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Leaf litter species identity alters the structure of pond communities

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The input of leaf litter resources is a major driver of ecosystem processes in terrestrial and freshwater habitats. Although variation exists in the quantity and composition of litter inputs due to natural and anthropogenic causes, few studies have examined how such variation influences the structure and composition of aquatic food webs. Using outdoor mesocosms, we examined the bottom–up effects of 10 chemically distinct tree litter species on microbial, algal, invertebrate and vertebrate fauna found in temperate ponds. We hypothesized that individual litter species, which differ in their traits, would differentially and predictably affect abiotic and biotic elements of pond communities. We further hypothesized that the presence of leaf litter, regardless of species, would elevate resource supply and increase the biomass of community members. Finally, we hypothesized that a mixture of litter species would have non-additive effects on community responses. We followed the system for >4 months and measured >30 abiotic and biotic responses related to primary and secondary production. The different species of leaf litter had major effects on abiotic and biotic responses, including phytoplankton, periphyton, zooplankton, snails, amphipods and tadpoles. Most biological responses were negatively associated with soluble carbon content of litter, or litter decay rate. Other litter traits, including phenolic concentrations and litter C:N were of secondary importance but did exhibit both positive and negative associations with several responses. The absence of litter had pervasive effects on abiotic attributes, but did not promote substantial changes in organism biomass. Most responses to the litter mixture were additive. Our results suggest that changes in temperate forest composition can strongly affect pond communities.

Shifts in the composition and diversity of primary producers can frequently have substantial effects on ecosystem function (Price et al. 1980). At both local and regional scales, plant chemistry exhibits interspecific variation in the composition of primary compounds (i.e. nutrients essential for growth and structure) and secondary compounds (i.e. defense compounds; Ollinger et al. 2002). It is well-known that such interspecific differences in living and senesced foliar chemistry can have unique effects on rates of herbivory and decomposition, and subsequently on the flow of energy through an ecosystem (Webster and Benfield 1986, Facelli and Pickett 1991, Scott and Binkley 1997, Lecerf et al. 2011, Eggert et al. 2012). However, we know far less regarding how variation in plant species composition alters the abiotic and biotic structure of the communities that process these inputs. As a consequence, we lack a mechanistic understanding for how changes in plant diversity translate to ecosystem processes.

Understanding the community effects of changing plant composition is particularly important in temperate forests, which have undergone massive shifts in vegetative composition over the past century from natural and human disturbances. In these systems, up to 90% of all plant material eventually senesces, often in a single seasonal pulse, and is processed by food webs in both aquatic and terrestrial systems (Facelli and Pickett 1991, Wallace et al. 1997). After falling, litter is immediately colonized by bacteria and fungi that nutritionally enrich the litter. Fragments of litter and colonies of microbes are subsequently consumed by grazers and their predators. Through respiration, excretion and egestion, energy and nutrients are released from the litter as inorganic compounds that are readily absorbed by primary producers (Gessner et al. 1999). Relative to terrestrial systems, the rate of this process is generally accelerated in freshwater environments (e.g. streams, ponds) where physical abrasion and leaching from water hasten the decomposition process, leading to relatively high biological activity and additional consumer biomass (Wallace et al. 1997, Wetzel 2001, Lecerf et al. 2007).

Although stream ecosystems have served as the primary system of interest for classic studies regarding the effects of litter on aquatic communities, recent studies indicate the importance of examining pond and wetland ecosystems. Like streams, ponds and wetlands are abundant features of a forest landscape and centers of relatively rapid nutrient cycling (Wetzel 2001). However, because these systems retain litter for longer periods of time relative to streams, consumers may have different responses to litter chemistry. Indeed, lab and field studies examining the growth and development of common wetland consumer species – such as larval anurans and mosquitos – demonstrate strong, positive relationships with nutrient content of litter inputs and negative relationships with the concentration of secondary compounds (e.g. phenolics, alkaloids) and lignin content (Tuchman et al. 2003, Maerz et al. 2005, Reiskind et al. 2009, Cohen et al. 2012). However, these studies have examined the effects of litter on only single species or a small subset of the species that are naturally found in wetland communities. To understand the more holistic effects of litter inputs on aquatic systems, we need to explore the effects of litter on diverse wetland communities.

In this study, we employed outdoor mesocosms to examine the effects of litter inputs, litter chemistry, and litter mixing on diverse pond communities containing species spanning multiple phyla. Mesocosms provide a useful starting point for generating predictions of what may occur in natural ecosystems, particularly for phenomenon that we are just beginning to understand. Similar to the approach of Cohen et al. (2012), we examined the effects of many different litter species to explore species-specific effects as well as general relationships of litter traits with community attributes (i.e. a trait-based approach; McGill et al. 2006). By using traits shared among all plant species (e.g. nitrogen content), it might be possible to generalize the effects of plant litter in ponds and wetlands within similar ecoregions (e.g. other temperate forests). We also examine effects of mixing litter species, which is known to have non-additive (i.e. interactive) effects on ecosystem processes in stream and terrestrial systems (Gessner et al. 2010).

We generated 12 treatments, including a no-litter treatment, 10 monoculture treatments of litter from different tree species that varied widely in chemistry, and a mixed-litter treatment to investigate possible interactions among leaf litter species. We hypothesized that individual litter species will differentially shape abiotic and biotic elements of pond communities as a consequence of their individual chemistries. More specifically, we predicted that the majority of responses will be negatively impacted by increasing levels of soluble carbon, phenolics, lignin and C:N, but positively influenced by increasing litter decay rate. We also hypothesized that the presence of leaf litter, regardless of species, will elevate resource supply and subsequently increase the biomass and survivorship of community members. Finally, we hypothesized that a mixture of all litter species will have non-additive effects on pond community responses.

Methods

Experimental design

The experiment was conducted at the University of Pittsburgh's Pymatuning Laboratory of Ecology in northwest Pennsylvania. We used a completely randomized design with 12 treatments, each replicated four times for a total of 48 experimental units. Based on a prior experiment (Stoler and Relyea 2011), this level of replication was expected to provide sufficient power to differentiate responses among treatments. The 12 treatments consisted of 10 litter species monocultures, a control treatment containing no leaves, and an even mixture of all 10 litter species with the same total litter biomass as the monocultures (Table 1). All litter species used in this study may be found around wetlands where amphibians breed and are common in western Pennsylvanian forests, or were once common in the case of American chestnut. In addition, many species are the focus of substantial conservation issues. For example, American elm and green ash are both declining due to invasive diseases and insect pests (Moser et al. 2009). In contrast, species such as red maple and black cherry are increasing in abundance due to overbrowsing of other species (e.g. oaks) by mammalian herbivores (Abrams 2003). Although many of the litter species are not likely to co-occur, the purpose of the litter mixing treatment was to test the effects of litter mixing and not to generate a realistic mixture.

Table 1. Treatments used in the experiment, including common names, codes and taxonomic family. For all single litter species treatments, the five litter traits used in the redundancy analysis are given. Values for soluble carbon, lignin and total phenolics are means from analyses performed in triplicate; values in parentheses represent 95% confidence intervals (CI). Note that values for the mixture treatment are averages of individual species traits. Values for C:N represent single samples analyzed in a CHN analyzer with 4% measured accuracy. Values for decay rate are means of decay coefficients expressed on a per week basis (sensu Petersen and Cummins 1974); values in parentheses represent 95% CI.

