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Long-term resource addition to a detrital food web yields a pattern of responses more complex than pervasive bottom-up control

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Background. Theory predicts strong bottom-up control in detritus-based food webs, yet field experiments with detritus-based terrestrial systems have uncovered contradictory evidence regarding the strength and pervasiveness of bottom-up control processes. Two factors likely leading to contradictory results are experiment duration, which influences exposure to temporal variation in abiotic factors such as rainfall and affects the likelihood of detecting approach to a new equilibrium; and openness of the experimental units to immigration and migration. To investigate the contribution of these two factors, we conducted a long-term experiment with open and fenced plots in the forest that was the site of an earlier, short-term experiment (3.5 months) with open plots (Chen & Wise 1999) that produced evidence of strong bottom-up control for 14 taxonomic groupings of primary consumers of litter and fungi (microbi-detritivores) and their predators. Methods. We added artificial high-quality detritus to ten 2 x 2-m forest-floor plots at bi-weekly intervals from April through September in three consecutive years (Supplemented treatment). Ten comparable Ambient plots were controls. Half of the Supplemented and Ambient plots were enclosed by metal fencing. Results. Arthropod community structure (based upon 18 response variables) diverged over time between Supplemented and Ambient treatments, with no effect of Fencing on the multivariate response pattern. Fencing possibly influenced only ca. 20% of the subsequent univariate analyses. Multi- and univariate analyses revealed bottom-up control by fall of Year 1 of some, but not all, microbi-detritivores and predators. During the following two years the pattern of responses became more complex than that observed by Chen & Wise (1999). Some taxa showed consistent bottom-up control whereas many did not. Variation across years could not be explained completely by differences in rainfall because some taxa exhibited negative, not positive, responses to detrital supplementation. Discussion. Our 3-yr experiment did not confirm the conclusion of strong, pervasive bottom-up control of microbi-detritivores and predators reported by
Chen and Wise (1999). Our longer-term experiment revealed a more complex pattern of responses, a pattern much closer to the range of outcomes reported in the literature for many short-term experiments. Much of the variation in responses across studies likely reflects variation in factors such as rainfall and the quality of added detritus. Nevertheless, it is also possible that long-term resource enhancement can drive a community towards a new equilibrium state that differs from what would have been predicted from the initial short-term responses exhibited by primary and secondary consumers.
Long-term resource addition to a detrital food web yields a pattern of responses more complex than pervasive bottom-up control

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Abstract

**Background.** Theory predicts strong bottom-up control in detritus-based food webs, yet field experiments with detritus-based terrestrial systems have uncovered contradictory evidence regarding the strength and pervasiveness of bottom-up control processes. Two factors likely leading to contradictory results are experiment duration, which influences exposure to temporal variation in abiotic factors such as rainfall and affects the likelihood of detecting approach to a new equilibrium; and openness of the experimental units to immigration and migration. To investigate the contribution of these two factors, we conducted a long-term experiment with open and fenced plots in the forest that was the site of an earlier, short-term experiment (3.5 months) with open plots (Chen & Wise 1999) that produced evidence of strong bottom-up control for 14 taxonomic groupings of primary consumers of litter and fungi (microbi-detritivores) and their predators.

**Methods.** We added artificial high-quality detritus to ten 2 x 2-m forest-floor plots at bi-weekly intervals from April through September in three consecutive years (Supplemented treatment). Ten comparable Ambient plots were controls. Half of the Supplemented and Ambient plots were enclosed by metal fencing.

**Results.** Arthropod community structure (based upon 18 response variables) diverged over time between Supplemented and Ambient treatments, with no effect of Fencing on the multivariate response pattern. Fencing possibly influenced only ca. 20% of the subsequent univariate analyses. Multi- and univariate analyses revealed bottom-up control by fall of Year 1 of some, but not all, microbi-detritivores and predators. During the following two years the pattern of responses became more complex than that observed by Chen & Wise (1999). Some taxa showed consistent bottom-up control whereas many did not. Variation across years could not be explained completely by
differences in rainfall because some taxa exhibited negative, not positive, responses to detrital supplementation.

