

Consequences of non-random species loss for decomposition dynamics: experimental evidence for additive and non-additive effects

Becky A. Ball^{1*}, Mark D. Hunter², John S. Kominoski¹, Christopher M. Swan³ and Mark A. Bradford¹

¹Odum School of Ecology, University of Georgia, Athens, GA 30602, USA; ²School of Natural Resources and Environment, and Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA; and ³Geography and Environmental Systems, University of Maryland Baltimore County, 211 Sondheim Hall, 1000 Hilltop Circle, Baltimore, MD 21250, USA

Summary

1. Although litter decomposition is a fundamental ecological process, most of our understanding comes from studies of single-species decay. Recently, litter-mixing studies have tested whether monoculture data can be applied to mixed-litter systems. These studies have mainly attempted to detect non-additive effects of litter mixing, which address potential consequences of random species loss – the focus is not on which species are lost, but the decline in diversity *per se*.

2. Under global change, species loss is likely to be non-random, with some species more vulnerable to extinction than others. Under such scenarios, the effects of individual species (additivity) as well as of species interactions (non-additivity) on decomposition rates are of interest.

3. To examine potential impacts of non-random species loss on ecosystems, we studied additive and non-additive effects of litter mixing on decomposition. A full-factorial litterbag experiment was conducted using four deciduous leaf species, from which mass loss and nitrogen content were measured. Data were analysed using a statistical approach that first looks for additive identity effects based on the presence or absence of species and then significant species interactions occurring beyond those. It partitions non-additive effects into those caused by richness and/or composition.

4. This approach addresses questions key to understanding the potential effects of species loss on ecosystem processes. If additive effects dominate, the consequences for decomposition dynamics will be predictable based on our knowledge of individual species, but not statistically predictable if non-additive effects dominate.

5. We found additive (identity) effects on mass loss and non-additive (composition) effects on litter nitrogen dynamics, suggesting that non-random species loss could significantly affect this system. We were able to identify the species responsible for effects that would otherwise have been considered idiosyncratic or absent when analysed by the methods used in previous work.

6. *Synthesis.* We observed both additive and non-additive effects of litter-mixing on decomposition, indicating consequences of non-random species loss. To predict the consequences of global change for ecosystem functioning, studies should examine the effects of both random and non-random species loss, which will help identify the mechanisms that influence the response of ecosystems to environmental change.

Key-words: biodiversity, decomposition, ecosystem function, litter mixtures, litter quality, non-random species loss, random species loss, species composition, species diversity

*Correspondence and present address: Becky A. Ball, Dartmouth College, Environmental Studies Program, 6182 Steele Hall, Hanover, NH 03755, USA. E-mail: rebecca.a.ball@dartmouth.edu

Introduction

Decomposition of plant litter is a fundamental ecological process, integral to nutrient cycling, energy flow in food webs, and the structure and dynamics of ecosystems (Schnitzer & Khan 1978; Swift *et al.* 1979; Stevenson 1994; Aber & Melillo 2001; Moore *et al.* 2004). Much of our understanding about which factors influence decomposition is derived from studies following the decay dynamics of single species. Whether this understanding can be used to predict how litters decompose within litter mixtures was the focus of a number of studies in the 1980s and 90s (Chapman *et al.* 1988; Blair *et al.* 1990; Fyles & Fyles 1993; Rustad 1994; Salamanca *et al.* 1998). These early litter-mixing studies followed from the suggestion that differences in substrate nutrient content between litters might generate non-additive decay dynamics (Seastedt 1984), thereby challenging our assumptions about nutrient cycling in multi-species plant communities (Rustad 1994). If decay dynamics in mixtures are the sum of their parts (i.e. additive), decay dynamics of single litters can then be used to predict decay dynamics in the generally multi-species litter layers of ecosystems. Alternatively, if decay dynamics of mixtures are non-additive, research on decay rates of mixtures is required for us to understand nutrient dynamics in multi-species systems.

Following from the study by Wardle *et al.* (1997), litter-mix studies have proliferated in the context of biodiversity and ecosystem function. In contrast to earlier studies, the central focus of this body of work (reviewed by Gartner & Cardon 2004; Hättenschwiler *et al.* 2005) has been whether biodiversity (primarily species richness and composition) is related to decomposition. The main conclusions from this work are: (i) there is little evidence that litter species richness generates non-additive decay dynamics; and (ii) the composition of the litter mixture (i.e. the identity of species involved) often but not always generates non-additivity (see reviews by Gartner & Cardon 2004; Hättenschwiler *et al.* 2005). Specifically, non-additive dynamics arising from interactions among species have been the primary focus of previous work, which investigates the consequences of random species loss (Gross & Cardinale 2005). As a consequence, additive dynamics, where the results of litter mixing can be statistically predicted based on the individual species present, has been largely ignored as a valid effect of mixing.

Global environmental changes, such as climate and land-use change and resource availability, are likely to affect biodiversity through non-random species loss (Vitousek *et al.* 1997; Grime 1998; Loreau *et al.* 2001; Smith & Knapp 2003; Ellison *et al.* 2005; Schläpfer *et al.* 2005). Non-random loss may generate different outcomes on ecosystem functioning than random species loss (Gross & Cardinale 2005; Schläpfer *et al.* 2005). The pressing need to understand how ecosystems will function as species are lost non-randomly requires experimental designs that remove vulnerable species (e.g. Smith & Knapp 2003; Larsen *et al.* 2005; Schläpfer *et al.* 2005) and/or statistical models that can identify additive and non-additive effects of component species (e.g. Kominoski

et al. 2007). These approaches explicitly recognize that effects of species identity (through additive effects), as well as species interactions *per se* (which result in non-additive dynamics), are a valid component of understanding how biodiversity change will impact ecosystem function. While work on non-random species loss has begun for plant productivity (Smith & Knapp 2003; Schläpfer *et al.* 2005; Suding *et al.* 2006; Cross & Harte 2007), it has not been addressed explicitly for litter decomposition.

In the context of non-random species loss, either additive or non-additive effects of a component species imply that ecosystem functioning will be altered because of a shift in community composition. These differential effects reflect either an independent influence of species on ecosystem functioning (additivity) vs. emergent dynamics that arise because species effects are dependent on the presence of other species (non-additivity; Johnson *et al.* 2006). Non-additive effects of litter species richness on decay dynamics have been detected (McTiernan *et al.* 1997; Wardle *et al.* 1997; Swan & Palmer 2004; Hättenschwiler & Gasser 2005; Leroy & Marks 2006). The mechanistic explanations for non-additivity in litter mixtures generally revolve around differences in litter quality among component species, where mass loss of lower-nutrient litters are stimulated by adjacent higher-nutrient litter, or vice versa (Seastedt 1984; Hättenschwiler *et al.* 2005). Possible mechanisms for this include nutrient transfer (e.g. Schimel & Hättenschwiler 2007), stimulation of microbial processing (e.g. Bardgett & Shine 1999) and alterations in detritivore behaviour (e.g. Swan & Palmer 2006). Given the well-established relationships between litter quality and the decay rates of single species (McClaugherty & Berg 1987; Aber *et al.* 1990; Aerts 1997), and also the role of litter quality in generating non-additive dynamics (Smith & Bradford 2003a; Gartner & Cardon 2006; Leroy & Marks 2006), changes in the composition of litters differing markedly in quality are likely to generate marked effects on decomposition dynamics through both additive and non-additive mechanisms.

