

## INCREASING LITTER SPECIES RICHNESS REDUCES VARIABILITY IN A TERRESTRIAL DECOMPOSER SYSTEM

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**Abstract.** Debate on the relationship between diversity and stability has been driven by the recognition that species loss may influence ecosystem properties and processes. We conducted a litterbag experiment in the Scottish Highlands, United Kingdom, to examine the effects of altering plant litter diversity on decomposition, microbial biomass, and microfaunal abundance. The design of treatments was fully factorial and included five species from an upland plant community (silver birch, *Betula pendula*; Scots' pine, *Pinus sylvestris*; heather, *Calluna vulgaris*; bilberry, *Vaccinium myrtillus*; wavy-hair grass, *Deschampsia flexuosa*); species richness ranged from one to five species. We tested the effects of litter species richness and composition on variable means, whether increasing litter species richness reduced variability in the decomposer system, and whether any richness–variability relationships were maintained over time (196 vs. 564 days). While litter species composition effects controlled variable means, we revealed reductions in variability with increasing litter species richness, even after accounting for differences between litter types. These findings suggest that higher plant species richness per se may result in more stable ecosystem processes (e.g., decomposition) and decomposer communities. Negative richness–variation relationships generally relaxed over time, presumably because properties of litter mixtures became more homogeneous. However, given that plant litter inputs continue to enter the belowground system over time, we conclude that variation in ecosystem properties may be buffered by greater litter species richness.

**Key words:** biodiversity; decomposition; ecosystem variability; litter identity; microbial biomass; nematodes; stability.

### INTRODUCTION

The diversity–stability debate has intensified recently due to the need to determine how species loss may influence ecosystem “functioning” (McCann 2000, Hooper et al. 2005). Moreover, it has become increasingly evident that species richness may have important consequences for the stability, as well as the magnitude, of ecosystem properties (Van der Heijden et al. 1998, Wardle et al. 2000, Dang et al. 2005). While increasing species richness can have synergistic effects on ecosystem

properties, it is also noted that stability of these properties may increase with species richness against a background of spatial and temporal fluctuations (Tilman 1999, Loreau et al. 2001, Hooper et al. 2005). Examining the relationship between species richness and stability is therefore of considerable importance in understanding the reliability of key ecosystem services in the face of human-induced environmental changes.

In terrestrial systems, the influence of plant diversity (both richness and composition) on ecosystem properties has been explored mainly in experimental grasslands (e.g., Tilman et al. 1996, Hector et al. 1999). Variability is frequently used as a measure of stability (McCann 2000), and in these systems, variability in primary productivity has typically been assessed across plant species richness gradients. In particular, recent work by Tilman et al. (2006) has highlighted a decrease in the

Manuscript received 21 August 2007; revised 23 January 2008; accepted 24 January 2008. Corresponding Editor: D. A. Wardle.

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temporal variability of aboveground biomass with increasing plant species richness. Since the majority of aboveground plant productivity enters the decomposer system as litter (McNaughton et al. 1989), many studies have examined the effects of altering plant litter richness on decomposition and the decomposer community (Wardle et al. 1997, 2006, Kaneko and Salamanca 1999, Hansen 2000). However, while the consequences of altering live plant species richness for aboveground community stability are increasingly well resolved, only a handful of studies have explored variability in the decomposer system (e.g., Schädler and Brandl 2005, Lecerf et al. 2007).

That litter-mixing experiments have shown evidence of positive (synergistic), negative (antagonistic), and neutral effects may suggest decomposition and decomposer communities respond unpredictably to changes in litter diversity (Gartner and Cardon 2004, Hättenschwiler et al. 2005). In fact, nonadditive effects (synergistic and antagonistic) of litter mixing are prevalent (e.g., Hättenschwiler and Gasser 2005, Kominoski et al. 2007), and moreover, a greater proportion of nonadditive effects are synergistic (Gartner and Cardon 2004, Hättenschwiler and Gasser 2005). These nonadditive effects can be explained by species interactions, in comparison to additive effects that are explained by species identity. Despite the prevalence of nonadditive effects, several studies have shown that decomposition and decomposers are unlikely to be affected by the number of levels of litter species richness (Wardle et al. 2006, Lecerf et al. 2007). How these findings relate to variability in the decomposer system remains to be explored.

