dropped (Table 1). These trends suggest that our survival estimates are not biased by low detections.

There were several ecological factors that we did not account for due to the small scale of the study, but should be investigated in the future. First, future studies should investigate the microhabitats and microclimates of oak and maple litter. We observed that, as in other studies, our maple litter appeared to decompose faster than oak litter. Rapid decomposition likely impacts the mobility and shelter for both the amphibians and their invertebrate prey. The invertebrates in enclosures with maple litter treatments may have had less shelter to avoid the amphibians, and so the amphibians in maple litter may have had easier access to food than amphibians in oak litter.

In light of our snake encounter, the role of predation and its intersection with litter type should be investigated as well. King and King (2011) observed that wood frogs may use their skin coloration to avoid predation, and coloration often develops to match the leaves near the frogs' breeding ponds. It would be beneficial to learn whether the color of maple litter facilitates camouflage better than oak litter. A related factor to investigate is the interaction of sex and litter type. Wood frog color is sexually dimorphic, and while sex determination occurs during the larval stages, color differentiation in sexes occurs in terrestrial juveniles leading up to the first winter (King and King 2011, Lambert et al. 2017). Such changing coloration may also intersect with leaf litter type due to the leaves' color difference, especially as the differentiation occurs in the same life stage and time frame as our experiment.

Further studies should focus on the maple litter invertebrate community in comparison to the oak community. Greater amphibian survival could negatively impact the populations of their prey. Reduced invertebrate populations may, in turn, reduce the rate of decomposition in the



forest floor. Alternatively, increased amphibian growth and survival in maple litter could result from an invertebrate community that is more diverse or has greater biomass than the oak litter community. The expansion of invasive earthworms is another confounding factor as the worms modify the soil and compete with native invertebrates. Earthworms such as *Dendrobaena octadra*, *Aporrectodea spp.*, and *Lumbricus spp.* interfere with the mixing of soil layers and litter decomposition. This process of interference can remove nutrients from the litter and upper soil, reduce understory plant diversity, and cause declines in mycorrhizal diversity (Frelich et al. 2006). The reduced soil, plant, and fungal quality are associated with poorer quality invertebrate communities. Over five study sites in New York, abundance of litter-dwelling arthropods declined by 69.9% when earthworms were introduced (Burtis et al. 2014).

Future studies should also investigate more complex and spacious plots of maple and oak litter. Previous studies have shown that features such as brush piles, downed wood, and canopy cover contribute to increased wood frog and American toad survival rates by preventing desiccation (Earl and Semlitsch 2015b, Rittenhouse et al. 2008). Leaf litter depth is also positively associated with growth (Earl and Semlitsch 2015), so future studies can add enough litter to not only cover the enclosure ground but also rise above it. Additionally, space for a wider range and greater dispersal allow many amphibians, including wood frogs, to persist even in heavily modified habitats (Harper, Patrick, and Gibbs 2015).

Finally, future research should study full amphibian life cycles to determine long-term impacts of maple litter expansion. Adults should be studied to determine whether they are as well-adapted to maple litter as juveniles, and multiple generations can be studied to test for adaptation to the different leaf litter environments.

## Conclusion

We sought to understand the impact of New England's changing forest composition on juvenile amphibian growth and survival. Unlike larvae, juvenile wood frogs and American toads had higher growth and survival rates in maple leaf litter than in oak litter. Furthermore, both amphibian species were affected by the treatments in spite of different habitat specialization. This research has strong implications for the future of forest floor and soil ecology, as stable or even increasing amphibian populations affect their prey abundance, habitat, and litter decomposition.

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doi:10.1371/journal.pone.0072540

## Tables and Figures

Table 1: Number of recaptured animals detected during sampling each week (a), and Minimum Known Number Alive (MNKA) each week (b).