To investigate the potential consequences of non-random species loss for litter decomposition dynamics, we utilized a 3-year, full-factorial, litter mixture study in a southeastern United States temperate forest. We used litters from four dominant tree species within our study system, which differed in their chemical composition and monoculture decomposition rate. We used a statistical model that sequentially tests for additive effects of each component species, then whether any of the remaining variance is explained by interactions among the main factors (i.e. whether a species is present or absent). Significant interactions indicate non-additivity, and this behaviour was explored using *post hoc* analyses to determine whether the non-additivity was explained by species richness and/or composition (Mikola *et al.* 2002; Drake 2003). Note that richness effects are by definition non-additive (arising only through interactions among species), whereas compositional effects may be additive or non-additive. The strength of the approach is that we could first consider whether loss of a particular species is likely to affect ecosystem functioning. If

it does, then second we could consider whether the effects of its loss are likely to be statistically predictable (i.e. arising through additive mechanisms) or whether the consequences of its loss will be dependent on the presence of some or all of the other species in the community (i.e. non-additivity). We hypothesised that (i) given that our chosen litters form a gradient in litter nutrient content, loss of any one of the four species will produce an additive change in decomposition dynamics; (ii) given the expectation that non-additive, compositional effects arise when litters of markedly differing nutrient content are present, non-additivity will only arise when a litter species is lost that is at the high or low end of the quality spectrum; and (iii) as the overwhelming evidence to date indicates species composition is more important than species richness *per se* for decay of mixed-species litter, there will be no relationship between litter species richness and decomposition rate.

Methods

STUDY SITE

The experiment was conducted at Coweeta Hydrologic Laboratory in the southern Appalachian Mountains, Macon County, NC, USA (35°00'N, 83°30'W; elevation 1300 m). Mean annual rainfall is c. 1700 mm and mean annual temperature 13 °C (Heneghan *et al.* 1999). The study was conducted in Watershed 20 on Ball Creek that drains into Coweeta Creek, a tributary of the Little Tennessee River.

EXPERIMENTAL DESIGN

Litters were collected from the four most abundant tree species at Coweeta: *Liriodendron tulipifera* L. (tulip poplar, L), *Acer rubrum* L. (red maple, A), *Quercus prinus* L. (chestnut oak, Q) and *Rhododendron maximum* L. (rhododendron, R). The litters from these species cover a range of chemical composition and decay rate in monoculture (Table 1). Senesced leaves of each species were collected in October 2003 and air-dried at room temperature in paper bags in the laboratory for 1 week. Leaves were put into litterbags in each of the possible 15 combinations of the four species. Litterbags (15 × 15 cm) were constructed from 1 mm nylon mesh and heat-sealed at the edges. Each litterbag contained 5 g of leaves, and all species in any one combination were equally represented in mass. On 17 November 2003, one set of all 15 combinations was placed in each of four replicate blocks for each of nine collection dates across 3 years: 0, 92, 181, 273, 365, 546, 730, 911 and 1065 days. At each collection date, one set from each replicate plot was randomly chosen for processing, and litterbags were transported back to the laboratory on ice. Litter was dried, ground

using a Spex CertiPrep 8000-D Mixer Mill (Spex CertiPrep, Metuchen, NJ), and the ash free dry mass (AFDM) remaining for each litterbag was determined by incineration at 550 °C for 1 h. Nitrogen content was determined by combustion in a Carlo Erba Elemental Analyser (Carlo Erba, Milan, Italy) and reported as percentage nitrogen (%N) of litter dry mass.

DATA ANALYSIS

Mass loss data were expressed as proportion AFDM remaining. These data were not adequately described by a linear model, so instead of decay rate (k), mass loss data were analysed *per se* using time (days) as a discrete, rather than continuous, factor. This approach avoids problems associated with averaging log-transformed data (see Ostrofsky 2007), and permitted us to test whether species effects were consistent across time. All statistical calculations were conducted in S-PLUS 7.0 (Insightful Corp., Seattle, WA) for Windows using 0.05 as the critical level of α .

TESTING FOR ADDITIVITY AND NON-ADDITIVITY

Following the approach of Kominoski *et al.* (2007), an analysis of variance (ANOVA), using Type I sums of squares (SS), was performed to test for additivity and non-additivity of species effects. Note, however, that our approach differed significantly from the approach of Kominoski *et al.* (2007) because time was treated as a discrete factor and because of the way in which we explored non-additive effects (see Results). Block, time and the presence/absence of each of the four species were added sequentially as terms to the model. Block had four levels and Time eight levels (the day 0 data were not included). The term representing each species had two levels: present or absent. A species interaction term (SpInt) was then included to test for non-additivity. This term had 11 levels, each representing one of the specific litterbag multi-species combinations. Lastly, interactions between time and block, the species and SpInt terms were included.

A significant SpInt term (and/or its interaction with time) indicates a significant non-additive interaction among species, due to richness and/or composition. To explore these possible drivers we replaced the SpInt term with a Richness term, composed of three levels (two to four species). In the absence of a significant effect of Richness or its interaction with Time, a significant SpInt term must arise through non-additive composition effects. If a Richness term is significant, a Composition term, with 11 possible levels and thereby equivalent to the SpInt term, can be added to the model, while retaining Richness, to evaluate if both non-additive richness and composition effects manifest.

If the SpInt term was not significant, the model was re-run with each of the four species' presence/absence terms added first because, given that Type I SS was used, the F -values of the species terms were sensitive to the order in which they were added. A significant species

Table 1. Summary of initial litter chemistries and the 3-year decay rate (k) in monoculture for each of the four tree species used. Numbers represent means \pm 1 SE; $n = 4$

	%N	%C	%P	% Lignin	% Total Phenolics	k day ⁻¹
<i>Liriodendron tulipifera</i>	0.95 \pm 0.04	47.87 \pm 0.60	0.43 \pm 0.002	8.58 \pm 0.36	74.46 \pm 15.17	0.00099
<i>Acer rubrum</i>	0.70 \pm 0.06	49.75 \pm 0.95	0.33 \pm 0.009	9.14 \pm 0.42	58.56 \pm 6.96	0.00097
<i>Quercus prinus</i>	1.25 \pm 0.09	50.06 \pm 1.15	0.52 \pm 0.004	13.55 \pm 0.37	20.5 \pm 1.92	0.00092
<i>Rhododendron maximum</i>	0.55 \pm 0.08	48.88 \pm 1.08	0.19 \pm 0.004	12.54 \pm 1.15	9.9 \pm 4.54	0.00086

term indicated additive effects of that species on decay dynamics. It follows then that a non-significant species effect suggests that the species lost is functionally replaceable by one of the other species used (Larsen *et al.* 2005; Suding *et al.* 2006).

ALTERNATIVE ANALYTICAL METHODS

Our approach, to determine whether there are neutral, additive or non-additive consequences of the loss of a particular species on ecosystem functioning, focuses on the scenario of non-random community change. To place our analyses in the context of previous work on the consequences of random species loss for decomposition dynamics, we evaluated a number of the analytical approaches commonly used in prior litter-mix studies. Specifically, we were interested in whether these approaches can identify compositional effects and whether these effects could be classified as additive or non-additive and linked to the identities of particular species.