We conducted a manipulative litterbag experiment to examine the effects of altering plant litter diversity (species richness and composition) on litter decomposition, microbial biomass, and microfaunal abundance. Specifically, we tested whether (1) the overall effects of increasing litter species richness were synergistic; (2) whether increasing litter species richness reduced variability; and (3) whether these relationships held over time (196 vs. 564 days) for litter mass loss, moisture content, C:N ratio, microbial biomass, and nematode abundance. Although previous studies have used linear mixed models to examine the effects of litter species richness and composition in fully factorial designs (e.g., Smith and Bradford 2003, Kominoski et al. 2007), we believe our paper is the first to use these models to assess influences on variances as well as means. To our knowledge, no other study has simultaneously used the fixed-effect part of these models to remove the effects of the individual species in different mixtures and the random-effect part to model the relationship between species richness and variance in a single, integrative analysis, thereby accounting for the confounding influence of differences in means on variance at different

levels of species richness. Here we demonstrate that, while there are generally no effects of increasing litter species richness on means of decomposition variables, there are decreases in the variability of both decomposition and the decomposer community, even after accounting for differences among litter species.

## METHODS

### *Study site*

A litterbag experiment was set up in the understory of a 40-year-old birch stand on Tulchan Estate, Morayshire, Scotland, United Kingdom (57°25' N, 3°27' W, 260 m above sea level). Tulchan has a mean annual temperature and mean annual rainfall of 7.3°C and 889 mm, respectively (Metereological Office, UK). Senescent leaf litter of two tree species (silver birch, *Betula pendula* and Scots' pine, *Pinus sylvestris*), two dwarf-shrubs (heather, *Calluna vulgaris* and bilberry, *Vaccinium myrtillus*), and one grass (wavy-hair grass, *Deschampsia flexuosa*) was collected between October 2003 and January 2004, air-dried, and stored at room temperature until needed. These plant species are the five most common in our upland successional study system (Hester et al. 1991), and represent a wide range of litter decomposability (see Appendix A).

### *Experimental design*

Litterbags (10 × 9.5 cm) were composed of a 500-μm mesh bottom layer and 1-mm mesh top layer. Litterbags immediately retrieved from the field demonstrated that the 500-μm mesh effectively reduced handling losses for finer litter compared to larger mesh sizes (A. M. Keith, *unpublished data*). Each litterbag contained a total of 2 g of dried leaf litter, with equal masses of each litter type in mixtures. Litter monocultures, and all possible litter mixtures from the five different species were used, giving 31 different litter treatments (species composition), with species richness ranging from one to five species. Replication of treatments was adjusted at each level of litter species richness to compensate for the different number of litter treatments (e.g., 6, 3, 3, 6, and 12 replicates of the 5, 10, 10, 5, and 1 treatments at each richness level, respectively). Replicates of each treatment were allocated equally among three blocks with the areas for each block being chosen to avoid rocks and vegetation hummocks (see Plate 1). On 1 April 2004, 528 litterbags were placed in the field. The litterbags were covered and held down by coarse-mesh fencing (25 mm), and this was lifted twice to remove litterfall from the surrounding vegetation between sampling times.

After both 196 days (25 October 2004) and 564 days (31 October 2005), 264 litterbags were retrieved from the field. On each sampling occasion, half of the available replicates were freeze-dried to measure moisture content, decomposition (percentage of dry mass loss), and microbial biomass. Total phospholipid fatty acids

(PLFA) extracted from milled samples (50- $\mu$ m mesh) were used as an index of active microbial biomass (Zelles et al. 1995), and expressed as nanomole per gram of litter remaining. Total nitrogen and carbon content of milled samples was determined using a Flash-EA1112 Elemental Analyzer (Thermo-Finnigan, Milan, Italy). The nematode fauna were extracted from remaining replicates using the tray version of the Baermann funnel method (Whitehead and Hemming 1965). Total numbers of nematodes were counted at 40 $\times$  magnification, and expressed per gram of litter remaining.

#### *Statistical analyses*

We used Type 1 sums of squares general linear models (GLM) to test the effects of litter species richness and composition on mean mass loss, moisture, C:N ratio, microbial biomass, and nematode abundance. Time was initially included in the models as a fixed effect, but the analyses were repeated for each time separately to examine any differences in significant terms between 196 and 564 days. Initial analyses found that litter species richness as a continuous variable was insignificant for all response variables, and subsequently, litter species richness was treated as a categorical variable (five levels). The effect of adding the species richness term to the model was tested against the effect of adding the species composition term (31 levels) to the model to obtain the appropriate *F* value with respect to the nesting of species composition within species richness (Schmid et al. 2002). Significant differences between levels of species richness were assessed using least-squares means with Tukeys' adjustment.