Treatment	Code	Family	Species	Soluble carbon (%)	Lignin (%)	Phenolics (%)	C:N (g g^{-1})	Decay coefficient (-k)
Red maple	RM	*Aceraceae*	*Acer rubrum*	40.0 (± 10.5)	30.0 (± 14.5)	8.04 (± 1.56)	57.7	0.088 (± 0.013)
Hybrid chestnut	CH	*Fagaceae*	*Castanea dentata × C. mollissima*	39.2 (± 7.7)	40.8 (± 9.4)	5.11 (± 0.57)	73.2	0.092 (± 0.011)
Black oak	OAK	*Fagaceae*	*Quercus velutina*	29.0 (± 3.5)	40.0 (± 7.0)	4.55 (± 0.28)	34.4	0.041 (± 0.007)
American beech	BCH	*Fagaceae*	*Fagus grandifolia*	23.4 (± 4.9)	39.0 (± 3.9)	4.21 (± 0.74)	65.2	0.039 (± 0.015)
Tulip poplar	TP	*Magnoliaceae*	*Liriodendron tulipifera*	43.8 (± 2.5)	38.8 (± 5.0)	0.63 (± 0.06)	55.7	0.093 (± 0.008)
Green ash	ASH	*Oleaceae*	*Fraxinus pennsylvanica*	26.3 (± 10.5)	52.4 (± 14.5)	3.76 (± 1.15)	36.1	0.099 (± 0.004)
Black cherry	CHER	*Rosaceae*	*Prunus serotina*	36.4 (± 6.8)	29.0 (± 12.0)	1.74 (± 0.49)	46.5	0.097 (± 0.011)
Black willow	BW	*Salicaceae*	*Salix nigra*	20.8 (± 1.3)	36.4 (± 2.3)	1.10 (± 0.06)	32.2	0.081 (± 0.007)
Bigtooth aspen	ASP	*Salicaceae*	*Populus grandidentata*	22.8 (± 3.1)	29.2 (± 14.9)	1.63 (± 0.05)	70.6	0.063 (± 0.015)
American elm	ELM	*Ulmaceae*	*Ulmus americana*	20.5 (± 3.1)	36.3 (± 11.7)	1.53 (± 0.10)	47.6	0.095 (± 0.007)
Mixture	MIX			*30.2*	*37.2*	*3.2*	*51.9*	*.079*
No litter	NL							

The experimental units were 800-l, black, polyethylene, cylindrical tanks that served as pond mesocosms. Each mesocosm was covered with a 60% shade cloth lid that prevented escape or entry of organisms and simulated moderate canopy cover (Schiesari 2006) while providing sufficient light for algal growth. On 16 April 2008, we added approximately 20 l of homogenized loamy soil to each mesocosm, which was then fully dried in the sun to desiccate and kill any soil macroinvertebrates. We then filled the mesocosms with well water between 18 and 21 April and allowed the soil to settle for 3 days (water depth = 46 cm). On 25 April, we collected 20-l buckets of water from five ephemeral forest ponds as sources of microbes and algae. From these same ponds, we collected zooplankton using a 250-µm zooplankton net, which was sufficiently small to collect many of the large-bodied zooplankton common of forest ponds. As is common to mesocosm experiments of this nature (Relyea 2005), we removed all predators to eliminate top–down pressure on herbivores and detritivores so that we could focus on the bottom–up effects of leaf litter. We mixed all zooplankton and water from the five ponds and introduced equal aliquots of the slurry to all mesocosms.

We added leaf litter to the mesocosms on 27 and 28 April. Therefore, 28 April was defined as day 1 of the experiment. We collected the litter from forests in western PA within one week after senescence during autumn 2007. We air dried litter for one week after collection and stored it in a dry area through the winter. Previous work demonstrates that litter in the benthos of ponds does not significantly decay during the winter (Stoler unpubl.). Although leached chemicals can photo-degrade or biologically decompose before the spring thaw, temperate forest ponds in our region are typically covered in ice during the winter and metabolic activity slows substantially. Hence, it is likely that chemicals are retained in the water through the winter, so our use of non-decomposed autumn litter is not likely to detract substantially from the realism of our experiment. For each litter species, we assessed four components of litter chemistry: soluble carbon, lignin, total phenolics, the ratio of carbon to nitrogen (C:N) and decay rate. Briefly, we assessed soluble carbon and lignin via carbon fractionation; total phenolics via the spectrophotometry after mixing with the Folin–Ciocaltea reagent; C:N via an automated CHN analyzer; and litter decay rate via the litter-bag method. We report C:N instead of percent nitrogen because C:N provides a more informative understanding of litter nutritional quality (Graças et al. 2005). Details of the methods used to assess litter traits are available in the Supplementary material Appendix 1.

We added a total of 250 g of leaf litter to each mesocosm, which represents a moderate input of litter for temperate forests (Rubbo et al. 2008). The total amount of litter was divided between 235 g of loose leaf litter and five mesh bags that each contained 3 g of litter (mesh size = 5 mm). Mesocosms assigned to the mixture treatment received equal proportions of all litter species, both as loose litter and in the mesh bags. The no-leaf treatment received empty mesh bags. At the same time as litter introduction, we added 25 g of rabbit chow to each mesocosm (including the no-litter control treatment), which are condensed pellets of ground plant material that acted as an initial source of nutrients. This initial pulse of organic nutrients is common in large mesocosm experiments (Morin 1983), and is needed to elevate nutrient levels in the water column and benthos to concentrations that would be present in natural ponds prior to litterfall. Although this input represents an artificial nutrient source, its presence among all treatments should only make it more difficult to detect treatment differences. Additionally, the presence of rabbit chow is highly ephemeral as animals rapidly consume the food and either assimilate or excrete the material into the system. On day 11, we added four ceramic tiles, oriented vertically on top of the litter and soil on the north side of the mesocosms, to serve as periphyton samplers.

We introduced several species of macroinvertebrates and anuran larvae into all mesocosms, including some of the most common consumers in our region. All introduced animals are likely to co-occur in the moderate-canopy pond environments that our mesocosms were designed to simulate (Werner et al. 2007). Between days 11 and 16, we added two species of benthic detritivores: isopods (*Asellus communis*) and amphipods (*Crangonyx psuedogracilis*). Using adults dipnetted from a local forest pond, we introduced 26 amphipods and 40 isopods to each mesocosm. To equalize early production of both species, we added the same number of gravid females to each mesocosm (8 amphipods, 6 isopods).

At the same time, we introduced two species of snails to each mesocosm: the pouch snail *Physa acuta* and ram's horn snail *Helisoma trivolvis*. Both species are generalist feeders, but are commonly considered to be periphyton grazers. The snails were introduced as eggs to eliminate the risk of introducing nematode parasites that frequently live in adult snails and subsequently parasitize tadpoles. To obtain snail eggs, we collected approximately 500 adult pouch snails and 300 adult ram's horn snails from natural ponds and held them in the laboratory to reproduce. After reproduction, we removed, mixed, and introduced 10 egg masses of each species to each mesocosm by sinking a small cup with the egg masses into each mesocosm.

We added five species of tadpoles to each mesocosm as they became available based on breeding phenology, including three spring-breeding species: wood frogs *Lithobates sylvatica*, leopard frogs *Lithobates pipies*, American toads *Anaxyrus americanus* and two summer-breeding species: spring peepers *Pseudacris crucifer* and gray treefrogs *Hyla versicolor*. Each mesocosm received 20 individuals of each species. Similar to the snails, tadpoles are generalist grazers and may even filter phytoplankton, although they are commonly considered as periphyton grazers. We collected amphibians as newly oviposited eggs from nearby ponds (8–29 egg masses per species), allowed them to hatch in pools containing aged well water, and fed them rabbit chow pellets ad libitum. Tadpoles of each species were early in development (Gosner stage 25; Gosner 1960) when added to the experiment and had the following initial masses (± 1 SE): wood frogs = 52 ± 19 mg, leopard frogs = 36 ± 5 mg, toads = 25 ± 4 mg, spring peepers = 21 ± 23 mg, and gray treefrogs = 26 ± 11 mg. We added wood frogs and leopard frogs on day 16, American toads on day 31, spring peepers on day 38, and gray treefrogs on day 57.