Observed vs. expected models

Following Wardle *et al.* (1997), expected values for a variable were calculated for each mixture as an average of the monoculture values for each species involved using the following equation:

$$R_e = \sum_{i=1}^S \frac{M_i}{S}$$

where M_i is the monoculture value for species i , and S is the total number of species in the mixture. This was then compared to the observed value that was found experimentally for the mixture treatment as:

$$100 \times \left[\frac{\text{observed} - \text{expected}}{\text{expected}} \right]$$

which was plotted against species richness. This was done for each sample, and the average was taken for each treatment. For each treatment, 95% confidence intervals (CI) were also calculated and if the CI for each point did not cross $y = 0$, the effect was considered non-additive. This approach was conducted for each sampling period separately.

Following Hättenschwiler & Gasser (2005), expected values were calculated for each mixture as above, and the relationship between expected and observed values was assessed through linear regression, with deviations from the 1 : 1 line indicating non-additivity. Deviations were considered significant if the CI, both on the x - and y -axis, did not cross the line. A single-factor ANOVA across treatments was used to test for significant differences between observed and expected values. A Calculation term was used to describe the values for each treatment that had two values: observed or expected. The ANOVA determined if there were significant differences between the two. As we had multiple sampling dates, an additional two-way ANOVA was run which included time as a main and interacting factor. Following others (Schweitzer *et al.* 2005; e.g. Johnson *et al.* 2006), we also utilized a paired t -test.

Nested model

Following Smith & Bradford (2003a), Block, Time, Richness and Composition were added to a nested model (Composition in Richness). Block and Time had the same number of levels as with the initial model, and Richness had four levels (one to four species) while Composition had 15 levels (one for each possible combination

at each richness level). Next, the interactions of Time with Richness and Composition were added to the model. The resulting F -values were recalculated for the Richness terms against the relevant Composition terms (Crawley 2002). Significant richness terms would then indicate significant non-additive effects between at least two richness levels, whereas a significant composition effect may arise through additive or non-additive effects.

Results

TESTING FOR ADDITIVITY AND NON-ADDITIVITY

Mass loss

Litter mixing did not have non-additive effects on mass loss, given that the SpInt term and its interaction with time were not significant ($P > 0.05$), but there were significant additive effects of composition (Table 2). Specifically, the presence/absence of each of the four species had a significant effect on mass loss, and those of *A. rubrum* and *L. tulipifera* were consistent over time. Their main effects could therefore be pooled across time, which in turn revealed that their presence in mixture accelerated mass loss (Fig. 1a). The additive effects

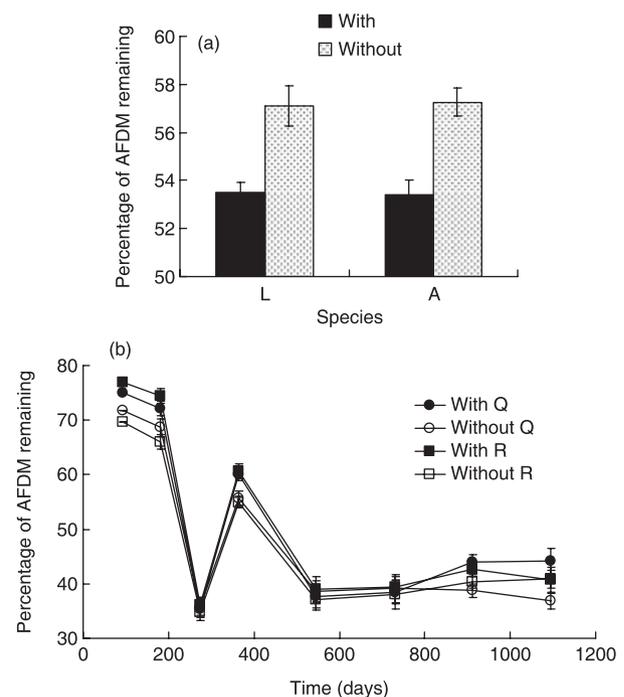


Fig. 1. Investigation of the direction of significant additive effects identified for %AFDM remaining. Letters refer to the genus of each of the four tree species: *L. tulipifera* (L), *A. rubrum* (A), *Q. prinus* (Q) and *R. maximum* (R). The ANOVA using Type I SS showed that the effects for (a) *L. tulipifera* and *A. rubrum* did not interact with time, and thus cumulative effects are shown for these species (see Results). However, the effects of (b) *Q. prinus* and *R. maximum* interacted with time and are expressed as a function of time. Solid bars or symbols represent all treatments that contained that species, and open ones include all treatments that did not. Values are means \pm 1 SE; $n = 4$. The spike at 365-day is due to organic sedimentation caused by a tropical storm that flooded the riparian zone. While inorganic sedimentation can be corrected in the analyses, organic sedimentation could not, so we considered it to be part of the natural dynamics.

Table 2. Summary of the ANOVA's testing for additive and non-additive effects of litter mixing on mass loss (%AFDM remaining) and nitrogen content (%N) of litter using Type I SS. The significance of the species terms is sensitive to the order in which they were added to the models. Hence, in the absence of a significant SpInt term, the models were re-run with each species being run first in the species order (see Results)

	d.f.	SS	MS	F	P
%AFDM remaining					
Block	3	588	196	2.97	0.032
Day	7	98 592	14 084	213	< 0.001
<i>Liriodendron tulipifera</i>	1	1884	1884	29.8	< 0.001
<i>Acer rubrum</i>	1	2114	2114	32.0	< 0.001
<i>Quercus prinus</i>	1	686	686	10.8	0.001
<i>Rhododendron maximum</i>	1	1415	1415	22.4	< 0.001
SpInt	10	868	86	1.32	0.221
Block × Day	21	9775	465	7.05	< 0.001
Day × <i>L. tulipifera</i>	7	379	54	0.82	0.571
Day × <i>A. rubrum</i>	7	550	78	1.19	0.308
Day × <i>Q. prinus</i>	7	882	126	1.91	0.067
Day × <i>R. maximum</i>	7	1051	150	2.27	0.028
Day × SpInt	70	3289	46	0.71	0.957
Residuals	328	21 672	66		
Total	471	143 454	21 158		
% Nitrogen					
Block	3	3.15	1.05	24.0	< 0.001
Day	8	45.5	5.68	130	< 0.001
<i>L. tulipifera</i>	1	3.02	3.02	69.0	< 0.001
<i>A. rubrum</i>	1	0.11	0.11	2.58	0.109
<i>Q. prinus</i>	1	2.88	2.88	65.9	< 0.001
<i>R. maximum</i>	1	6.52	6.52	149.3	< 0.001
SpInt	10	3.61	0.36	8.27	< 0.001
Block × Day	24	10.8	0.45	10.2	< 0.001
Day × <i>L. tulipifera</i>	8	0.49	0.06	1.39	0.200
Day × <i>A. rubrum</i>	8	0.47	0.06	1.35	0.220
Day × <i>Q. prinus</i>	8	0.31	0.04	0.89	0.521
Day × <i>R. maximum</i>	8	0.53	0.07	1.51	0.153
Day × SpInt	80	3.59	0.04	1.03	0.423
Residuals	370	16.2	0.04		
Total	531	97.1	20.4		

of *R. maximum* and *Q. prinus* were, however, time dependent. In general, the presence of these two species decreased rates of mass loss, but at days 273, 546 and 730, mass loss appears to be equivalent in both their presence and absence (Fig. 1b).