<b>Week</b>	<b>1a</b>	<b>1b</b>	<b>2a</b>	<b>2b</b>	<b>3a</b>	<b>3b</b>	<b>4a</b>	<b>4b</b>	<b>5a</b>	<b>5b</b>	<b>6a</b>	<b>6b</b>	<b>7a</b>	<b>7b</b>
<i>L. sylvaticus</i>	15	20	9	15	6	14	7	13	8	13	8	10	8	8
<i>A. americanus</i>	25	27	16	21	11	20	15	17	14	15	13	14	13	13
<b>Individuals Recaptured</b>	40	47	25	36	17	34	22	30	22	27	21	24	21	21

Table 2: Kaplan-Meier Survival Estimate: cumulative survival probability from the beginning of the study through to Week 7.

<b>Treatment</b>	<b><math>\delta S</math></b>
1 (Maple ANAM)	0.266666667
2 (Oak ANAM)	0.25
3 (Maple LISY)	0.333333333
4 (Oak LISY)	0.2

Table 3: Three candidate models of growth ranked by AIC value demonstrate that the addition of enclosure within the model is not informative.

<b>Model</b>	<b>Log Likelihood</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>	<b>w</b>
Mass~Species*Litter+Litter*Week+Species*Week+(1 Individual)	-47.2	112.4	0	0.312
Mass~Species*Litter+Litter*Week+Species*Week+(1 Individual) +Enclosure	-46.6	113.3	0.9	0.199
Mass~Species*Litter+Litter*Week+Species*Week+(1 Individual) +(1 Enclosure)	-45.8	111.5	-0.9	0.4891 8945



Table 4: Mixed effects model of amphibian mass in response to litter type, species, and week.

	<b>Estimate</b>	<b>Standard Error</b>	<b>Degrees of Freedom</b>	<b>T value</b>	<b>P value</b>
Intercept	0.534701566	0.083	68.243	6.429	1.281e-10
Species	0.189938929	0.126	69.91	1.502	1.331e-01
Litter	0.002806206	0.123	64.99	0.0228	9.819e-01
Week	0.160303145	0.011	183.906	14.958	0.000
Species by Litter	0.039876366	0.173	59.506	0.230	8.177e-01
Litter by Week	-0.056172922	0.016	193.033	-3.505	4.572e-04
Species by Week	0.031815623	0.015	191.085	2.063	3.908e-02

Figure 1: Random assignment of experimental treatments to enclosures. Diagram not to scale.