Abiotic measurements

To document how the leaf litter treatments affected abiotic conditions of the mesocosms, we quantified light attenuation, dissolved oxygen, pH, temperature, and temperature stratification at four sample dates (i.e. every four weeks). We measured light attenuation as the difference in photosynthetically active radiation between 2 cm and 22 cm below the water surface. We measured dissolved oxygen and pH just above the litter layer, which was approximately the same depth in all mesocosms. We measured temperature just under the water surface, and calculated temperature stratification as the difference in temperature just under the water surface and just above the litter layer. Details of these measurements can be found in the Supplementary material Appendix 1.

Biotic measurements

At multiple times during the experiment, we measured several biotic response variables. To quantify a rate of litter decay, we recorded the mass loss of litter in mesh litterbags on five sample dates (days 20, 34, 62, 90 and 118). On each sample date, we used mass loss values to calculate a rate coefficient ($-k$; sensu Petersen and Cummins 1974). To quantify algal and microbial biomass (i.e. basal production), we measured phytoplankton density and periphyton biomass monthly (phytoplankton on days 26, 48, 81 and 108; periphyton on days 33, 59, 82 and 111). Details regarding the sampling methods are provided in the Supplementary material Appendix 1.

We began estimating the abundance of the invertebrates after two months. Although earlier samples were taken, population sizes were very small and it was evident that most species had not reached carrying capacity. Hence, we do not report these earlier samples. We quantified the density of zooplankton on two sample dates (days 81 and 109). *Daphnia pulex* and *Scapholeberis mucronata* constituted 100% of all cladoceran species on both sample dates, and *Skistodiaptomus oregonensis* constituted between 95% and 92% of all copepod species on the first and second sample date, respectively. The remaining rare species were excluded from the analysis. We measured abundance and biomass of amphipods and isopods on days 62 and 90 and of the two snail species on days 66 and 94. At the same time, we also quantified the number of snail egg masses of each species on the walls of the mesocosm.

For amphibians, we collected individuals as they metamorphosed and recorded each individual's time to metamorphosis (i.e. time to Gosner stage 45). When the experiment was terminated on day 145, we collected all remaining tadpoles. For each amphibian species, our response variables were total survival in a mesocosm (i.e. survival of tadpoles + metamorphs), total biomass in a mesocosm (i.e. biomass of tadpoles + metamorphs), mean individual mass of metamorphs from a mesocosm (i.e. for those species that completed metamorphosis), and mean time to metamorphosis from a mesocosm (i.e. for those species that completed metamorphosis).

Statistical analysis

Trait-based analysis

To illustrate the effects of individual litter species and to explore generalities in the relationships between litter traits (i.e. litter chemistry and decay rate) and the abiotic and biotic responses, we employed redundancy analysis (RDA). RDA is a constrained, linear, multivariate ordination analysis that explores how variation within an independent dataset (e.g. litter chemistry; litter decay coefficients) explains variation of a dependent dataset (e.g. abiotic and biotic response variables). Canonical axes (i.e. ecological gradients) for each data set are derived such that the first ecological gradient derived from the independent dataset explains the maximum variation within the dependent dataset. The amount of response variation explained by ecological gradients is determined, and the ability of ecological gradients to significantly explain variation in the dependent dataset is then determined with a Monte Carlo permutation test. Methods of interpreting biplots of an RDA can be found in the Supplmentary material Appendix 1.

In conducting the RDA, we included five leaf litter traits in the independent dataset: total phenolics, C:N content, percent lignin content, percent soluble carbon and litter decay rate. We verified that these traits were not correlated with each other prior to analysis. Because we wanted to explore how litter traits caused the abiotic and biotic responses to change through the growing season, we conducted a separate analysis at each time point (i.e. four total analyses) to visually interpret temporal changes in trait–response correlations. We conducted a fifth analysis to explore relationships between litter traits and amphibian responses. Time to metamorphosis and mass at metamorphosis for leopard frogs, gray treefrogs, and spring peepers were excluded from the RDA due to missing data that resulted from high amounts of tadpole mortality in some treatments. We excluded the no-litter and mixture treatments from all RDAs because these treatments did not have singular values for chemical traits.

To help interpret the importance of different litter traits in composing ecological gradients, we examined the canonical loadings of each trait on each canonical axis. Following the recommendation of Tabachnick and Fidell (2001), we considered any trait with a loading of ± 0.45 as important for interpreting an axis. To determine whether a biotic or abiotic response significantly associated with an ecological gradient, we conducted regression analyses of individual responses versus the canonical scores of all replicates on a single gradient. Due to the large number of responses, we adjusted all p-values with the Bonferroni method. We centered and standardized all data prior to analysis, and transformed data when necessary to achieve normal distributions. We verified multivariate normality of data for each analysis by examining the scatterplot of χ^2-values with squared Mahalanobis distances, and assuming normality if the line was reasonably straight. We conducted all ordination analyses using the 'vegan' package in R (ver. 3.1.2, <www.r-project.org>).

Litter species-based analysis

We supplemented the exploratory statistics of RDA by testing for differences among leaf litter treatments using analysis of variance techniques. All species-level analyses were conducted using IBM SPSS ver. 19.

We tested for differences in decay rate constants among litter species with a univariate analysis of variance ANOVA. Average decay constants for each treatment are provided in Table 1. Test results and mass loss curves are provided in the Supplementary material Appendix 2.

To assess the effects of litter on the abiotic responses (pH, DO, temperature, temperature stratification and light attenuation) we used a repeated-measures multivariate analysis of variance (rm-MANOVA). To interpret significant multivariate results, we conducted univariate analyses to explore treatment differences, followed by Tukey's post hoc treatment comparisons. A full description of our analysis is described in Supplementary material Appendix 1. To test if the no-litter treatment (i.e. NL) was associated with responses different from the mean of the other litter species treatments (excluding the mixture treatment), we conducted weighted planned comparisons that resulted in the comparison of no-litter treatment responses with the average of all litter species treatment responses. In a similar manner, we conducted weighted planned comparisons to determine if mixture treatment responses were non-additive (i.e. comparing the expected and observed responses of the mixture treatment where expected responses were calculated as the mean treatment response of all monoculture litter species).

To assess the effect of litter treatment on the biotic responses that were measured at more than one time point, we again used rm-MANOVAs. We conducted one rm-MANOVA for response variables that were measured at two time points, including all invertebrate responses (i.e. responses associated with snails, detritivores and zooplankton). We conducted a second rm-ANOVA for response variables that were measured at four time points (i.e. phytoplankton and periphyton). To interpret significant multivariate results, we conducted univariate analyses and Tukey's post hoc comparisons as described for the abiotic analyses.

Because the amphibian response variables were only measured at a single time point, we separately analyzed these data using a combination of a MANOVA and several ANOVAs. The MANOVA included each amphibian species' survival and total biomass. Because mass at metamorphosis and time to metamorphosis had missing values due to complete mortality or incomplete development to metamorphosis for several species, these responses were analyzed separately using univariate ANOVAs. After finding significant univariate effects, we used Tukey's post hoc test to determine which litter treatments differed and we conducted planned comparisons identical to those in the abiotic and biotic analyses.

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.dg4mc > (Stoler and Relyea 2015).

Results

Trait-based analysis

For all RDAs, litter traits explained a significant amount of variation in response variables (17% to 53%), as determined by Monte Carlo permutation tests (number of permutations = 999). The results of permutation tests, as well as the amount of variation in responses explained by each ecological gradient in each analysis are provided in Supplementary material Appendix 3. In all cases, the first two gradients explained the most amount of variation among responses; additional gradients only explained minor amounts of additional variation.

Overall, the concentration of litter soluble carbon and litter decay rate were consistently important components of ecological gradients that accounted for a substantial amount of variation among abiotic and biotic responses. Litter C:N and phenolic concentrations were also important to at least one ecological gradient in each analysis, but were associated with fewer responses. Lignin did not load onto any gradient in our analyses. Below, we describe the RDA results for each sample date.