Nitrogen

In contrast to mass loss, there were significant non-additive effects of litter mixing on N content of litter (Table 2). Replacing the SpInt term with Richness did not identify richness to be driving the non-additivity ($F_{2,442} = 0.54$, $P > 0.50$), indicating that the non-additivity arose from compositional effects. Given that the composition effect did not interact with time, results were pooled across time.

To detect which species contributed to non-additive interactions, we compared the observed value for all mixtures involving each species against those that would be expected based on the average of that species in monoculture and the treatment that contained the other species involved. For example, to explore possible non-additivity of *L. tulipifera*, we compared the observed and expected values for LA, LQ, LR, LAQ, LAR, LQR and LAQR (where each of these is the mixture treatment consisting of the species each letter

represents; see Methods). The expected values were the average between the observed values for treatments L and A, Q, R, AQ, AR, QR and AQR, respectively. Observed minus expected values were plotted, and CIs that did not cross the x -axis were considered to be non-additive (Fig. 2). By doing this we found that each species contributed to non-additive dynamics, and this non-additivity was usually restricted to mixes of three and four species (Fig. 2). *Liriodendron tulipifera* and *Q. prinus* tended to decrease %N, while *A. rubrum* and *R. maximum* tended to increase it.

TESTING ALTERNATIVE MODELS

Mass loss

The observed/expected model showed idiosyncratic, sometimes non-additive, effects of litter mixing on mass remaining (Fig. 3). Mixing effects were strongly non-additive for some compositions at some time points, but in most cases the difference between observed and expected did not appear to differ significantly from zero, therefore showing only additive effects. There was also the potential for the relationship to vary with time, with stronger interactions occurring later in

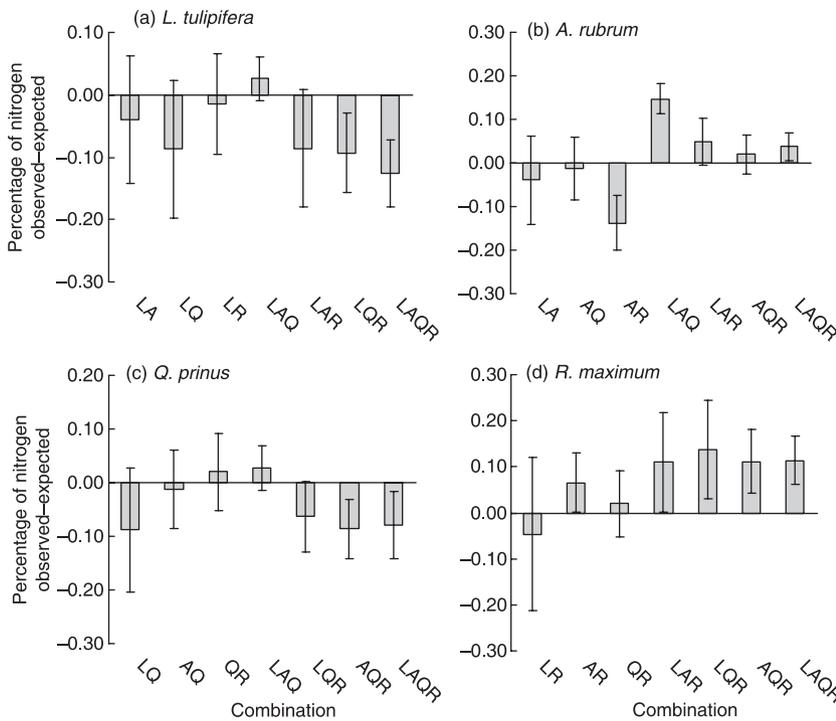


Fig. 2. Investigation into potential non-additive interactions driven by each of the four species used. Observed values were compared to expected values calculated as the average between the observed monoculture of each species and all of its possible interaction treatments (see Results). Error bars represent 95% CI, and treatments for which the CIs do not cross $y = 0$ are considered to be significantly non-additive.

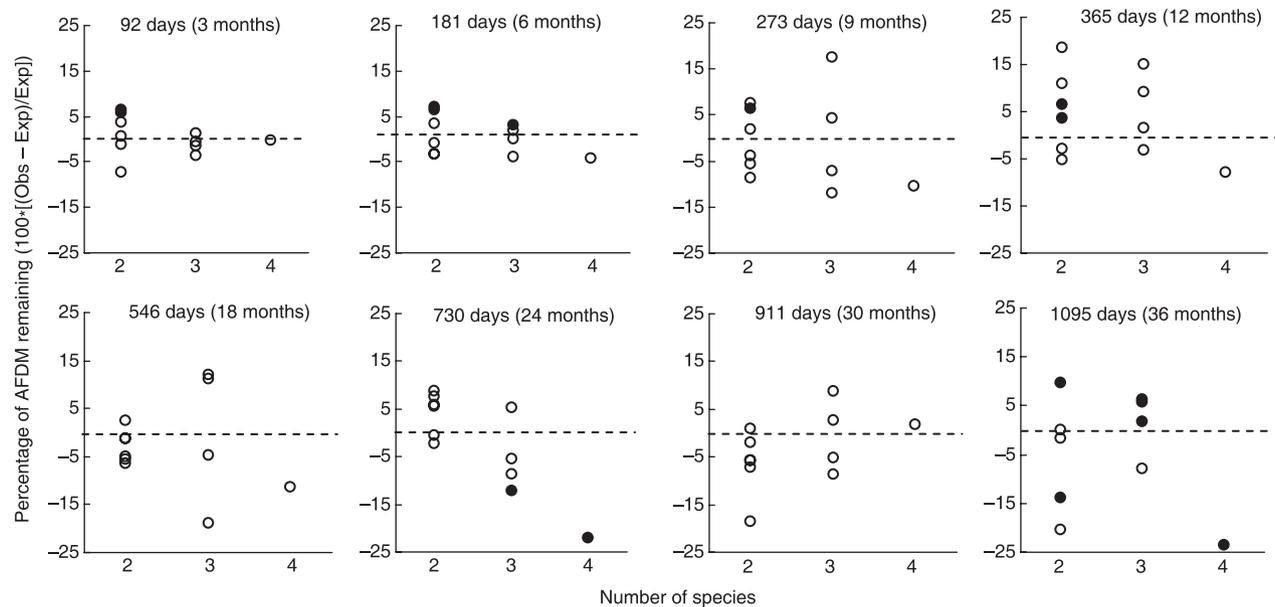


Fig. 3. Litter %AFDM remaining in the mixture litterbags in relation to the expected values calculated from the corresponding monoculture litterbags. Values are plotted against the number of species involved in the mixtures. Closed circles represent points for which the 95% CI did not cross $y = 0$, suggesting significant non-additivity. Open circles represent points for which they did, suggesting additive effects. For clarity, CIs are not shown.

time. However, error also increased (data not shown), and it was difficult to identify a significant relationship with certainty. The regression method showed no significant difference between observed and expected values when averaged over time ($F_{1,652} = 0.21$, $P = 0.65$, Fig. 4a), so there was no overall mixing effect. Again, stronger effects tended to occur later in time, but when time was added to the model, there was still no significant Calculation effect ($F_{1,650} = 0.80$, $P = 0.37$)

or its interaction with time ($F_{1,650} = 1.38$, $P = 0.24$). The nested model identified significant composition effects (Table 3), but we could not determine whether these were additive and/or non-additive. In agreement with the previous models, there was no interaction of either composition or richness with time, so effects were consistent throughout the experiment. Neither of the methods that test for an effect of species richness identified a significant impact on mass loss.