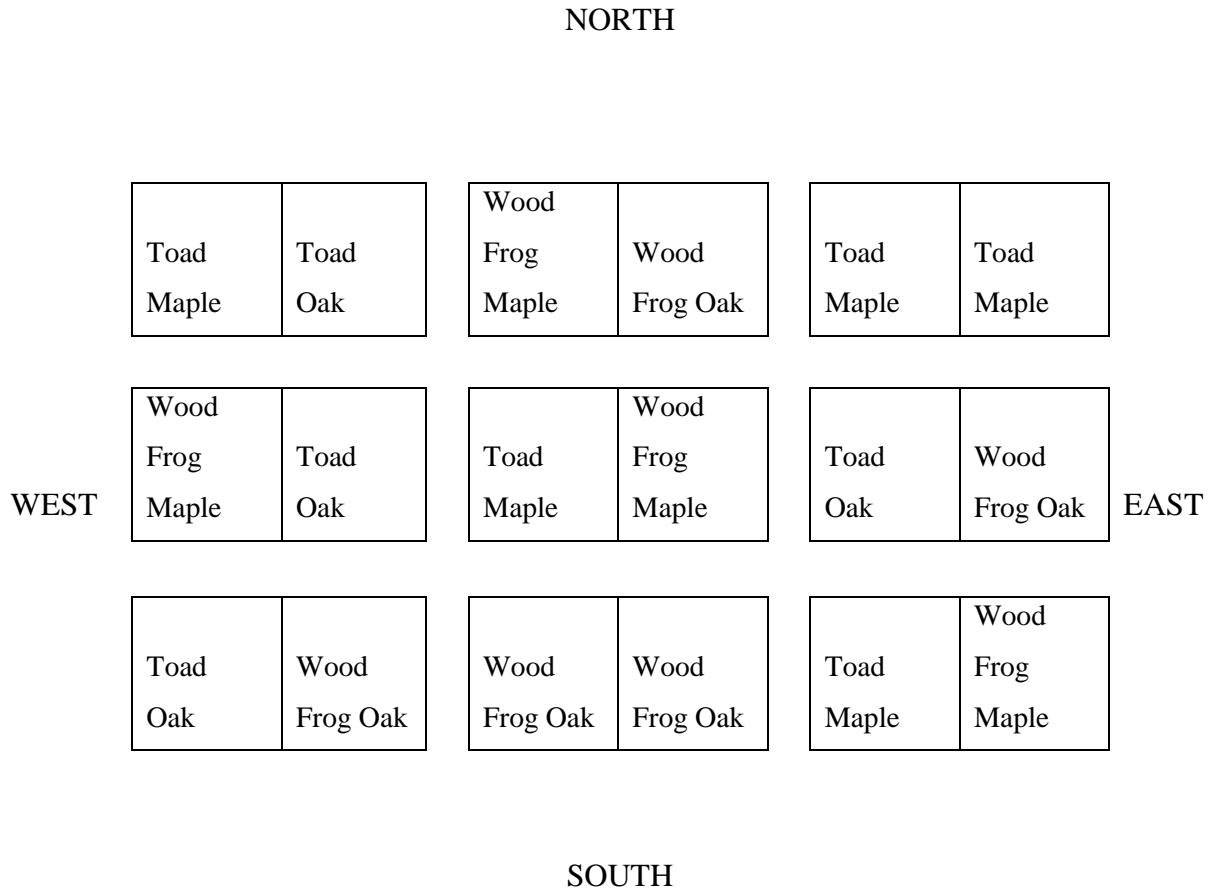


Figure 2: Photo of terrestrial enclosures for amphibian with the lids open



Figure 3: q-q normal plot of best growth model.