First sample date

Soluble carbon and litter decay rate loaded negatively on the first ecological gradient. Phenolics and C:N loaded positively on the second ecological gradient, whereas litter decay rate loaded negatively on this gradient. Regarding response associations, dissolved oxygen and pH were positively correlated with the first gradient whereas light attenuation, temperature, and temperature stratification were negative correlated with this gradient. Temperature, temperature stratification, and phytoplankton concentrations were positively correlated with the second ecological gradient (Fig. 1a).

Second sample date

Soluble carbon and litter decay rate negatively loaded onto the first ecological gradient. Litter decay rate loaded positively onto the second ecological gradient, whereas phenolics and C:N loaded negatively onto this gradient. Regarding response associations, temperature, dissolved oxygen and pH were positive correlated to the first ecological gradient, whereas temperature stratification and light attenuation were negative correlated to this gradient. Phytoplankton concentrations and pH were negatively correlated with the second ecological gradient (Fig. 1b).

Third sample date

Soluble carbon, litter decay rate and litter C:N positively loaded on the first ecological gradient. Phenolics loaded positively onto the second gradient. Regarding response associations, light attenuation was positively correlated with the first ecological gradient, whereas pouch snail biomass, density and egg mass density were negatively correlated with this gradient. Periphyton biomass and the egg mass density of ram's horn snails was also negatively correlated with the first gradient. Isopod biomass, isopod density, copepod density and pouch snail egg mass density were positively correlated with the second gradient (Fig. 1c).

Fourth sample date

Soluble carbon negatively loaded onto the first ecological gradient. Litter decay rate loaded positively onto the second ecological gradient, whereas litter C:N and phenolics loaded negatively onto this gradient. Regarding response associations, phytoplankton concentrations and pouch snail biomass positively correlated with the first ecological gradient, whereas ram's horn snail egg density and copepod density were negatively correlated with this gradient. Dissolved oxygen, pH and phytoplankton concentrations were positively correlated with the second ecological gradient (Fig. 1d).

Amphibians

Litter phenolic concentrations loaded positively onto the first ecological gradient whereas litter decay rate loaded

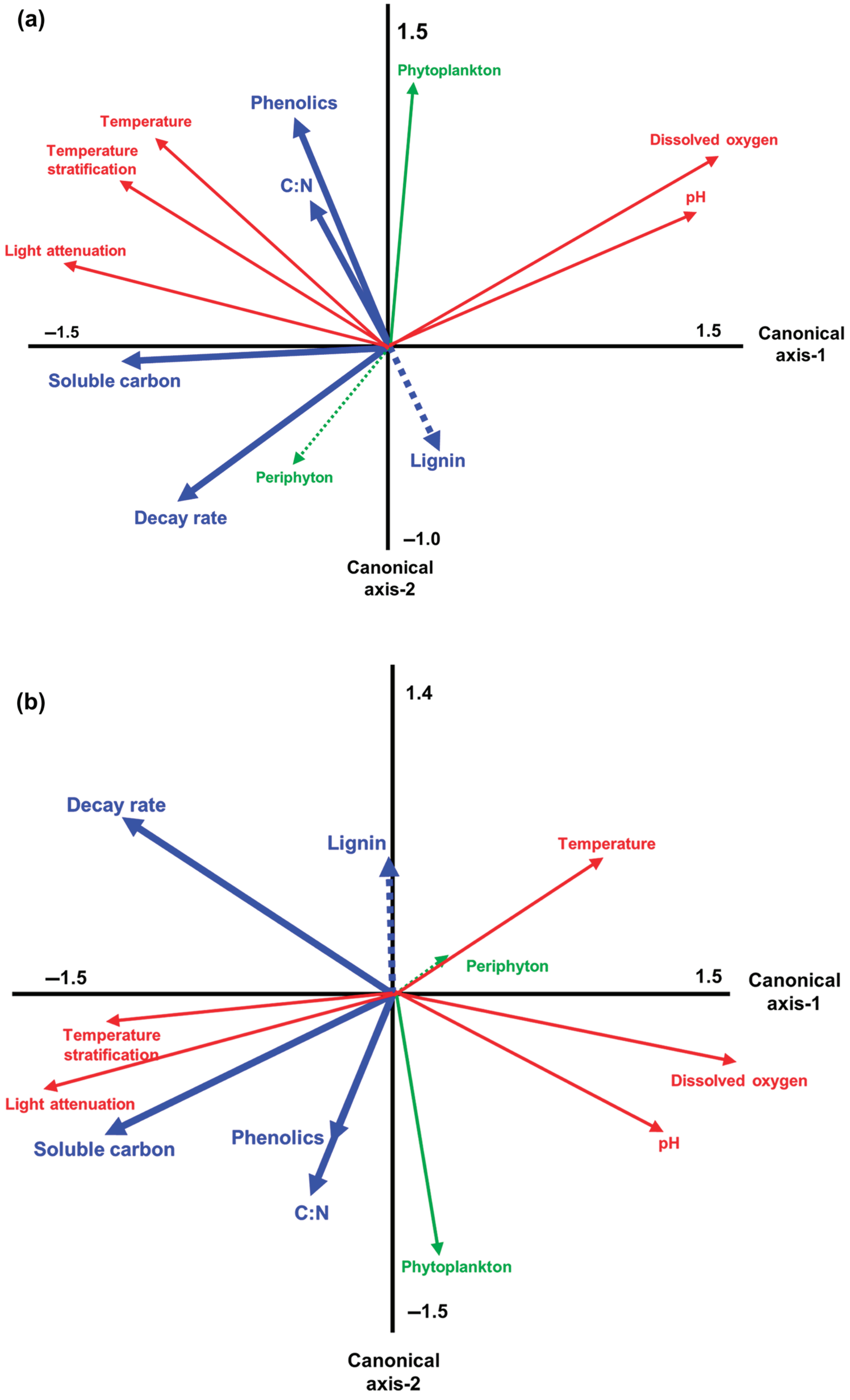

Figure 1. Biplot of redundancy analysis for responses taken during the (a) first sample period, (b) second sample period, (c) third sample period, and (d) fourth sample period. Independent values (blue arrows) are litter traits; dependent values are the abiotic (red arrows) and abiotic responses (primary producers = green arrows; primary consumers = brown arrows) to the 10 litter-species treatments (excluding the no-litter and mixture treatments). The angle of the arrows with respect the axes indicate the magnitude of correlation between a variable and a canonical variate. Solid arrows indicate variables that exhibit significant correlations with one or more canonical variates. Note that the length of the arrow only approximates the strength of this correlation.