**Discussion.** Our 3-yr experiment did not confirm the conclusion of strong, pervasive bottom-up control of microbi-detritivores and predators reported by Chen and Wise (1999). Our longer-term experiment revealed a more complex pattern of responses, a pattern much closer to the range of outcomes reported in the literature for many short-term experiments. Much of the variation in responses across studies likely reflects variation in factors such as rainfall and the quality of added detritus. Nevertheless, it is also possible that long-term resource enhancement can drive a community towards a new equilibrium state that differs from what would have been predicted from the initial short-term responses exhibited by primary and secondary consumers.
Introduction

Classical theory predicts extensive bottom-up control in detritus-based food webs. However, accumulating empirical findings and modeling research suggest that bottom-up control may not be as strong and pervasive as hypothesized, and that a mixture of bottom-up and top-down control processes characterizes soil food webs (e.g. Bardgett & Wardle 2010; McCann 2012; Moore & deRuiter 2012; Pimm 2002; Wardle 2002). Debates over the strength of bottom-up and top-down control in food webs with many generalist predators (a characteristic of soil communities) intensified in parallel with increasing reliance on controlled field experiments to test theory (e.g. Hairston 1989; Hairston & Hairston 1993; McCann 2012; Menge 2000; Moore et al. 2004; Moore & deRuiter 2012; Polis & Strong 1996; Polis 1996; Resetarits 1998).

Making inferences about population control processes from field experiments is not straightforward (Raffaelli & Moller 2000). Two major challenges are space and time. Species interactions occur over a spectrum of spatial scales. Finding an appropriate size for experimental units is difficult, especially given opposing constraints imposed by the desire for realism, the requirement of sufficient replication for adequate statistical power, and the frequent need to impose barriers to migration by using cages or fencing (Gardner et al. 2004; Hurlbert 1984; Raffaelli & Moller 2000; Resetarits 1998). Perhaps an even greater challenge is time. Short-term experiments often fail to capture the spectrum of responses caused by temporal variation in abiotic factors such as rainfall. Furthermore, short-term experiments are unlikely to reveal new equilibria because detecting the consequences of time lags within chains of indirect effects requires many generations of interacting organisms (Bender et al. 1984; Osenberg & Mittelbach 1996; Yodzis 1988).
The most direct way to uncover the strength of bottom-up control and its pervasiveness across trophic levels is to observe how adding energy- and/or nutrient-rich detritus to replicated plots in a field experiment alters densities of major taxa of primary and secondary consumers. Such experiments in terrestrial ecosystems have been conducted in prairies and grasslands (Fountain et al. 2008; Hoekman et al. 2011; Oelbermann et al. 2008; Patrick et al. 2012) and forests (Chen & Wise 1999; David et al. 1991; Lessard et al. 2011; Maraun et al. 2001; Raub et al. 2014; Salamon et al. 2006; Scheu & Schaefer 1998; Yang 2006). Most experiments uncovered some evidence for bottom-up control, but the strength and pervasiveness across trophic levels of the responses varied substantially. In some studies, supplementing detrital input resulted in increased populations of primary consumers and their predators. In other experiments the predators showed no response. Sometimes effects occurred across many taxa, sometimes they were limited to a few, and in some instances effects of detrital supplementation were negative. Such variability in outcomes likely reflects differences between experiments in many factors, both environmental and logistical: levels of limiting abiotic factors (i.e. rainfall and temperature) during the experiment; type, quality, and amount of added detritus; taxonomic resolution of the response variables; plot size; number of replicates; whether the plots were open or fenced; and duration of the experiment.

Long-term experiments are more likely to capture the influence of variation in abiotic factors and also are more likely to reveal indirect effects that propagate at different rates through a complex food web. Among experiments conducted to date, densities of some trophic groups occasionally responded negatively to addition of detritus. Do these negative effects reflect differential responses by predators to resource-addition combined with intensification of top-down control processes along a subset of trophic pathways due to the indirect effects of trophic-level omnivory in a detritus-based food web (Polis & Strong 1996, Halaj & Wise 2002, Oelbermann et al. 2008)?
Were different pathways of top-down control processes modulating the strength of bottom-up control, producing different responses among trophic levels as the system moved towards a new equilibrium state? Direct manipulation of predator densities in similar detritus-based food webs has revealed top-down control, including trophic cascades affecting decomposition rates (Kajak 1997; Kajak & Jakubczyk 1977; Lawrence & Wise 2004; Lensing & Wise 2006; Wardle 2002; Wise 2004). However, negative effects of detrital enhancement on densities of primary consumers and predators were only infrequently observed in previous experiments. A caveat is needed, though, as most resource-enhancement experiments have been relatively brief compared to the generation times of species in the community [one exception is the 4-yr manipulation of nutrients in a grassland (Patrick et al. 2012)]. Furthermore, no experiments of both short-and long-term duration have been conducted with the same system, so the question remains unanswered of whether short-term resource enhancement produces patterns predictive of longer-term resource-enhancement experiments.