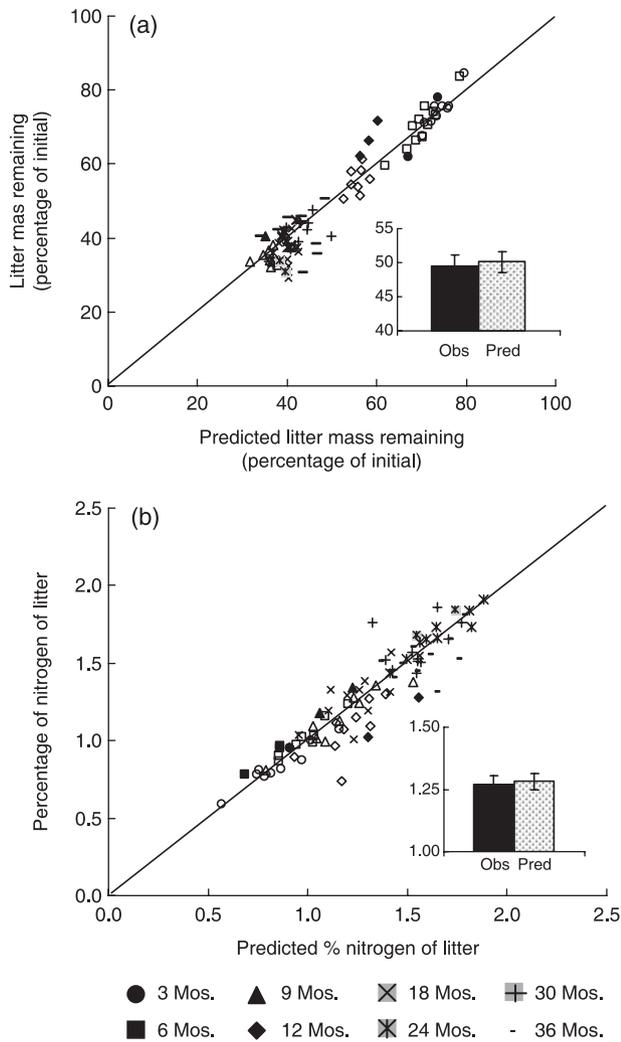


Fig. 4. (a) Observed %AFDM remaining and (b) observed %N in litter in relation to the expected values calculated from the corresponding monoculture litterbags. The line indicates the 1 : 1 relationship along which observed and expected values are equal. Data points represent averages across treatments over time, where solid symbols are significantly different from 1 : 1 (based on the 95% CI). For clarity, CIs are not shown. The inset shows the average observed (solid) and expected (open) values across all treatments.

Nitrogen

As with mass loss, the observed/expected model showed idiosyncratic effects on N content, with both additive and non-additive effects present (Fig. 5). Again, strength varied with time, but a trend was difficult to determine. The regression method showed that actual %N was lower than expected, but not significantly so ($F_{1,652} = 0.05$, $P = 0.83$, Fig. 4b). Again, the strength of this appeared to vary with time, but an interaction with time was not identified as significant if added to the ANOVA model ($F_{1,650} = 1.88$, $P = 0.17$). It is important to note that the overall average showed that observed and expected %N were virtually the same, but the majority of samples were above the 1 : 1 line, showing positive effects, for all but two time points. The nested model shows that there

Table 3. Summary of the nested ANOVA testing for composition and richness effects of litter-mixing on mass loss (%AFDM remaining) and nitrogen content (%N) of litter

	d.f.	SS	MS	F	P
%AFDM remaining					
Block	3	588	196	2.18	0.090
Time	7	98 593	14 085	157	<0.001
Richness	3	463	154	0.27	0.840
Composition	11	6210	565	6.29	<0.001
Time: Richness	21	947	45.1	0.65	0.866
Time: Composition	77	5332	69.3	0.77	0.916
Residuals	349	31 322	89.8		
Total	471	143 454	305		
%Nitrogen					
Block	3	3.15	1.05	15.48	<0.001
Time	8	45.54	5.69	83.97	<0.001
Richness	3	0.07	0.02	0.02	0.997
Composition	11	16.08	1.46	21.57	<0.001
Time: Richness	24	0.77	0.03	0.58	0.933
Time: Composition	88	4.87	0.06	0.82	0.876
Residuals	394	26.71	0.07		
Total	531	97.18	0.18		

Quality richness terms (indented) are tested against the quality composition terms, while other terms are tested against the model residual.

was an effect of composition on %N, but does not identify if it is due to additive or non-additive mechanisms (Table 3). As with mass loss, no effects of richness were identified by any of the methods.

Discussion

We sought to determine if there were additive or non-additive effects of litter species diversity, through richness or composition, on litter mass loss and N content in a southern Appalachian riparian forest. We were primarily interested in the relative importance of additive and non-additive effects to assess potential consequences of non-random species loss. Given the variation in litter quality represented by our four species (Table 1), we expected additive effects on decomposition based on species identity. This was confirmed for mass loss, where there were significant effects of the presence/absence of each of the four species. Given previous work (Wardle *et al.* 1997; Hättenschwiler & Gasser 2005), we also expected non-additive effects due to the large difference in litter quality between some of the species. Indeed, non-additive effects on litter N content were detected and determined to be due to species composition rather than species richness. Overall, our data suggest that effects of litter diversity on the decomposition process are mediated by species composition rather than species richness.

The presence of significant additive and non-additive effects of species composition on litter decay in our study suggests that non-random species loss from our system will influence significantly the dynamics of decomposition. The influence of each of the four species on decomposition dynamics shows that our four dominant species are not functionally substitutable (Larsen *et al.* 2005; Suding *et al.*