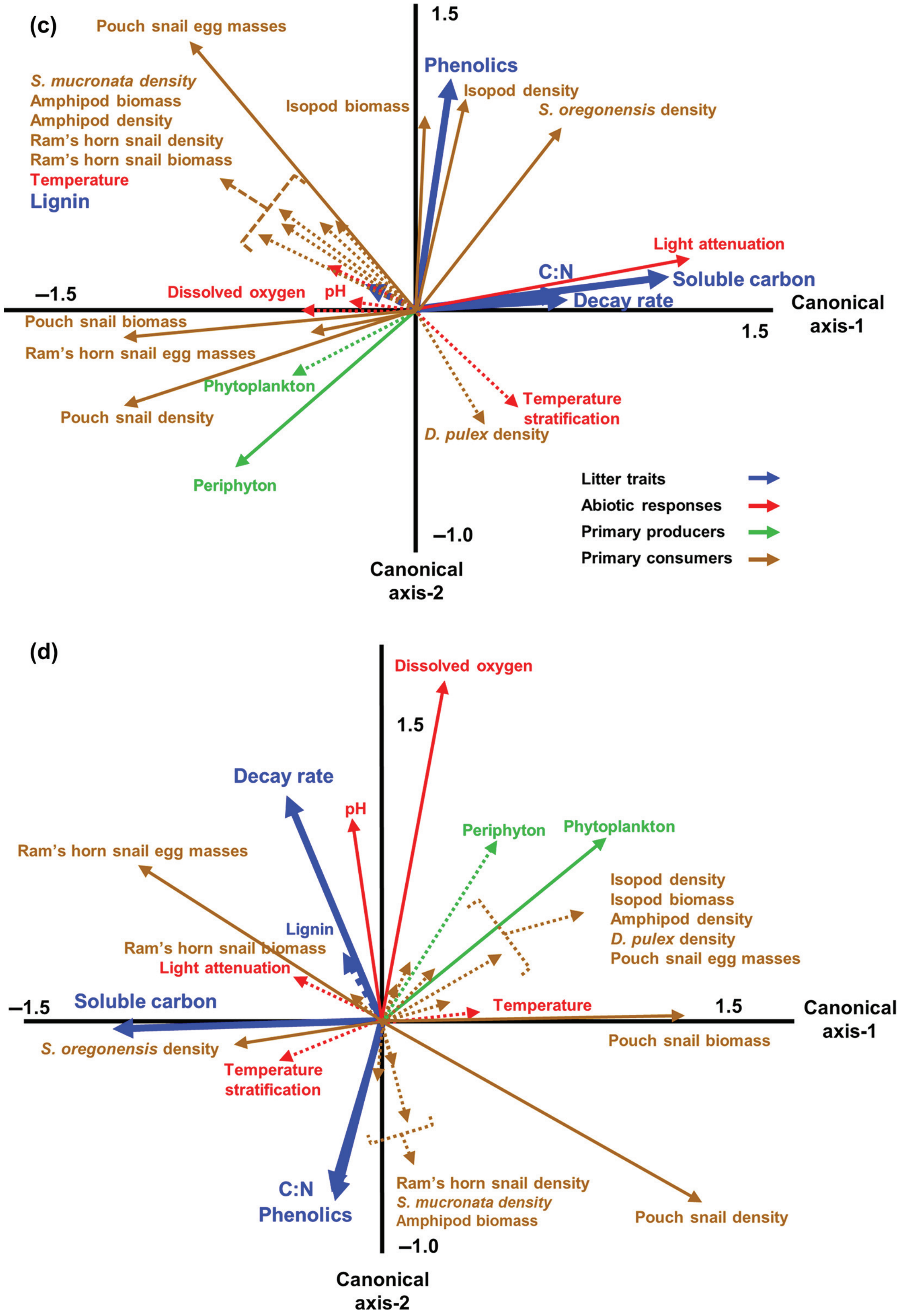

Figure 1. Continued.

negatively onto this gradient. Soluble carbon and C:N loaded negatively onto the second ecological gradient. Regarding response associations, the survival of leopard frog, spring peepers and gray tree frogs was negatively correlated with the first ecological gradient. The total biomass of spring peepers, as well as the mass at metamorphosis and time to metamorphosis of wood frogs and American toads was also negatively correlated with the first ecological gradient. The survival of leopard frogs, wood frogs and American toads, as well as the total biomass of wood frogs and American toads

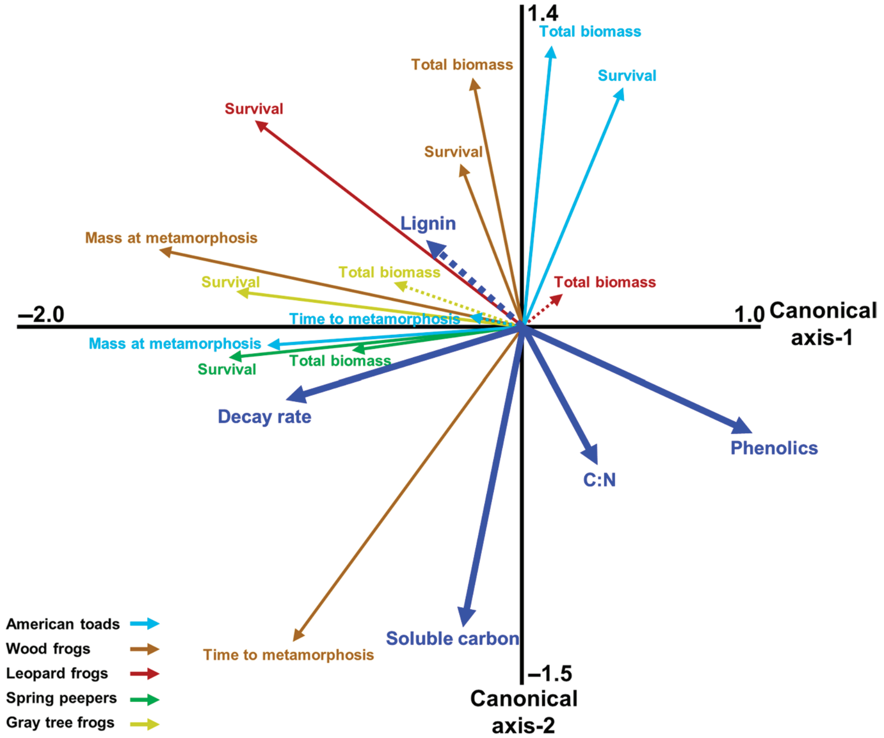

Figure 2. Biplot of redundancy analysis for litter traits and amphibian responses. Independent values are litter traits; dependent values are amphibian responses (American toads = green arrows; wood frogs = brown arrows; leopard frogs = red arrows; spring peepers = green arrows; gray treefrogs = yellow arrows) among the 10 litter species treatments (excluding the no-litter and mixture treatments). Individual size at metamorphosis and time to metamorphosis for leopard frogs, gray treefrogs, and spring peepers were omitted due to missing values (see text for further explanation). Interpretation as in Fig. 1.

were all positively correlated with the second gradient. Wood frog time to metamorphosis was negatively correlated with this gradient (Fig. 2).

Litter species-based analysis

We supplemented the exploratory statistics of RDA with ANOVAs on individual responses. Because of the large number of treatments and responses, we have documented descriptions and test statistics of all species-level differences for each response variable in Supplementary material Appendices 4 and 5. Here, we highlight responses that exhibit variability among litter species treatments, and provide information on no-litter and mixture effects. We then provide the results of our trait-based analysis of the population, community, and ecosystem responses based on the redundancy analyses. All litter treatments are coded as listed in Table 1.

Abiotic responses

Overall, we found strong effects of litter species on all abiotic responses, including light attenuation, dissolved oxygen, temperature, temperature stratification, and pH (Supplementary material Appendix 5 Table A5.1–2, Fig. A61). Analyses within sample dates revealed several significant effects that tended to attenuate later in the study (Table 2). Although we found a wide range of effects that varied in strength across sample dates, TP, RM and CH treatments had the highest light attenuation and lowest levels of dissolved oxygen. RM and TP treatments exhibited the lowest temperature and highest levels of temperature stratification, but only on the first two sample dates. The RM treatment exhibited the lowest pH, but only on the first two sample dates.

Basal production and invertebrates

We found effects of individual litter species on the biotic responses measured throughout our study including chlorophyll a concentration (i.e. a surrogate for phytoplankton biomass), periphyton biomass, densities of *D. pulex* zooplankton, pouch snail responses (i.e. biomass, density and egg production), egg production of ram's horn snails, and amphipod responses (i.e. biomass and density; Supplementary material Appendix 5 Table A5.3–A5.6; Fig. A6.2–A6.4). Several of these responses also exhibited effects of time, as well as time-by-treatment interactions (Table 2). In contrast, the biomass and density of isopods, as well as the densities of *S. mucronata* and ram's horn snails exhibited only effects of time and were not affected by litter species. The biomass of ram's horn snail was not affected by time, litter species or their interaction.

Unlike abiotic responses, there was no litter species treatment that exhibited consistent high or low biotic response values. In general, BW exhibited relatively high phytoplankton concentrations whereas the more recalcitrant species (e.g. BCH) tended to exhibit relatively high periphyton biomass. Pouch snail biomass and density significantly decreased in TP. Similarly, pouch snail egg production decreased in TP, whereas egg production of ram's horn snails increased in the same treatment. Biomass and density of amphipods both decreased in TP.