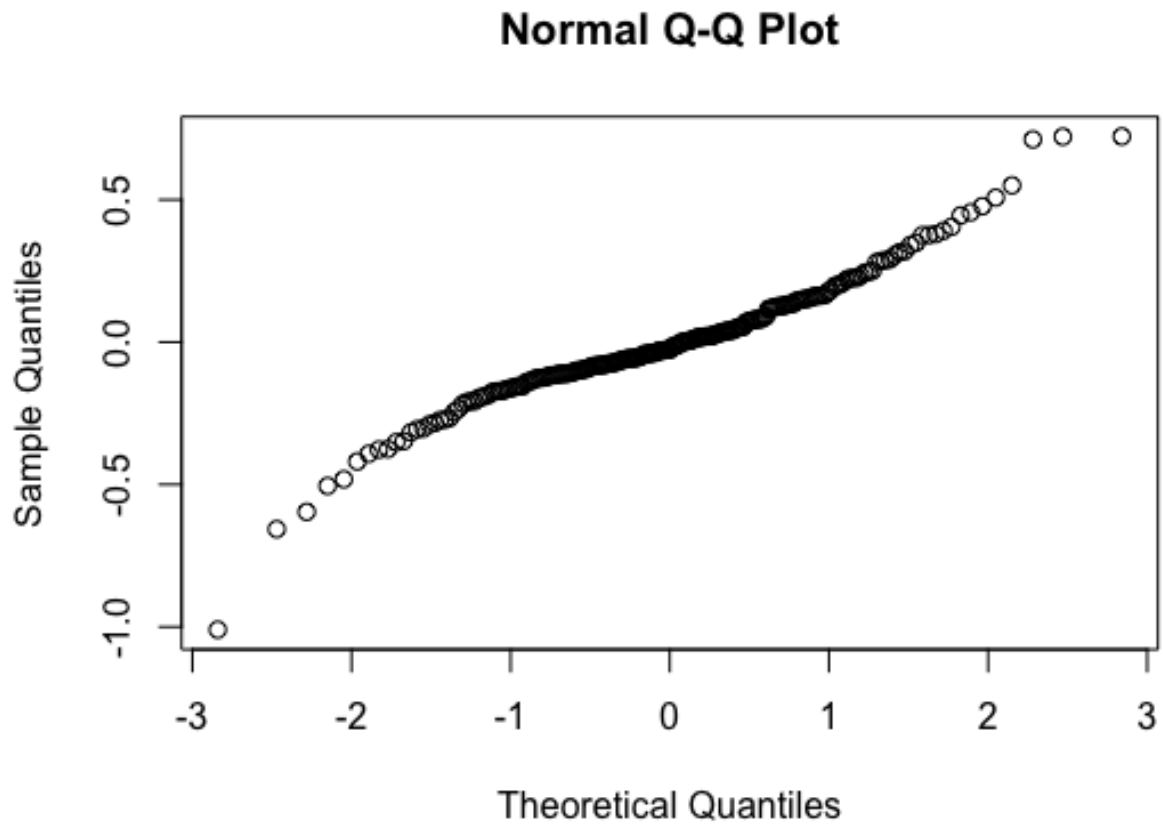


Figure 4: Residual plot of best growth model.

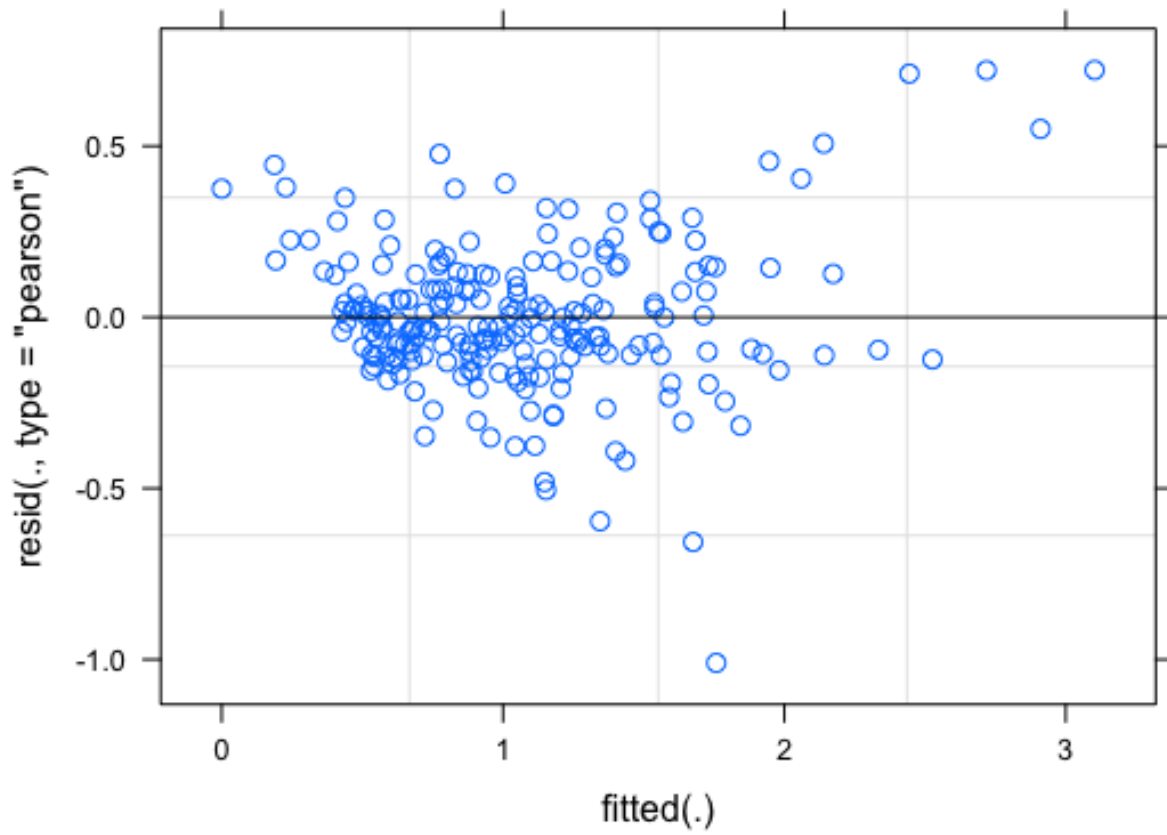


Figure 5: Kaplan-Meier Survival Estimate of probability of surviving to a given week. American toad (ANAM) treatments in blue; Wood frog (LISY) treatments in green; dark colors are Maple litter; light colors are Oak litter