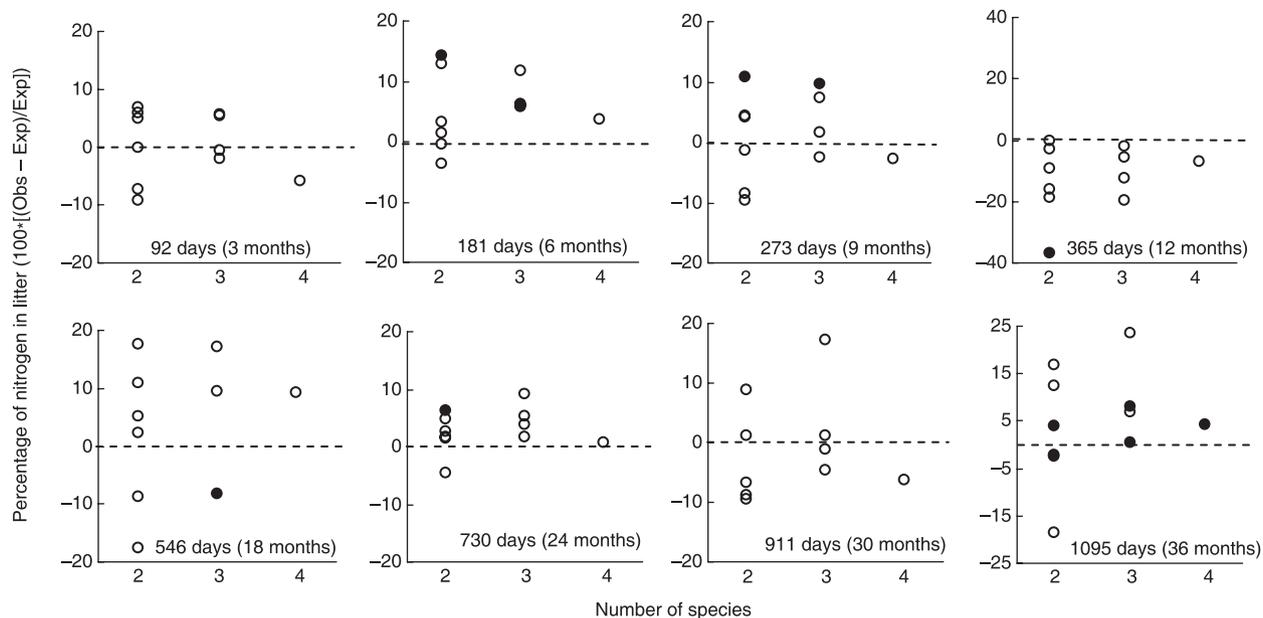


Fig. 5. Litter %N content in the mixture litterbags in relation to the expected values calculated from the corresponding monoculture litterbags. Values are plotted against the number of species involved in the mixtures. Closed circles represent points for which the 95% CI did not cross zero, suggesting significant non-additivity. Open circles represent points for which they did, suggesting additive effects. For clarity, CIs are not shown.

2006). Given that additive effects alone drive mass loss, the consequences of species loss on this variable should be predictable from studies of individual species. Given the plethora of work investigating the decay rate of single plant species, we may already have abundant information to predict the consequence of species loss and/or gain on litter decay rates. This is valuable given the changing distribution and abundances of species. For example, the invasive hemlock woolly adelgid (*Adelges tsugae*) is projected to extirpate eastern hemlock from much of its range, which at our field site is likely to be replaced by tulip poplar or rhododendron (Orwig & Foster 1998; Ellison *et al.* 2005). Replacement by tulip poplar is likely to increase rates of litter loss (Fig. 1a), whereas replacement with rhododendron is likely to decrease rates of litter loss (Fig. 1b). Similarly, potential declines in chestnut oak and rhododendron caused by the invasive pathogen sudden oak death (*Phytophthora ramorum*; Rizzo *et al.* 2002), are likely to increase rates of litter decay, although the strength of the influence on mass loss is likely to vary over time (Fig. 1b). A concomitant study in the stream associated with the riparian zone in which we worked (Kominoski *et al.* 2007) identified non-additive effects of species diversity on litter mass loss dynamics. This non-additivity was caused by both positive effects of species richness and negative effects of certain species compositions (Kominoski *et al.* 2007). In the aquatic system, there, therefore, appears to be a greater influence of species interactions on decomposition dynamics than in the terrestrial system. This may arise because of the different physical factors and biota which affect decomposition rates in stream and terrestrial systems. What seems certain is that the consequences of non-random species loss may differ for aquatic and terrestrial systems, with the impacts being less (statistically) predictable in streams.

That the effects of the lower-quality species in our study were not consistent across time, while they were for the higher-quality litters (Fig. 1), may be due to a greater influence of physical and biotic factors on the degradation of slower-decomposing species. For example, litter quality can interact with the biota degrading litter to alter mass loss throughout decomposition, and these biota are often considered to play a more important role in regulating the decay rates of lower quality litters (Smith & Bradford 2003b; Moorhead & Sinsabaugh 2006). Alternatively, the inhibition of biotic activity by low-quality litter may dissipate with time, altering the role of these species in decay across time. Notably, *R. maximum* and *Q. prinus* were only similar in their initial lignin concentrations, contradicting the hypothesis that lignin concentration is more important in later stages of decay (McClaugherty & Berg 1987; Taylor *et al.* 1989; Berg 2000). More research is necessary to clarify the mechanism behind the interaction of low quality species with time, but it is clear that the loss of higher-quality species from this system may cause patterns of mass loss to be less predictable over the decomposition continuum.

Changes in N dynamics caused by species loss may not be statistically predictable from knowledge of the main effects of each species, given that we observed pervasive non-additive effects on litter N content (Fig. 2). Investigating the interactions which gave rise to this non-additivity is complicated; even full-factorial diversity studies present a special case because there is no true control. That is, the response variable (e.g. plant productivity or decomposition) is normally a property of the main effects (i.e. species), and a true control would be where these main effects are not applied. Mass loss would be zero, as there would have been no litter to decompose. The approach we took to investigate interactions was relevant to

scenarios of non-random species loss. We explored non-additive interactions using an altered observed/expected method that tests for non-additive interactions driven by losing a particular species from a mixture (see Results). Certainly the method used here is not the only possible method, and more work on the best way to explore non-additive composition effects is necessary. What our method did show is that each of the four species contributed to non-additive interactions, but this was not only true for mixtures containing species of very different initial chemical qualities, in contrast to our hypothesis and the general theory behind litter-mixing studies (Seastedt 1984; Blair *et al.* 1990). Notably, non-additivity was generally apparent only in three- and four-species mixtures. In species-rich mixtures, species high in initial N (*L. tulipifera* and *Q. prinus*) acted to decrease total N content in comparison to what would be expected, whereas those low in initial N (*A. rubrum* and *R. maximum*) increased it. Overall, these results suggest that N dynamics will be altered, through both species identity and interaction effects, by the loss of any one of the dominant tree species in our system.

Prior to the 365-day sampling, a tropical storm deposited organic sedimentation in the litter. Tropical storm systems are a natural disturbance in the southern Appalachians (Swank & Crossley 1988), with an average of five affecting the area each decade to varying degrees of severity (Atlantic Oceanographic and Meteorological Laboratory 2006). As organic sedimentation cannot be corrected by measuring AFDM, we treated this sedimentation as a natural part of the system. We would not expect sedimentation to strongly influence the results, as it is unlikely that sediment was deposited unevenly amongst the different treatments. Compositional effects of each of the four species were detected, so individual species' influences were not masked by the sedimentation event. In addition, only the additive effects of *Q. prinus* and *R. maximum* on mass loss interacted with time; had the impacts of the sedimentation been large we would have expected more statistical interactions with time for both mass loss and N. The absence of time interactions on N dynamics under hurricane events is consistent with soil nutrient dynamics (Wright & Coleman 1999). Sedimentation may, however, have reduced the magnitude of the species effects on mass loss that we observed, and so our data should be viewed as a conservative representation of possible effects of non-random species loss in our system. Our data may be most relevant to the many other systems that regularly experience hurricane phenomena, such as the humid tropics of Asia and the Caribbean (Beard *et al.* 2005; Hou *et al.* 2005), as well as the eastern United States (Swank & Crossley 1988; Schwarz *et al.* 2001).

Using a full-factorial design and a model that allows us to look for additive and non-additive effects of species composition allowed us to explore the effects of both random and non-random species loss on ecosystem processes, an issue that has been brought forth for diversity studies of productivity (Smith & Knapp 2003; Gross & Cardinale 2005; Schläpfer *et al.* 2005), but not yet decomposition. The advantages of this method are that it: (i) places an equal emphasis on species

identity effects, which is important if species are lost non-randomly as anticipated under global change, by looking for effects of the presence of each species; (ii) permits us to consider whether there are overall effects of particular species that would otherwise appear idiosyncratic; and (iii) identifies whether impacts of species loss are statistically predictable (i.e. based on single-species decay dynamics). Conversely, most litter mixing studies do not address additive effects and focus on the effects of random species loss. If non-random species loss is also likely in other systems, it is important to realize that the consequences of species loss may differ from those represented in the literature. Schläpfer *et al.* (2005) point out that the assumption of random species loss can cause results to be either over- or underestimated, depending on the correlation between species persistence and performance. To determine how information yielded from previous studies compares with our data, and what previous methods tell us about additivity and non-additivity, we used several common methods for analysing litter mixture decomposition data.