Table 2. Instances of univariate effects of litter species on abiotic and biotic responses across the four sample dates. An 'X' indicates a significant univariate effect and the presence of treatment differences. Asterisks indicate responses for which values were averaged across sample dates because they lacked a time-by-treatment interaction. Note that zooplankton, pouch snail, ram's horn snail, amphipod and isopod responses were only measured on the third and fourth sample dates.

		Time 1	Time 2	Time 3	Time 4
Abiotic measurements	Light attenuation	X	X	X	X
	Dissolved oxygen	X	X	X	X
	Temperature	X	X		
	Temperature stratification	X	X	X	
	pH	X	X	X	X
Basal production	Phytoplankton	X	X		X
	Periphyton	X			X
Zooplankton	*D. pulex**			X	X
	S. mucronata				
	*S. oregonensis**			X	X
Pouch snails	Density*			X	X
	Biomass			X	X
	Egg production			X	X
Ram's horn snails	Density				
	Biomass				
	Egg production				X
Amphipods	Density*			X	X
	Biomass*			X	X
Isopods	Density				
	Biomass				

Amphibians

We found a significant multivariate effect of litter treatment on amphibian responses (Supplementary material Appendix 5 Table A5.7, Fig. A6.5). The survival of all tadpole species was affected by litter species. Total biomass of toads, wood frogs, and spring peepers, as well as the individual mass at metamorphosis of American toads, wood frogs and leopard frogs were affected by litter species. Only wood frog and gray tree frog time to metamorphosis were affected by litter species. In general, amphibian species that metamorphosed earlier in the season (i.e. wood frogs and American toads) were strongly and negatively affected by more soluble litter species treatments (e.g. TP and RM). In contrast, species that metamorphosed later in the season (i.e. spring peepers and gray tree frogs) were positively affected by those same treatments.

Effects of litter absence (Supplementary material Appendix 5 Table A5.8)

In the absence of litter, light attenuation tended to be lower, whereas both pH and dissolved oxygen were consistently higher in the absence of litter on all sample dates. Average temperature was lower in the NL treatment, but only during the first half of the experiment. In contrast, temperature stratification in the NL treatment was never different from the average of all litter treatments.

We also observed several effects of litter absence on biotic responses. Concentrations of chl a were higher in the absence of litter on the second sample date, but lower on the third sample date. Periphyton biomass was higher in the NL treatment, but only on the first sample date. We also found a greater density of pouch snails in the absence of litter and fewer egg masses, although this effect was only significant on the first sample date. Lastly, we found a lower biomass of amphipods in the absence of litter. We found no effects of litter absence on zooplankton densities at any time throughout the study.

Regarding amphibian responses, toads experienced higher survival and larger mass of metamorphs in the NL treatment relative to the average of all litter treatments. Similarly, we observed larger total biomass of leopard frogs in the NL treatment. In contrast, wood frog metamorphs were smaller in absence of litter. Both leopard frogs and gray tree frogs had a shorter time to metamorphosis in the NL treatment. We could not conduct planned comparisons for spring peepers in the NL treatment due to complete mortality among no-litter replicates.

Mixture effects (Supplementary material Appendix 5 Table A5.9)

Comparisons revealed that abiotic responses to litter mixing were entirely additive. Most biotic responses exhibited additive effects as well, yet there were a few exceptions. Litter mixing had an antagonistic effect on pouch snail density and total pouch snail biomass on both sample dates, and on spring peeper individual metamorph mass. In contrast, litter mixing had a synergistic effect on egg production of ram's horn snails, but only on the first sample day.

Discussion

By examining the effects of litter species monocultures on community responses across multiple trophic levels and time points, we are able to illustrate potential relationships between forest tree composition and the attributes of pond ecosystems. Moreover, the design of our study enables us to generalize the effects of litter in terms of litter chemistry. This approach, similar to that of Cohen et al. (2012), is useful in broadening the applicability of our results to a wider range of litter species than the 10 species used in our study. Indeed, we found that only two litter traits (i.e. soluble carbon and litter decay rate) accounted for much of the variation among mesocosm communities, thereby suggesting that the effects of litter on pond communities may be predictable based on litter traits. Overall, our study is the first to test the effects of a wide range of litter species on multiple trophic levels in a controlled pond ecosystem, and also to provide generality regarding the effects of broad litter traits rather than specific litter species.

Responses of the community to different species of litter

Our primary hypothesis was that individual litter species would have different impacts on abiotic and biotic effects as a consequence of the traits of the litter. Indeed, most responses exhibited a wide range of values across litter species treatments and we found that much of this variation could be explained by relatively few litter traits. For example, litter decay rate exhibited positive associations with several responses throughout our study. This is most likely because rapidly decomposing leaf litter provides a valuable resource for consumers. However, positive associations with decay rate were not ubiquitous throughout the study. Indeed, other studies have found relatively weak correlations of litter decay rate with consumer growth (Sayer 2006). One possible explanation is that both harmful and beneficial compounds can be released from rapidly decomposing litter. As further evidence of this, decay rate often loaded onto ecological gradients with other litter traits (e.g. soluble carbon). Decay rate only exhibited an independent association with an ecological gradient on the final sampling period, and was not strongly associated with any response. Hence, pond responses to litter inputs might be better predicted by the chemical attributes of litter that determine decay rates, rather than decay rate itself.

Among the chemical traits we measured, soluble carbon was among the most important components in all redundancy analyses. Dissolved organic carbon (DOC), derived from soluble carbon, is known to reduce ultraviolet radiation, bind to contaminants, and provide valuable sources of organic energy (Williamson et al. 1999, Wetzel 2001). Under low to moderate levels of DOC, phytoplankton can benefit from DOC whereas benthic primary production becomes limited as a result of increased light attenuation (Klug 2002, Karlsson et al. 2009). In contrast, high levels of soluble carbon can be toxic to some species (Horne and Dunson 1995) and also attenuate enough light to inhibit rates of photosynthesis and increase microbial growth, leading to reductions in dissolved oxygen that might impair animal growth and survival (Klug 2002, McIntyre and McCollum 2000). Given these trends, it is not surprising that we saw increased mortality of animals in treatments with high light attenuation, including 80% American toad mortality in the red maple treatment and the complete absence of pouch snails in the tulip poplar treatment. However, it is worth noting that some species that inhabit closed-canopy wetlands may possess adaptations to such harsh conditions (McIntyre and McCollum 2000, Horne and Dunson 1995, Skelly et al. 2002, Schiesari et al. 2009). For example, tadpole species with primitive lungs (e.g. wood frogs) can bob to the surface for air when dissolved oxygen is low whereas toads do not possess such lungs (Feder and Moran 1985). Hence, it is important to consider the physiological attributes of organisms when predicting the effects of litter inputs on pond and wetland communities.

Our analyses also indicated that total phenolic content exhibited negative associations with several biotic responses. The most pronounced effects were negative associations between phenolic concentrations and American toad mass at metamorphosis, as well as survival of leopard frogs, spring peepers and gray treefrogs. The negative influence of phenolics on the survival of amphibians has been well documented (Maerz et al. 2005, Cohen et al. 2012) and is likely a result of direct toxicity and bottom–up inhibition of resource availability. The effects of phenolic acids on other biotic responses may be more complex. For example, phytoplankton are negatively influenced by high phenolic concentrations, yet low levels may be beneficial as a resource and by removing nutrient competitors (Herrera-Silveira and Ramirez-Ramirez 1996). Indeed, we saw a positive association between phytoplankton and phenolic acids. Phenolic acids are also implicated as deterrents to microbial growth in aquatic systems since they can be toxic and energetically expensive to break down (Ardón and Pringle 2008). However, we saw no association between periphyton and phenolic acids, and actually observed a positive association between phenolic acids and the biomass of isopods, pouch snails and copepods. Since it is unlikely that phenolic acids are directly beneficial to these consumers, our results suggest that the relative effects of phenolic acids likely depend on other factors.