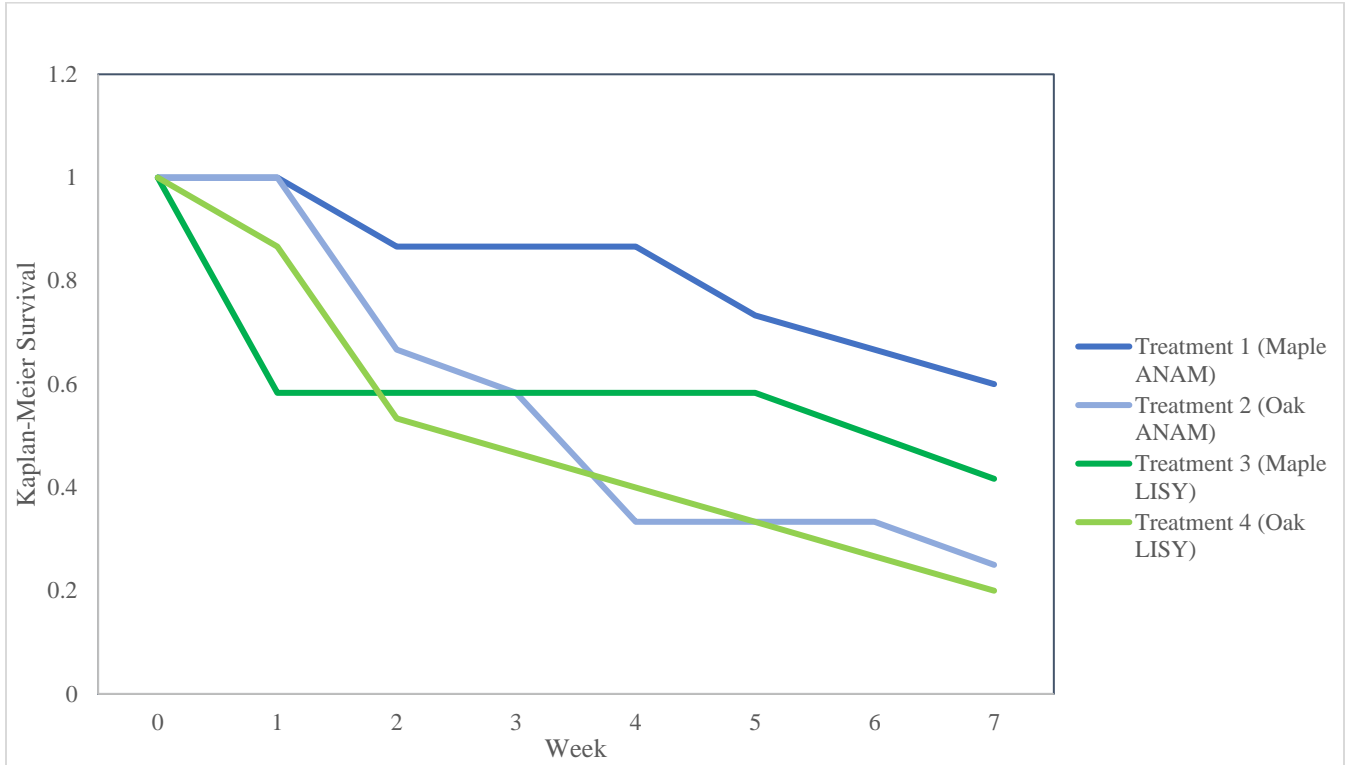


Figure 6: Probability of surviving within a specific week. American toad (ANAM) treatments in blue; Wood frog (LISY) treatments in green.