In a further analysis, we compared Type 1 sums of squares attributed to species composition when entered in the GLM (after fitting time and block) either alone or after fitting five species-specific covariates (which we call litter identity terms). For each species, the corresponding litter identity term consisted of the initial proportion that each species placed in the litterbags (e.g., 0, 0.20, 0.25, 0.33, 0.5, and 1). Using these initial proportions of each litter species as terms in the model, rather than dummy variables for presence/absence (e.g., 0 and 1), explained a greater amount of variation in all response variables (see Appendix B: Table B1). This was performed to determine whether litter species identity could explain the variation associated with species composition.

We then fitted linear mixed models (LMMs) to each response variable in turn to model random variation as a function of litter species richness by the method of residual maximum likelihood. These analyses were carried out for each time separately, and with categorical variables for block (three levels as fixed effect) and species richness included in the models. Three possible models were considered for the variance of residuals. Firstly, this variance was taken to have a common value



PLATE 1. Experimental block of litterbags in the birch stand on the day they were placed in the field (1 April 2004). Photo credit: G. H. R. Osler.

for all observations. Secondly, the variances of residuals were taken to have unrelated values for each level of species richness (displayed as data points in Fig. 1). Finally, the variance,  $v$ , was assumed to follow a power function in species richness,  $s$ , with equation  $v = a \cdot s^{-b}$  (displayed as lines in Fig. 1). With this formulation, positive values of  $b$  indicate variance decreasing as species richness increases. LMMs with variances following the power function for given values of  $b$  were fitted by declaring observations weights of  $s^b$ , and optimal values of  $b$  were determined by fitting a range of values of  $b$  (−2.5 to 2.5 in increments of 0.01) and selecting the value that maximized the residual log-likelihood (equivalent to minimizing the  $-2 \times \log$ -likelihood deviance). Differences in deviance were assessed against  $\chi^2$  distributions, with degrees of freedom taken to be the difference in the number of variance parameters. However, these analyses do not account for the influence of different mean values of the different species compositions: Instead, variation due to different composition means within species richness levels contributes to the estimated residual variation. Therefore, the above analysis (described as “Total variance” in Fig. 1), does not allow us properly to examine whether variances were