Detrital-enhancement experiments have been conducted with both fenced and open plots. Fencing, which can limit confounding effects of emigration and immigration on responses of the target taxa to resource enhancement, is potentially most critical for smaller experimental units. This is especially true if the experiment is conducted over many generations of the affected organisms. Positive responses in open plots possibly underestimate the actual strength of bottom-up control because populations that increased in response to detrital supplementation can decline as emigrants leave for areas outside the plots where densities are lower. Similarly, unexpected decreases in density in supplemented unfenced plots might be masked by augmentation of densities due to immigration from outside. Thus, we hypothesized that fencing the plots would
produce more realistic estimates of the strength of bottom-up control, or conversely, would more likely reveal population declines resulting from cascading indirect effects.

Despite the perceived need to impose barriers to migration, possible impacts of fencing on results are difficult to interpret because some animals can cross the barrier, whereas others cannot. In a 1.5-yr predator-reduction experiment conducted with 2x2-m plots in the same forest as the current research, fencing had no impact upon densities of potential prey (families of Collembola) in non-manipulated plots (Wise 2004), which implies that the results obtained in fenced predator-reduction plots reflected processes occurring on the open forest floor. However, this conclusion is not entirely without reservations because it was not possible to achieve persistent predator-reductions without fencing. Therefore, in that experiment it was not possible to establish a completely balanced design [predator treatment (2 levels) x fencing treatment (2 levels)]. In the current research, however, we could evaluate the impact of fencing directly and unambiguously because the detrital-enhancement treatment was imposed equally in open and fenced plots.

Here we report results of a 3-year detrital-addition experiment in a secondary oak-maple-hickory forest, with a few scattered pine trees, in Madison Co., Kentucky, USA. Our experiment was conducted within ~0.5 km of the sites of a previous similar, but short-term (3.5-months), experiment that utilized open (unfenced) forest-floor plots (Chen & Wise 1999) — referred to as “CW99” from now on. The earlier experiment in this forest produced clear evidence of detrital resource limitation [sensu Osenberg & Mittelbach (1996)] i.e. relatively rapid elevation of population densities of both primary and secondary consumers in response to addition of high-quality detritus. Major groups of primary consumers, the microb-detritivores (grazers of fungi and consumers of organic debris), were at least 2-3x more abundant in supplemented than
control plots. Major arthropod predators were ~ 2x as abundant. No taxa were less abundant in
the resource-supplemented treatment. Because the plots were not fenced, emigration of some
taxa that responded positively to resource supplementation might have weakened the observed
magnitude of bottom-up control. Similarly, immigration of taxa that had actually declined in
density might have erased the negative treatment response. Our experiment expanded the design
of CW99 to answer two questions (the first, logistical; the second, conceptual): (1) How would a
barrier to emigration/immigration of some groups of ground arthropods affect conclusions about
bottom-up control? (2) Would a longer-term experiment reveal inconsistencies in responses that
would suggest either tempering of bottom-up control by variation in abiotic factors and/or
movement of the perturbed community in the direction of a new equilibrium?

Methods

Experimental design

The experiment started two years after CW99 and ran from 1997 through 1999 (hereon
designated Years 1, 2, and 3). Each experimental unit (20 in total) was a 2 x 2-m area of forest
floor, separated from each other by at least 10 m. Experimental units were randomly assigned to
one of two levels of a resource treatment and one of two levels of a fencing treatment, yielding
five replicates of each of the four combinations of treatment levels. Thus, half of the units
received a detrital supplement (Supplemented), the others none (Ambient), and half of the plots
in each resource treatment were open to emigration and immigration (Open), while the others
were enclosed with 35-cm aluminum flashing inserted 8 cm into the ground (Fenced). The fence was topped with a 15-cm horizontal strip of flashing that formed two lips coated on the underside with a tree-banding compound (Tanglefoot®, Grand Rapids, Michigan) to further retard movement of epigeic (ground-active) arthropods across the barrier. This design is more complex than that of CW99, which had no fenced plots but employed the same total number of experimental units: twenty 2 x 5-m open plots, half of which received a detrital supplement.