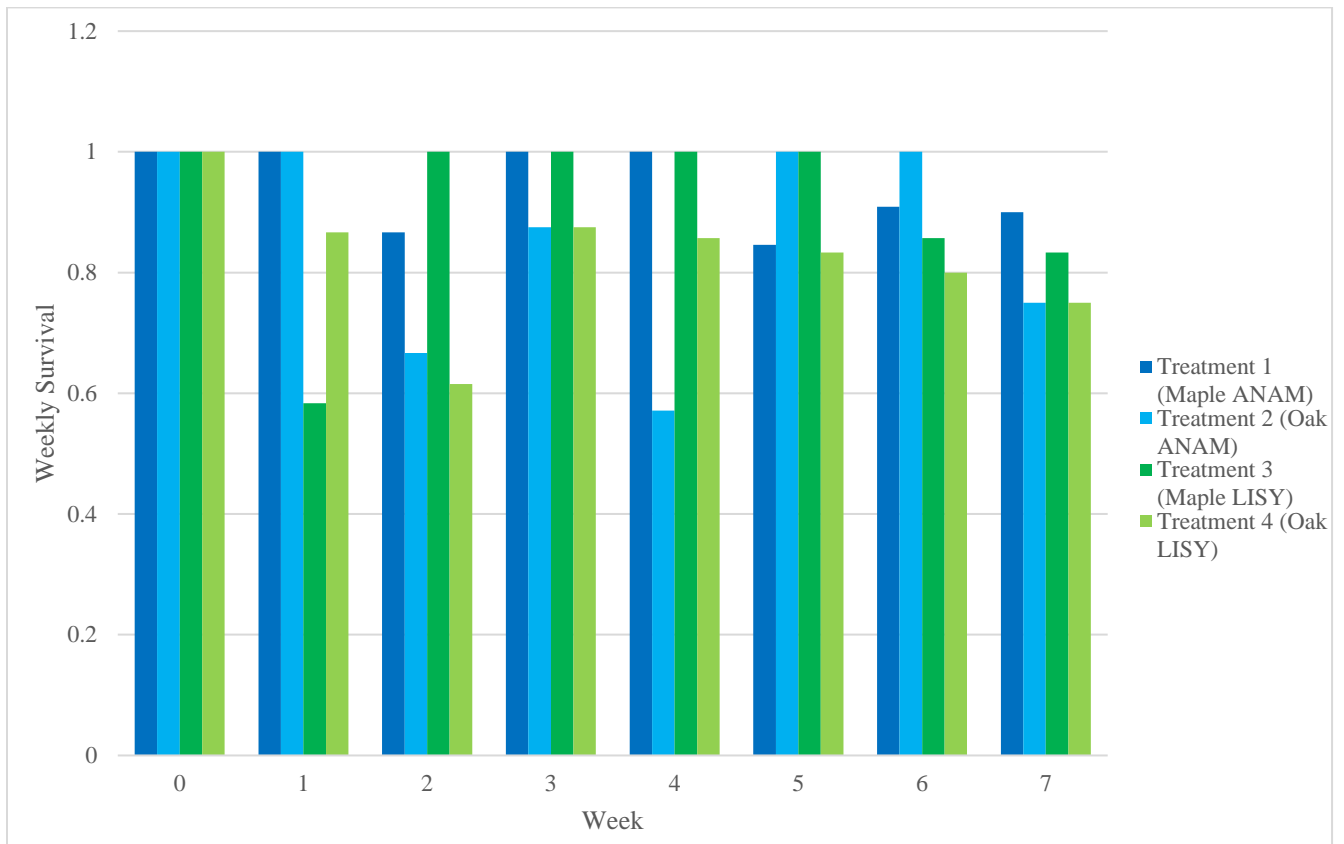


Figure 7: American toad (ANAM) and wood frog (LISY) weekly mass in response to leaf litter type by week, amphibian species by week, and interaction between amphibian species and leaf litter.