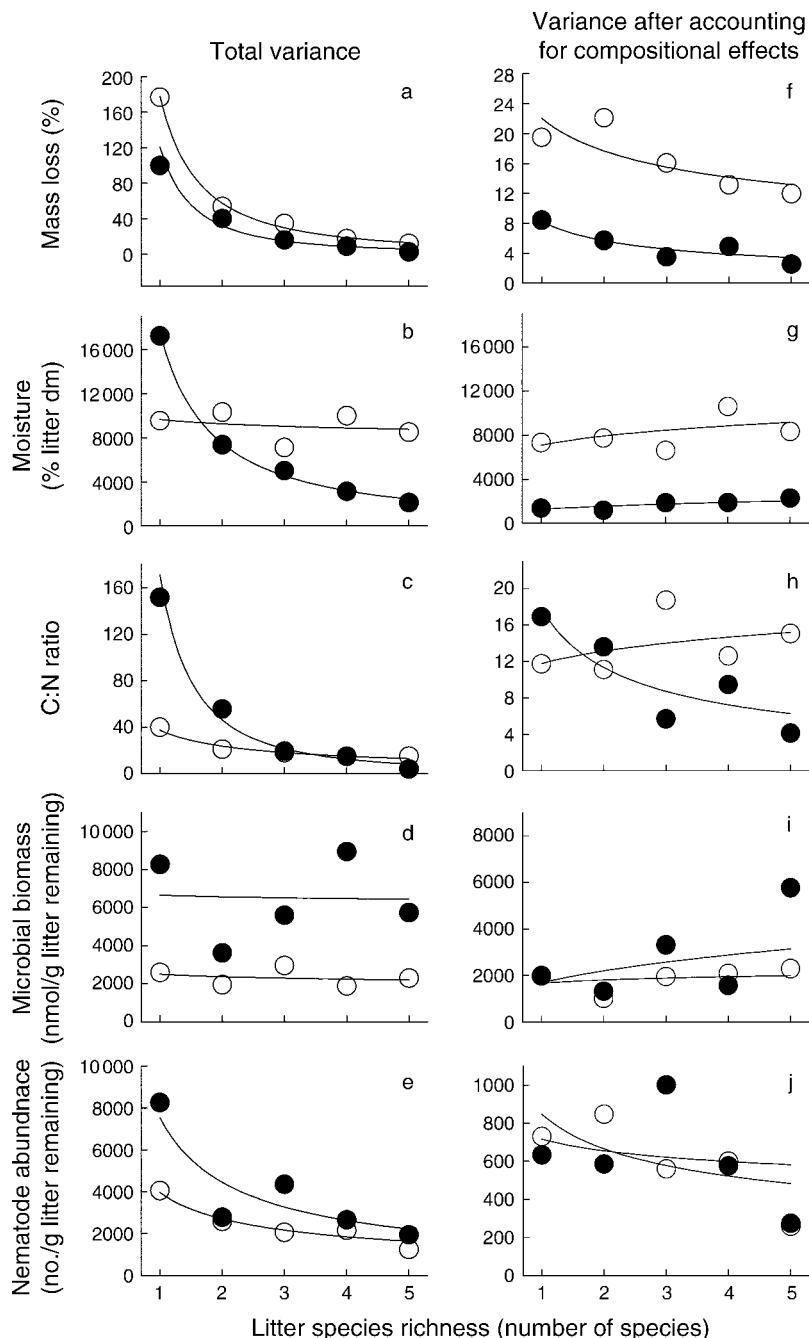


FIG. 1. The effect of litter species richness on (a–e) total variance and (f–j) variance once species composition has been accounted for, after 196 days (solid symbols) and 564 days (open symbols), for (a, f) mass loss, (b, g) moisture content, (c, h) C:N ratio, (e, j) microbial biomass, and (d, i) nematode abundance. Lines represent the richness–variance relationships modeled by optimized power-law functions.

influenced by differences in species richness. Consequently, the former procedures were repeated but this time species composition (31 levels) was included as a fixed effect in the LMM (Fig. 1f–j).

Response variables were transformed where necessary, the appropriate transformation being selected by inspection of residual plots. All statistical analyses were carried out using PROC GLM and PROC MIXED

TABLE 1. Summary of fully factorial GLM analyses of litter species richness and composition effects on decomposition and decomposer variables (percentage of sums of squares [%SS] and *F* values) after 196 and 564 days.

		Mass loss (%)		Moisture (% litter dm)		C:N ratio		Microbial biomass (nmol/g litter dm)		Nematode abundance (no./g litter dm)	
Source of variation	df	%SS	<i>F</i>	%SS	<i>F</i>	%SS	<i>F</i>	%SS	<i>F</i>	%SS	<i>F</i>
196 days											
Block	2	2.1	8.9**	0.8	2.3	0.8	2.9	3.4	8.0**	4.1	0.7
Species richness†	4	2.0	0.2	1.3	0.1	3.2	0.3	25.8	3.4*	2.5	0.9
Species composition (nested in species richness)	26	84.2	27.4**	81.3	18.7**	81.2	21.0**	50.0	9.2**	18.9	0.0
Error	99	11.7		16.6		14.7		20.8		74.5	
564 days											
Block	2	3.3	8.4**	12.1	10.3**	3.6	4.4*	2.7	2.2	1.1	0.7
Species richness†	4	1.4	0.1	5.1	1.4	8.6	1.2	1.8	0.3	5.2	1.9
Species composition (nested in species richness)	26	75.9	14.9**	24.4	1.6	47.7	4.5**	35.7	2.3**	18.3	0.9
Error	99	19.4		58.4		40.0		59.8		75.4	

Note: See Appendix C for full GLM tables.

† Species richness term tested against species composition to obtain appropriate *F* value.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ .

(SAS Institute 2002) or the REML command of GenStat v9.2 (VSN International 2007).

## RESULTS

There were large differences in decomposability between litter species monocultures with nearly a twofold difference in mass loss between *V. myrtillus* and *D. flexuosa* after 564 days (Appendix A). Despite these differences, litter species richness did not significantly influence means in the decomposer system with the exception of microbial biomass after 196 days ( $F_{4,99} = 3.4$ ,  $P = 0.024$ ; Table 1; see Appendix C for full

GLM tables). This particular significant species richness term resulted from the higher microbial biomass at the one- and five-species richness levels, and lower microbial biomass at the two-species richness level (Table 2). In contrast, litter species composition had a considerable impact on all variables except nematode abundance, and explained a large proportion of variation of these variables (Table 1; see Appendix C for full GLM tables). Nematode abundance was not influenced by any term in the model, and ~75% of variation remained in the residual error at both sampling times (Table 1).