We employed the detritus-supplementation protocol of CW99, which has also been used in other experiments (Chen & Wise 1997; Raub et al. 2014). Our goal was not to determine which components of the resource base (bacteria, fungi, and organic debris) were possibly limiting densities of microbivores and detritivores, as was the aim of Salamon et al. (2006). Rather, our goal was to follow the community response to long-term enhancement of a broadly defined resource base. This experimental approach, including that of Salamon et al. (2006) and others, involves adding artificial forms of organic matter and nutrients. Every two weeks from April through September we added chopped “fresh” (i.e. not dried) mushrooms and potatoes, and dry flakes of *Drosophila* medium (Carolina Biological Supply; Burlington, North Carolina, USA; Formula 4-24) to the Supplemented plots.

We decided initially to supplement at a rate approximately 1/3 that of CW99 because we hypothesized that the strong responses exhibited in the earlier experiment were due to a high level of detrital enhancement. We planned to continue this rate of supplementation in the following years, but decided to increase the rate because the increase in densities of most taxa in response to the detrital enhancement in Year 1 was much less (including no responses) than that observed by CW99. Therefore, in Years 2 and 3 we increased the rate of supplementation to a level similar to CW99. In Year 1 each Supplemented plot received 195 g (dry wt.) m⁻² of detritus
(26 g m\(^{-2}\), 79 g m\(^{-2}\) and 90 g m\(^{-2}\) of mushrooms, potatoes, and *Drosophila* medium, respectively).

In Years 2 and 3 the rate of detritus supplementation was increased ca. 4x (to 770 g m\(^{-2}\) and 874 g m\(^{-2}\) total dry wt., respectively). The slightly larger amount of detritus added during Year 3 reflects a slightly longer period of detrital addition than in Year 2. Biweekly rates were the same in Years 2 and 3.

Adding artificial detritus can influence the structure of the leaf-litter layer, so it is instructive to compare amounts added with litter standing crops. In Year 1 the average (± SE) standing crop of litter (dry wt. m\(^{-2}\)) in Ambient plots was 671 ± 43 g (\(n = 10\)). Thus, the dry weight of detritus added throughout Year 1 was ~ 30% of the average standing crop of detritus, compared to an addition rate of ~100% of the litter standing crop in CW99. In Years 2 and 3 each Supplemented plot received ~136% and ~122% of that year’s average standing crop of litter, respectively. By the end of Year 3 litter weight was only 13% higher in Supplemented than Ambient plots (\(F_{1, 16} = 4.93, P = .04\)), compared to a ~30% increase at the end of CW99.

Due to our decision to increase the supplementation rate in Years 2 and 3 to ~4x the rate of Year 1, differences in response patterns between Year 1 and the following two years can be attributed not only to differences in abiotic factors between years and time lags in the appearance of direct and indirect effects, but also to markedly different rates of detrital supplementation. In contrast, differences between Years 2 and 3 must have been due primarily to factors other than a difference in the rate of resource addition, since biweekly rates of supplementation in Years 2 and 3 were the same.

**Fungal biomass**
Differences in fungal abundance between Supplemented and Ambient plots at the end of the experiment were estimated by assaying leaf litter for ergosterol (Appendix S1), a common sterol in fungal hyphae that is nearly absent from plants (Weete & Weber 1980). The amount of ergosterol is correlated with both total hyphal mass and membrane content and likely assayed both living and dead hyphae (Mille-Lindblom et al. 2004; Ruzicka et al. 2000; Zhao et al. 2005).

Arthropods

Selected taxa of arthropods active within and on the surface of leaf litter were sampled three times in Year 1 (18 July, 15 August, 13 October), twice in Year 2 (20 June, 23 September) and twice in Year 3 (3 June, 5 September). Values for the first two dates in Year 1 were averaged, yielding two values (Summer and Fall) for each year. Densities of most taxa were estimated by litter extraction and/or litter sifting. Sticky traps were used to measure activity-densities of adult flies (Diptera) just above the litter layer.

Litter extraction

Densities (measured as number per .05-m$^2$ of forest floor) of 15 taxonomic groupings [six families of springtails (Collembola), thrips (Thysanoptera), larval moths (Lepidoptera), larval and adult beetles (Coleoptera), larval and adult flies (Diptera), pseudoscorpions (Pseudoscorpiones), centipedes (Chilopoda) and spiders (Araneae)] were estimated by taking litter from .05-m$^2$ of forest floor per plot and using a temperature/humidity gradient in a modified Kempson-McFadyen apparatus (Kempson et al. 1963; Schauermann 1982) to extract animals
into 50% ethylene glycol over 10 days. Extracted arthropods were washed and stored in 70% ethyl alcohol until identified.