Litter C:N loaded onto at least one ecological gradient on all sample dates. However, our results suggest that the relative role of C:N in structuring pond communities may be less than the role of more soluble litter attributes (Moran and Hodson 1989). Similarly, Cohen et al. (2012) found that the more aqueous components of litter chemistry (e.g. phenolics) generally have a stronger impact on larval anurans than litter nutrient content. These findings contrast with predictions; elevated C:N (i.e. lower nutritional quality) is regularly implicated as a factor that slows litter decomposition and reduces available nutrients (Melillo et al. 1982, Scott and Binkley 1997). Moreover, stoichiometric theory suggests that elevated C:N should limit N-rich producers and consumers, and subsequently change community composition (Sterner and Elser 2002). However, Hall et al. (2004) demonstrates that other factors, such as light levels and consumer metabolic efficiencies, are more likely to describe energy limitations of individual consumer species. Additionally, nutrient ratios of basal resources might not adequately describe the edibility of food, which also has strong influences on community structure (Hall et al. 2006).

Effect of litter absence

Our second hypothesis was that the presence of leaf litter, regardless of species, would increase resource supply and subsequently increase the biomass and survivorship of community members. Throughout the duration of the experiment, the absence of litter led to low light attenuation values that were similar to treatments containing the most recalcitrant litter species (e.g. beech, oak). In turn, pH and dissolved oxygen increased in the absence of litter. These effects may result from reduced microbial respiration or increased algal production, which typically lowers the amount of carbonic acid in aquatic systems (Wetzel 2001). Indeed, periphyton and phytoplankton initially increased in the absence of litter, likely due to the initial pulse of nutrients in rabbit chow as well as low light attenuation. However, these effects were short-lived and phytoplankton decreased below the average of all litter treatments by the end of the study. This is likely due to rapid rates of herbivory, although there were no differences in in zooplankton density between no-litter and litter treatments. However, we did find that the biomass of some consumers (e.g. American toads, pouch snails) increased in the absence of litter. This contrasts with previous evidence that the removal of litter inputs in wetlands decreases secondary production (Rubbo et al. 2006, Sayer 2006, Earl and Semlitsch 2013). However, it is worth noting that such studies have focused on the effects of litter removal without considering the specific quality of litter removed. Our study demonstrates that the quality of litter is an important factor in structuring pond communities, and that the effects of litter removal must be considered relative to litter quality.

Effects of mixing litter

In contrast to our third hypothesis, most responses to litter mixing were additive. Among the 44 tests for non-additivity that we conducted in our analysis, pouch snail biomass, density and egg production exhibited non-additive antagonistic responses to litter mixing. Given their low densities in some treatments (i.e. tulip poplar and red maple), these results suggest pouch snails are particularly sensitive to presence of those leaf species in mixture, and possibly to high levels of soluble carbon. Lack of additional non-additive results is surprising; past studies have commonly observed non-additive responses to litter mixtures in lotic ecosystems (i.e. streams) including both antagonistic and synergistic effects (Gessner et al. 2010). Although this may be a consequence of differences between lotic ecosystems and lentic ecosystems, our lack of non-additivity might also result from the high diversity of our mixed litter assemblage. Most non-additive responses are observed using low species richness (i.e. two to four species) whereas our mixture treatment included 10 litter species. Indeed, our previous work has found that gray tree frogs respond non-additively to diverse (12 species) mixtures of litter species that included many of the litter species represented in the current study (Stoler and Relyea 2011). Non-additivity may be more prevalent in less diverse mixtures if the effects are due to the relatively strong influence of individual litter species (i.e. selection effects; Kominoski et al. 2009).

Effects of time

Despite several strong associations between litter traits and abiotic and biotic responses, generalized trends were elusive across the full duration of the study. Inconsistency in trends is likely due to changing environmental conditions as the experiment progressed, such as changes in air temperature and sunlight availability. The quality of litter can also change substantially over time as compounds are leached and mineralized (Melillo et al. 1982). Indeed, the amount of response variation explained by litter traits decreased as our study progressed, suggesting that the pulse of litter introduced to our mesocosms exerted a diminishing effect on the communities over time. Similar results have been observed in past studies (Moran and Hodson 1989) and are likely due to an increasing percentage of relatively non-influential, recalcitrant compounds (e.g. lignin) that remain in the litter during later stages of decay (Melillo et al. 1982). Although it is also possible that other components of litter chemistry that we did not measure might influence pond communities, the broad traits that we used are the most often cited determinants of litter palatability and quality (Taylor et al. 1989, Ardón and Pringle 2008).

Temporal changes in environmental conditions and litter chemistry are particularly relevant for amphibian species, which have different breeding and metamorphosing times. Indeed, Cohen et al. (2012) also found different amphibian species with different larval durations were each affected by different environmental variables. Similarly, we found that early-metamorphosing species (i.e. wood frogs and American toads) were most strongly affected by soluble carbon, whereas late-metamorphosing species (i.e. leopard frogs, spring peepers and gray tree frogs) were most strongly affected by litter decay rate and phenolics. These results suggest that interactions of litter traits with time may be important to consider when predicting effects of litter inputs on aquatic organisms with varying phenologies.

Consequences of leaf litter inputs to ecological function and changing forest composition

The results of this experiment are meant to provide predictions for the consequences of historic and current shifts in tree diversity on wetland ecological function in North American temperate forests. Mesocosms provide a useful tool for generating such predictions, and future work should explore this question in a more natural context by incorporating other natural elements (e.g. other organic and inorganic inputs, pre-existing detritus). Despite the artificial nature of our experiment, our results do suggest that both natural- and human-derived changes in temperate forest composition have led to substantial changes in wetland communities. For example, American chestnut has dramatically declined throughout much of its original range due to an invasive fungal disease, and has been replaced by oak trees (Moser et al. 2009). Our study suggests that this turnover led to increased pond clarity and dissolved oxygen as well as changes in community composition and biomass, particularly among snail species. Similarly, Dutch elm disease and emerald ash borers threaten most northeastern populations of elm and ash (Moser et al. 2009). Our study suggests that the loss of either species might lead to the reduction of amphibian and snail biomass from wetlands in elm and ash dominated forests.

In addition to demonstrating the consequences of human-derived changes in forest composition, our study suggests how pond and wetland communities change with natural forest succession. For example, early-succession species in forest include bigtooth aspen, black willow and tulip poplar. Of those species, tulip poplar has the most pronounced influence on pond dynamics, with extreme reductions in water clarity, dissolved oxygen, and consumer biomass. In contrast, the nutrient-rich chemistry of black willow litter was associated with high primary producer biomass and substantial improvement in the survival of spring-breeding amphibians.

Shifts in tree composition are likely to be most influential when major changes in functional traits are involved. In this regard, of particular importance is the replacement of oak and beech stands by red maple and cherry due to overbrowsing by deer (Abrams 2003). Relative to many oak and beech, red maple and cherry exhibit relatively rapid decay rates and high levels of soluble carbon. Our study suggests that this may dramatically alter the profile of wetland communities and lead to substantial animal mortality. Rubbo and Kiesecker (2004) specifically examined the effects of maple and oak litter on wood frogs and two salamander species, and found that inputs of red maple litter decreased survival of all three species by up to 20% relative to inputs of oak litter. Although they did not attempt to relate this effect with litter chemistry, our current analysis strongly suggests this to be the case.

The effects of species turnover are likely to be strongly mediated by litter mixing effects, since temperate forests are often comprised of diverse tree species assemblages. Responses from our mixture treatment suggest that the combined effects of multiple litter species on pond and wetland ecosystems are largely additive, in contrast to findings from streams and terrestrial systems (Lecerf et al. 2007, Kominoski et al. 2009). Future work should concentrate on three goals. First, we need to understand which components of food webs exhibit non-additive responses to litter mixtures and the mechanisms underlying this non-additivity. As we understand these mechanisms, we can predict the effects of realistic litter species mixtures. Second, we need to understand the role of litter species evenness; realistic mixtures are frequently comprised of rare and dominant species, and it is possible that the biomass of any single litter species in mixture is not linearly related to its biological effects (Hillebrand et al. 2008). Finally, these questions should be approached from both species- and trait-based perspectives to move from species-specific case studies to a broad understanding of mechanisms.