The various observed/expected models tend to treat additive effects as a null effect (see Introduction), thereby not addressing the potential for a lack of diversity effects of composition. A lack of non-additive effects may be due to individual (additive) effects of species, where observed values equal expected due to a dominance of species identity over interactions among species. Conversely, the species examined may be functionally redundant so that when one species is lost, another species compensates (Suding *et al.* 2006; Cross & Harte 2007). In this case, observed would still equal expected, though it is not due to any species effects. It may not be an unreasonable assumption that diversity effects exist, given that most studies see some sort of effect, though they do not always differentiate between additive or non-additive, and cannot always identify the species driving those effects (Gartner & Cardon 2004; Hättenschwiler *et al.* 2005).

In our comparison of analytical methods, we found that all methods converged on one result: that there was no effect of species richness on either litter mass loss or N content. In contrast, the methods of analysis provided different interpretations of the effects of species composition on litter decay. This is due to the differences in how additive and non-additive effects are treated by each model. Overall, all of the methods can detect additive and non-additive composition effects, but only our Type I SS model and the nested model treat additive effects as a legitimate compositional effect, though the nested model cannot differentiate them specifically from non-additivity. While non-additive effects (that can be identified by observed/expected models) drive litter N content, mass loss is driven by additive composition effects, which are identified as idiosyncratic or nonexistent by some models. Though additivity is not explicitly addressed, the information still exists via the lack of non-additive effects, but these effects tend not to be explained or investigated further. They offer no specific identification of the strength of a certain species' effect, which is an important factor in the case of non-random species loss. For models that can detect additivity but not

identify it, such as the nested method, we are able to predict that there are consequences of non-random species loss, but are not able to identify which species are likely to generate consequences or how predictable those consequences will be. Therefore, we may be missing out on important information by using only methods that do not or cannot specifically identify additive effects.

To detect both additive and non-additive effects of species on ecosystem processes, a full-factorial design is necessary, which generally limits species mixtures to low richness levels given the number of species combinations necessary. Patches of leaf litter in temperate forest soils are generally occupied by only a few species, so this is not unreasonable. If simpler questions pertaining to only non-additivity, and therefore random species loss, are being asked, then it is appropriate to use the methods already frequent in litter-mixing literature. However, our method allows us to look for potential effects of non-random species loss without having to identify *a priori* the most susceptible species and eliminate them. While it is often pointed out that it may be more appropriate to study the decomposition of mixed litter through identification of the litter remaining in bags (Hättenschwiler & Gasser 2005; Gartner & Cardon 2006), it is not always possible or practical to do this. Over long-term studies such as ours, litter species become indistinguishable later in decomposition. Our method allows us to look for the species driving compositional effects without having to identify individually their leaves in the litter layer and measure their contribution to mass remaining.

Conclusion

We have shown significant additive effects of litter mixing on mass loss and non-additive effects of species composition on N content in decomposing litter. These results suggest that the consequences of non-random species loss for our system will be statistically predictable for mass loss but not for N dynamics. Given that non-random (as opposed to random) species loss is likely to be the result of current global change drivers, much more attention needs to be paid to its effects on decomposition in litter-mix studies. We have shown here that the additive effects of species identity have a large impact on decomposition dynamics; such additive effects are usually not resolved in diversity studies, although that species identity effects may be large is recognised in studies of random species loss. Given that the dominant tree species used in our study are likely to change in relative abundance due to invasive pathogens and pests, our research suggests that the consequences will include marked changes in organic matter processing and nutrient dynamics. Our findings highlight that diversity studies considering scenarios of non-random species loss will facilitate predictions of the consequences of global change for ecosystem functioning that result from the effects of both species identity and interactions. This will permit mechanisms such as the presence and/or absence of functional redundancy and complementarity to be identified and addressed.

Acknowledgements

We thank Kyle Wickings and Bas Boots for comments on an earlier draft, and Jimmy Blackmon, Rose Cannon and Ryan Malloy for their help in the field and laboratory. We thank Tom Maddox in the Analytical Chemistry Laboratory of the Odum School of Ecology for elemental analyses. This research was supported by National Science Foundation grants DEB-9632854 and DEB-0218001 to the Coweeta LTER Program.

References

- Aber, J.D. & Melillo, J.M. (2001) Chemical properties of litter and soil organic matter: the decomposition continuum. *Terrestrial Ecosystems*, pp. 205–226. Academic Press, San Diego.
- Aber, J.D., Melillo, J.M. & McLaugherty, C.A. (1990) Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. *Canadian Journal of Botany*, **68**, 2201–2208.
- Aerts, R. (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, **79**, 439–449.
- Atlantic Oceanographic and Meteorological Laboratory (2006) *HURDAT Re-analysis Project*. <<http://www.aoml.noaa.gov/hrd/hurdat/>>.
- Bardgett, R.D. & Shine, A. (1999) Linkages between plant litter diversity, soil microbial biomass and ecosystem function in temperate grasslands. *Soil Biology and Biochemistry*, **31**, 317–321.
- Beard, K.H., Vogt, K.A., Vogt, D.J., Scatena, F.N., Covich, A.P., Sigurdardottir, R., Sicama, T.G. & Crowl, T.A. (2005) Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. *Ecological Monographs*, **75**, 345–361.
- Berg, B. (2000) Litter decomposition and organic matter turnover in northern forest soils. *Forest Ecology and Management*, **133**, 13–22.
- Blair, J.M., Parmelee, R.W. & Beare, M.H. (1990) Decay-rates, nitrogen fluxes, and decomposer communities of single-species and mixed-species foliar litter. *Ecology*, **71**, 1976–1985.
- Chapman, K., Whittaker, J.B. & Heal, O.W. (1988) Metabolic and faunal activity in litters of tree mixtures compared with pure stands. *Agriculture Ecosystems and Environment*, **24**, 33–40.
- Crawley, M.J. (2002) Nested designs and variance components analysis. *Statistical Computing: An Introduction to Data Analysis using S-Plus*, pp. 361–375. John Wiley & Sons, Ltd., West Sussex.
- Cross, M.S. & Harte, J. (2007) Compensatory responses to loss of warming-sensitive plant species. *Ecology*, **88**, 740–748.
- Drake, J.M. (2003) Why does grassland productivity increase with species richness? Disentangling species richness and composition with tests for overyielding and superyielding in biodiversity experiments. *Proceedings of the Royal Society of London Series B – Biological Sciences*, **270**, 1713–1719.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B. & Webster, J.R. (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, **3**, 479–486.
- Fyles, J.W. & Fyles, I.H. (1993) Interaction of douglas-fir with red alder and salal foliage litter during decomposition. *Canadian Journal of Forest Research – Revue Canadienne De Recherche Forestiere*, **23**, 358–361.
- Gartner, T.B. & Cardon, Z.G. (2004) Decomposition dynamics in mixed-species leaf litter. *Oikos*, **104**, 230–246.
- Gartner, T.B. & Cardon, Z.G. (2006) Site of leaf origin affects how mixed litter decomposes. *Soil Biology and Biochemistry*, **38**, 2307–2317.
- Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.
- Gross, K. & Cardinale, B.J. (2005) The functional consequences of random vs. ordered species extinctions. *Ecology Letters*, **8**, 409–418.
- Hättenschwiler, S. & Gasser, P. (2005) Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 1519–1524.
- Hättenschwiler, S., Tiunov, A.V. & Scheu, S. (2005) Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology Evolution and Systematics*, **36**, 191–218.
- Heneghan, L., Coleman, D.C., Crossley, D.A. & Zou, X.M. (1999) Nitrogen dynamics in decomposing chestnut oak (*Quercus prinus* L.) in mesic temperate and tropical forest. *Applied Soil Ecology*, **13**, 169–175.
- Hou, P.C.L., Zou, X.M., Huang, C.Y. & Chien, H.J. (2005) Plant litter decomposition influenced by soil animals and disturbance in a subtropical rainforest of Taiwan. *Pedobiologia*, **49**, 539–547.