TABLE 2. Effects of litter species richness on means of decomposition and decomposer community variables after 196 and 564 days.

Variable and period	Litter species richness (no. species)				
	1	2	3	4	5
Mass loss (%)					
196 days	30.1	31.0	30.8	31.8	30.4
564 days	49.9	50.5	50.4	50.2	49.1
Moisture (% litter dm)					
196 days	492.5	506.4	490.7	486.1	485.8
564 days	245.7	237.5	195.6	196.5	242.2
C:N ratio					
196 days	37.8	34.5	33.8	33.9	33.2
564 days	25.3	26.6	23.9	25.1	26.0
Microbial biomass (nmol/g litter dm)					
196 days	3055.0 <sup>a</sup>	1994.1 <sup>c</sup>	2499.2 <sup>b</sup>	2597.6 <sup>b</sup>	3052.7 <sup>a</sup>
564 days	2788.7	2685.9	2689.5	2798.3	2814.1
Nematode abundance (no./g litter dm)					
196 days	164.4	139.4	154.2	141.9	166.6
564 days	112.8	91.4	106.4	90.4	120.1

Note: Different superscript letters within the same row indicate significantly different means (Tukey contrasts,  $P < 0.05$ ).

Including litter identity terms before species composition in the GLM model consumed much of its variation, and rendered species composition insignificant for all variables except microbial biomass (Appendix B: Table B2). This suggests that effects of increasing species richness on the decomposer system are largely additive. That the species composition term remained significant for microbial biomass indicates that species interactions are important. In turn, all pairwise interactions between litter species were antagonistic for microbial biomass (data not shown).

In comparison to the limited effects of species richness on means, the effect of litter species richness on variances was substantially greater (Fig. 1). Modeling variance with a power-function as opposed to a variance parameter at each level of species richness ( $v_1$ – $v_5$ ; Appendix D) resulted in very similar deviances, but because it concentrated the signal into a single degree of freedom, it almost always led to lower  $P$  values in  $\chi^2$  tests (Appendix D). Considering total variance as a function of species richness, negative relationships between litter diversity and variability were evident for all response variables except microbial biomass (Fig. 1a–e). These negative richness–variability relationships were generally stronger (optimal value of  $b$  more positive in power-law model; see Appendix D) after 196 days than after 564 days (Fig. 1a–e). Specifically, there was strong evidence for such negative power-function relationships between litter species richness and variability in mass loss (196 days and 564 days,  $P < 0.001$ ; Fig. 1a), moisture (196 days,  $P = 0.007$ ; Fig. 1b), C:N ratio (196 days,  $P < 0.001$ ; and 564 days,  $P = 0.039$ ; Fig. 1c), and nematode abundance (196 days,  $P = 0.031$ ; 564 days,  $P = 0.059$ ; Fig. 1e). Accounting for variation due to differences between individual litter species (Fig. 1f–j), the reduction in variability with increasing litter species richness was less strong (optimal value of  $b$  reduced in power-law model; see Appendix D), but there was still good evidence for the power-function relationship between litter species richness and variability in C:N ratio (196 days,  $P = 0.070$ ; Fig. 1h) and mass loss (564 days,  $P = 0.045$ ; Fig. 1h), and weaker evidence for the power-function relationship between litter species richness and variability in nematode abundance (564 days,  $P = 0.190$ ; Fig. 1j). Only variability in microbial biomass showed no relation with litter species richness in either analysis (Fig. 1e, j).

#### DISCUSSION

Our study has explicitly demonstrated a reduction in the variability of the decomposer system with increasing plant litter species richness. While others have also shown reductions in variability with increasing litter species richness (e.g., Schädler and Brandl 2005, Lecerf et al. 2007), we believe that none have taken such a holistic approach to remove the confounding influence

of differences in means, and then to model the variances associated with different levels of species richness. In diversity–function experiments, richness effects can be confounded through increasing similarity of species combinations at higher levels of species richness, and this compositional artifact itself has been considered a “hidden” effect of diversity (Huston 1997). However, given that previous studies have not examined whether richness-specific variances were influenced by differences between species through the correct statistical modeling of variance, any negative richness–variability relationships found may be misleading.