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References

Abrams, M. D. 2003. Where has all the white oak gone? – BioSci. 53: 927–939.

Ardón, M. and Pringle, C. M. 2008. Do secondary compounds inhibit microbial- and insect-mediated leaf breakdown in a tropical rainforest stream, Costa Rica? – Oecologia 155: 311–323.

Cohen, J. S. et al. 2012. Traits, not origin, explain impacts of plants on larval amphibians. – Ecol. Appl. 22: 218–228.

Earl, J. E. and Semlitsch, R. D. 2013. Spatial subsidies, trophic state, and community structure: examining the effects of leaf litter input on ponds. – Ecosystems 16: 639–651.

Eggert, S. L. et al. 2012. Storage and export of organic matter in a headwater stream: responses to long-term detrital manipulations. – Ecosphere 3: 1–25.

Facelli, J. M. and Pickett, S. T. 1991. Plant litter: its dynamics and effects on plant community structure. – Bot. Rev. 57: 1–32.

Feder, M. E. and Moran, C. M. 1985. Effect of water depth on costs of aerial respiration and its alternatives in tadpoles of *Rana pipiens*. – Can. J. Zool. 63: 643–648.

Gessner, M. O. et al. 1999. A perspective on leaf litter breakdown in streams. – Oikos 85: 377–384.

Gessner, M. O. et al. 2010. Diversity meets decomposition. – Trends Ecol. Evol. 25: 372–380.

Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. – Herpetologica 16: 183–190.

Graças, M. A. et al. 2005. Methods to study litter decomposition: a practical guide. – Springer.

Hall, S. R. et al. 2004. Stoichiometry and planktonic grazer composition over gradients of light, nutrients and predation risk. – Ecology 85: 2291–2301

Hall, S. R. et al. 2006. Inedible producers in food webs: controls on stoichiometric food quality and composition of grazers. – Am. Nat. 167: 628–637.

Herrera-Silveira, J. A. and Ramirez-Ramirez, J. 1996. Effects of natural phenolic material (tannin) on phytoplankton growth. – Limnol. Oceanogr. 41: 1018–1023.

Hillebrand, H. et al. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. – Ecology 89: 1510–1520.

Horne, M. and Dunson, W. 1995. The interactive effects of low pH, toxic metals and DOC on a simulated temporary pond community. – Environ. Pollut. 89: 155–161.

Karlsson, J. et al. 2009. Light limitation of nutrient-poor lake ecosystems. – Nature 460: 506–509.

Klug, J. L. 2002. Positive and negative effects of allochthonous dissolved organic matter and inorganic nutrients on phytoplankton growth. – Can. J. Fish. Aquat. Sci. 59: 85–95.

Kominoski, J. S. et al. 2009. Does mixing litter of different qualities alters stream microbial diversity and functioning on individual litter species? – Oikos 118: 457–463.

Lecerf, A. et al. 2007. Decomposition of diverse litter mixtures in streams. – Ecology 88: 219–227.

Lecerf, A. et al. 2011. Incubation time, functional litter diversity, and habitat characteristics predict litter-mixing effects on decomposition. – Ecology 92:160–169.

Maerz, J. C. et al. 2005. Can secondary compounds of an invasive plant affect larval amphibians? – Funct. Ecol. 19: 970–975.

McGill, B. J. et al. 2006. Rebuilding community ecology from functional traits. – Trends Ecol. Evol. 21: 178–185.

McIntyre, P. B. and McCollum, S. A. 2000. Responses of bullfrog tadpoles to hypoxia and predators. – Oecologia 125: 301–308.

Melillo, J. M. et al. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. – Ecology 63: 621–626.

Moran, M. and Hodson, R. E. 1989. Bacterial secondary production on vascular plant detritus: relationships to detritus composition and degradation rate. – Appl. Environ. Microb. 55: 2178–2189.

Morin, P. J. 1983. Predation, competition and the composition of larval anuran guilds. – Ecol. Monogr. 53: 119–138.

Moser, W. K. et al. 2009. Impacts of nonnative invasive species on US forests and recommendations for policy and management. – J. For. 107: 320–327.

Ollinger, S. V. et al. 2002. Regional variation in foliar chemistry and N cycling among forests of diverse history and composition. – Ecology 83: 339–355.

Petersen, R. C. and Cummins, K. W. 1974. Leaf processing in a woodland stream. – Freshwater Biol. 4: 343–368.

Price, P. W. et al. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. – Annu. Rev. Ecol. Syst. 11: 41–65.

Reiskind, M. H. et al. 2009. Leaf species identity and combination affect performance and oviposition choice of two container mosquito species. – Ecol. Entomol. 34: 447–456.

Relyea, R. A. 2005. The impact of insecticides and herbicides on the biodiversity and productivity of aquatic communities. – Ecol. Appl. 15: 618–627.

Rubbo, M. J. and Kiesecker, J. M. 2004. Leaf litter composition and community structure: translating regional species changes into local dynamics. – Ecology 85: 2519–2525.

Rubbo, M. J. et al. 2006. Terrestrial subsidies of organic carbon support net ecosystem production in temporary forest ponds: evidence from an ecosystem experiment. – Ecosystems 9: 1170–1176.

Rubbo, M. J. et al. 2008. Differential responses of aquatic consumers to variations in leaf-litter inputs. – Hydrobiologia 605: 37–44.

Sayer, E. J. 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. – Biol. Rev. Camb. Phil. Soc. 81: 1–31.

Schiesari, L. 2006. Pond canopy cover: a resource gradient for anuran larvae. – Freshwater Biol. 51: 412–423.

Schiesari, L. et al. 2009. Carnivory and resource-based niche differentiation in anuran larvae: implications for food web and experimental ecology. – Freshwater Biol. 54: 572–586.

Scott, N. A. and Binkley, D. 1997. Foliage litter quality and annual net N mineralization: comparison across North American forest sites. – Oecologia 111: 151–159.

Skelly, D. et al. 2002. Forest canopy and the performance of larval amphibians. – Ecology 83: 983–992.

Sterner, R. W. and Elser, J. J. 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. – Princeton Univ. Press.

Stoler, A. B. and Relyea, R. A. 2011. Living in the litter: the influence of tree leaf litter on wetland communities. – Oikos 120: 862–872.

Stoler, A. B. and Relyea, R. A. 2015. Data from: Leaf litter species identity alters the structure of pond communities. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.dg4mc>.

Tabachnick, B. G. and Fidell, L. S. 2001. Using multivariate statistics. – Pearson.

Taylor, B. R. et al. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. – Ecology 70: 97–104.

Tuchman, N. C. et al. 2003. Nutritional quality of leaf detritus altered by elevated atmospheric CO_2: effects on development of mosquito larvae. – Freshwater Biol. 48: 1432–1439.

Wallace, J. B. et al. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. – Science 277: 102–104.

Webster, J. and Benfield, E. 1986. Vascular plant breakdown in freshwater ecosystems. – Annu. Rev. Ecol. Syst. 17: 567–594.

Werner, E. E. et al. 2007. Amphibian species richness across environmental gradients. – Oikos 116: 1697–1712.

Wetzel, R. G. 2001. Limnology: lake and river ecosystems. – Academic Press.

Williamson, C. E. et al. 1999. Dissolved organic carbon and nutrients as regulators of lake ecosystems: resurrection of a more integrated paradigm. – Limnol. Oceanogr. 44: 795–803.

Supplementary material (available online as Appendix oik-02480 at <www.oikosjournal.org/appendix/oik-02480>). Appendix 1–6.