- Johnson, M.T.J., Lajeunesse, M.J. & Agrawal, A.A. (2006) Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters*, **9**, 24–34.
- Kominoski, J.S., Pringle, C.M., Ball, B.A., Bradford, M.A., Coleman, D.C., Hall, D.B. & Hunter, M.D. (2007) Nonadditive effects of leaf litter species diversity on breakdown dynamics in a detritus-based stream. *Ecology*, **88**, 1167–1176.
- Larsen, T.H., Williams, N.M. & Kremen, C. (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, **8**, 538–547.
- Leroy, C.J. & Marks, J.C. (2006) Litter quality, stream characteristics and litter diversity influence decomposition rates and macroinvertebrates. *Freshwater Biology*, **51**, 605–617.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, **294**, 804–808.
- McClaugherty, C. & Berg, B. (1987) Cellulose, lignin and nitrogen concentrations as rate regulating factors in late stages of forest litter decomposition. *Pedobiologia*, **30**, 101–112.
- McTiernan, K.B., Ineson, P. & Coward, P.A. (1997) Respiration and nutrient release from tree leaf litter mixtures. *Oikos*, **78**, 527–538.
- Mikola, J., Salonen, V. & Setälä, H. (2002) Studying the effects of plant species richness on ecosystem functioning: does the choice of experimental design matter? *Oecologia*, **133**, 594–598.
- Moore, J.C., Berlow, E.L., Coleman, D.C., de Ruiter, P.C., Dong, Q., Hastings, A., Johnson, N.C., McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K., Rosemond, A.D., Post, D.M., Sabo, J.L., Scow, K.M., Vanni, M.J. & Wall, D.H. (2004) Detritus, trophic dynamics and biodiversity. *Ecology Letters*, **7**, 584–600.
- Moorhead, D.L. & Sinsabaugh, R.L. (2006) A theoretical model of litter decay and microbial interaction. *Ecological Monographs*, **76**, 151–174.
- Orwig, D.A. & Foster, D.R. (1998) Forest response to the introduced hemlock woolly adelgid in southern New England, USA. *Journal of the Torrey Botanical Society*, **125**, 60–73.
- Ostrofsky, M.L. (2007) A comment on the use of exponential decay models to test nonadditive processing hypotheses in multispecies mixtures of litter. *Journal of the North American Benthological Society*, **26**, 23–27.
- Rizzo, D.M., Garbelotto, M., Davidson, J.M., Slaughter, G.W. & Koike, S.T. (2002) *Phytophthora ramorum* as the cause of extensive mortality of *Quercus* spp. and *Lithocarpus densiflorus* in California. *Plant Disease*, **86**, 205–214.
- Rustad, L.E. (1994) Element dynamics along a decay continuum in a red spruce ecosystem in Maine, USA. *Ecology*, **75**, 867–879.
- Salamanca, E.F., Kaneko, N. & Katagiri, S. (1998) Effects of leaf litter mixtures on the decomposition of *Quercus serrata* and *Pinus densiflora* using field and laboratory microcosm methods. *Ecological Engineering*, **10**, 53–73.
- Schimel, J.P. & Hättenschwiler, S. (2007) Nitrogen transfer between decomposing leaves of different N status. *Soil Biology and Biochemistry*, **39**, 1428–1436.
- Schläpfer, F., Pfisterer, A.B. & Schmid, B. (2005) Non-random species extinction and plant production: implications for ecosystem functioning. *Journal of Applied Ecology*, **42**, 13–24.
- Schnitzer, M. & Khan, S.U. (1978) *Soil Organic Matter*. Elsevier Scientific Publishing Company, New York, NY.
- Schwarz, P.A., Fahey, T.J., Martin, C.W., Siccama, T.G. & Bailey, A. (2001) Structure and composition of three northern hardwood-conifer forests with differing disturbance histories. *Forest Ecology and Management*, **144**, 201–212.
- Schweitzer, J.A., Bailey, J.K., Hart, S.C. & Whitham, T.G. (2005) Nonadditive effects of mixing cottonwood genotypes on litter decomposition and nutrient dynamics. *Ecology*, **86**, 2834–2840.
- Seastedt, T.R. (1984) The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology*, **29**, 25–46.
- Smith, M.D. & Knapp, A.K. (2003) Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters*, **6**, 509–517.
- Smith, V.C. & Bradford, M.A. (2003a) Do non-additive effects on decomposition in litter-mix experiments result from differences in resource quality between litters? *Oikos*, **102**, 235–242.
- Smith, V.C. & Bradford, M.A. (2003b) Litter quality impacts on grassland litter decomposition are differently dependent on soil fauna across time. *Applied Soil Ecology*, **24**, 197–203.
- Stevenson, F.J. (1994) *Humus Chemistry: Genesis, Composition, Reactions*. John Wiley & Sons, Inc., New York, NY.
- Suding, K.N., Miller, A.E., Bechtold, H. & Bowman, W.D. (2006) The consequence of species loss on ecosystem nitrogen cycling depends on community compensation. *Oecologia*, **149**, 141–149.
- Swan, C. & Palmer, M. (2006) Composition of speciose leaf litter alters stream detritivore growth, feeding activity and leaf breakdown. *Oecologia*, **147**, 469–478.
- Swan, C.M. & Palmer, M.A. (2004) Leaf diversity alters litter breakdown in a Piedmont stream. *Journal of the North American Benthological Society*, **23**, 15–28.
- Swank, W.T. & Crossley, D.A. (1988) Forest hydrology and ecology at Coweeta. *Ecological Studies: Analysis and Synthesis* (eds W.D. Billings, F. Golley, O.L. Lange, J.S. Olson & H. Remmert), p. 469. Springer-Verlag, New York.
- Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) *Decomposition in Terrestrial Ecosystems*. University of California Press, Los Angeles.
- Taylor, B.R., Parkinson, D. & Parsons, W.F.J. (1989) Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology*, **70**, 97–104.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494–499.
- Wardle, D.A., Bonner, K.I. & Nicholson, K.S. (1997) Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos*, **79**, 247–258.
- Wright, C.J. & Coleman, D.C. (1999) The effects of disturbance events on labile phosphorus fractions and total organic phosphorus in the southern Appalachians. *Soil Science*, **164**, 391–402.

Received 28 September 2007; accepted 28 November 2007

Handling Editor: Richard Bardgett