Here, we accounted for the variation attributed to litter species composition across the litter richness gradient, thereby allowing us to detect genuine effects of litter species richness on variance. When differences between species were taken into account, although variance was lower overall, the variability of mass loss, C:N ratio, and nematode abundance still decreased across the litter richness gradient. This suggests an effect of litter species richness per se on variability in the decomposer system over and above that of any compositional effects. That variability in active microbial biomass showed no relation to litter species richness at either sampling date may suggest that microbes respond to finer scales of resource diversity (e.g., Orwin et al. 2006). It also highlights that we do not always necessarily find negative relationships between litter species richness and variability in the decomposer system.

Where negative richness–variability relationships were present, they generally relaxed over time, with a decrease in the magnitude of variability at lower levels of species richness after 564 days. The notable exception was mass loss, whose variability increased considerably over time for litter monocultures. Since mass loss is an accumulative measure, this is perhaps not surprising, and we may expect a reduction in variability after a greater length of time. This suggests that litter species richness may influence the various properties of the decomposer system over different timescales.

Despite differences in variability, particularly for mass loss and litter C:N ratio, there were only limited differences in mean values of measured variables over the gradient of litter species richness. In particular, there was no straightforward explanation for the significant impact of litter species richness on microbial biomass after 196 days. In turn, we found no support for any synergistic effects of increasing litter species richness on variable means, and this may be unexpected given that nonadditive effects are prevalent in litter mixing experiments (Gartner and Cardon 2004, Hättenschwiler and Gasser 2005). However, in a similar experiment, Wardle et al. (2006) also found few effects of litter mixing on decomposition or decomposer abundance. Like other studies, we found that litter species compo-

sition had an overwhelming influence on decomposition and the decomposer community (Wardle et al. 2006, Lecerf et al. 2007). Furthermore, the large influence of species composition on all variables, except microbial biomass, could be explained by litter identity thus indicating additivity in our litter mixtures.

That the effects of litter mixing in our study were largely additive indicates that richness–variability relationships were not being influenced by over-yielding or mean–variance rescaling mechanisms (see Cottingham et al. 2001). Hence, likely candidates are those mechanisms that promote negative covariance in species responses to changing environmental conditions over space. These include statistical averaging (or “portfolio” effect sensu Doak et al. [1998]), the insurance effect, and species evenness. However, regardless of the mechanisms involved, the reductions in variability highlight the significant role that litter richness may play in determining the stability of the decomposer system.

The trend of decreasing variability at lower levels of litter species richness, and over time, suggest that properties of the different litter treatments are becoming more homogeneous. However, the litterbags contain a finite quantity of substrate and given that plant litter inputs will continue to enter the belowground system over time, we conclude that greater plant species richness may be important for maintaining the stability of ecosystem processes (e.g., decomposition) and components of the decomposer community.

#### ACKNOWLEDGMENTS

This research was funded by a Natural Environment Research Council studentship awarded to A. M. Keith, and was linked to the SEERAD-funded MOORCO project. Tulchan Estate granted access to the litterbag study site, and the Meteorological Office (UK) provided climatic data. Claire Cameron and Brian Ord at the Macaulay Institute provided assistance with PLFA analysis. We thank two anonymous reviewers whose comments have greatly improved the manuscript.

#### LITERATURE CITED

- Cottingham, K. L., B. L. Brown, and J. T. Lennon. 2001. Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters* 4:72–85.
- Dang, C. K., E. Chauvet, and M. O. Gessner. 2005. Magnitude and variability of process rates in fungal diversity–litter decomposition relationships. *Ecology Letters* 8:1129–1137.
- Doak, D. F., D. Bigger, E. K. Harding, M. A. Marvier, R. E. O'Malley, and D. Thomson. 1998. The statistical inevitability of stability–diversity relationships in community ecology. *American Naturalist* 151:264–276.
- Gartner, T. B., and Z. G. Cardon. 2004. Decomposition dynamics in mixed-species leaf litter. *Oikos* 104:230–246.
- Hansen, R. A. 2000. Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. *Ecology* 81:1120–1132.
- Hättenschwiler, S., and P. Gasser. 2005. Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences USA* 102:1519–1524.
- Hättenschwiler, S., A. V. Tiunov, and S. Scheu. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution and Systematics* 36:191–218.
- Hector, A., et al. 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286:1123–1127.
- Hester, A., J. Miles, and C. H. Gimingham. 1991. Succession from heather moorland to birch woodland. I. Experimental alteration of specific environmental conditions in the field. *Journal of Ecology* 79:303–315.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110:449–460.
- Kaneko, N., and E. Salamanca. 1999. Mixed leaf-litter effects on decomposition rates and soil microarthropod communities in an oak-pine stand in Japan. *Ecological Research* 14: 131–138.
- Kominoski, J. S., C. M. Pringle, B. A. Ball, M. A. Bradford, D. C. Coleman, D. B. Hall, and M. D. Hunter. 2007. Nonadditive effects of leaf litter species diversity on breakdown dynamics in a detritus-based stream. *Ecology* 88:1167–1176.
- Lecerf, A., G. Risnoveanu, C. Popescu, M. O. Gessner, and E. Chauvet. 2007. Decomposition of diverse litter mixtures in streams. *Ecology* 88:219–227.
- Loreau, M. S., et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808.
- McCann, K. S. 2000. The diversity–stability debate. *Nature* 405: 228–233.
- McNaughton, S. J., M. Oesterheld, D. A. Frank, and K. J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* 341:142–144.
- Orwin, K. H., D. A. Wardle, and L. G. Greenfield. 2006. Ecological consequences of carbon substrate identity and diversity in a laboratory study. *Ecology* 87:580–593.
- SAS Institute. 2002. SAS version 9.1. SAS Institute, Cary, North Carolina, USA.
- Schädler, M., and R. Brandl. 2005. Do invertebrate decomposers affect the disappearance rate of litter mixtures? *Soil Biology and Biochemistry* 37:329–337.
- Schmid, B., A. Hector, M. A. Huston, P. Inchausti, I. Nijs, P. W. Leadley, and D. Tilman. 2002. The design and analysis of biodiversity experiments. Pages 61–75 in M. Loreau and P. Inchausti, editors. *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford, UK.
- Smith, V. C., and M. A. Bradford. 2003. Do non-additive effects on decomposition in litter-mix experiments result from differences in resource quality between litters? *Oikos* 102: 235–242.
- Tilman, D. D. 1999. The ecological consequences of changing biodiversity: a search for general principles. *Ecology* 80: 1455–1474.
- Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441:629–632.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379:718–720.
- Van der Heijden, M. G. A., J. N. Klironomos, M. Ursic, P. Moutoglou, R. Streitwolf-Engel, T. Boller, A. Wiemken, and I. R. Sanders. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396:69–72.
- VSN International. 2007. GenStat version 9.2. VSN International, Hemel Hempstead, UK.

- Wardle, D. A., K. I. Bonner, and G. M. Barker. 2000. Stability of ecosystem properties in response to above-ground functional group richness and composition. *Oikos* 89:11–23.
- Wardle, D. A., K. I. Bonner, and K. S. Nicholson. 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos* 79:247–258.
- Wardle, D. A., G. W. Yeates, G. M. Barker, and K. I. Bonner. 2006. The influence of plant litter diversity on decomposer abundance and diversity. *Soil Biology and Biochemistry* 38: 1052–1062.
- Whitehead, A. G., and J. R. Hemming. 1965. A comparison of some quantitative methods of extracting small vermiform nematodes from soil. *Annals of Applied Biology* 55:25–38.
- Zelles, L., O. Y. Bai, R. Rackwitz, D. Chadwick, and F. Beese. 1995. Determination of phospholipid- and lipopolysaccharide-derived fatty acids as an estimate of microbial biomass and community structures in soils. *Biology and Fertility of Soils* 19:115–123.

#### APPENDIX A

Initial litter properties and litter decomposition for monocultures after 196 and 564 days (*Ecological Archives* E089-150-A1).

#### APPENDIX B

GLM summary statistics relating to litter identity effects (*Ecological Archives* E089-150-A2).

#### APPENDIX C

Full GLM summaries from analysis of litter species richness and composition after 196 and 564 days for mass loss, moisture, C:N ratio, microbial biomass, and nematode abundance (*Ecological Archives* E089-150-A3).

#### APPENDIX D

Summary statistics for modeling random variation as a function of litter species richness (*Ecological Archives* E089-150-A4).