**Litter sifting**

Litter extraction is not the best way to sample densities of active, larger spiders that often are less abundant than smaller life stages and species (Chen & Wise 1999). Therefore, densities of cursorial spiders (primarily Corinnidae, Clubionidae, Gnaphosidae, and Lycosidae) and web-weaving spiders (primarily Linyphiidae and Dictynidae) were assessed by carefully sifting and searching, in the field, one 0.2-m² sample of litter per plot (different from the .05- m² sample).

**Sticky traps**

Densities (number per .05-m²) of larval and adult Diptera within the litter were determined by Kempson extractions. In addition, activity-densities (combined result of density and activity; number captured per trap) of selected families of adult Diptera were assessed with aerial traps placed just above the litter layer. Two 10 x 10-cm vertical pieces of metal insect screening attached to thin steel rods were coated with Tanglefoot® and placed 0.5m apart and perpendicular to each other in each plot for 24 hours.

**Taxonomic resolution of response variables**

Several criteria dictated the taxonomic resolution of the response variables: (1) a close-as-feasible match to the degree of resolution reported in CW99; (2) logistical constraints (e.g. time and technical help) related to sorting and identifying the number of arthropods collected; (3) the overall pattern of relative abundance (i.e. numbers of each family of Collembola were greater
than numbers for each of the other categories, all of which were orders or selected families within orders); and (4) the fact that trophic position (i.e. predator or detritivore) was broadly similar for organisms within orders, with the exception of Coleoptera (CW99 reported total Coleoptera and Staphylinidae, but did not distinguish other families; results were similar in CW99 for total Coleoptera and Staphylinidae). Diptera in the litter were fungivorous families. Only fungivorous families (Mycetophilidae, Sciaridae, and Phoridae) are included in the Diptera numbers from the sticky traps. Note that Diptera adults and spiders each are represented in Kempson samples and also in a different response variable, either sticky traps (Diptera) or litter-sifting (cursorial and web-building spiders). Cursorial and web-building families utilize very different foraging modes (Wise 1993) and could easily be distinguished in sifting samples. They were pooled for Kempson samples due to the challenge of correctly identifying small specimens to family. Logistical constraints forced us to exclude mites (Acarina), a group that is abundant in leaf litter and was sampled in CW99.

Statistical analyses

The core structure of the experiment is a repeated-measures 2 x 2 x 3 design [Resource (Ambient, Supplemented) x Fencing (Open, Fenced) x Year (1, 2, and 3)] analyzed separately for summer and fall samples (rationale for separating seasons is explained below). Methodological details of statistical analyses appear in Appendix S2. The complete arthropod data set is described in Appendix S7 and presented in Supplemental Data S8. Below we present an overview of our approach to data analysis.
The central conceptual question addressed by our field experiment is: *How does the response of the system to resource supplementation change over time?* The focus of our analyses is the statistic that directly addresses this question, the Resource x Year interaction. We evaluated this interaction by relying on a combination of multivariate and univariate statistical techniques. We first used multivariate analyses to determine how detrital supplementation changed arthropod community structure over time and which response variables were most closely linked to these changes. Multivariate analyses were performed first because if there is no multivariate effect, there is no justification for doing separate univariate analyses. Because multivariate effects were present we then conducted independent univariate analyses and compared patterns of change over time of individual response variables with the multivariate patterns.

We postulated that the system would respond differently in summer and fall because summer samples had been exposed to detrital enhancement for fewer months than fall samples and because life histories of many taxa show pronounced seasonal patterns. Multivariate analysis of the community distance matrix based on the entire data set confirmed this expectation, as there was an interaction between [Resource x Year] and Season (Tables S3.1, S3.2 in Appendix S3). Thus, we divided the community distance matrix into summer and fall subsets, yielding one distance matrix for each season. All subsequent multivariate and univariate analyses were done separately for summer and fall samples.

The central logistical question addressed by our field experiment is: *How does the openness of the plots affect the observed pattern of responses to detrital supplementation?* Thus, we first tested for an interaction between [Resource x Year] and Fencing. If there was no evidence for an interaction (*P* value of the 3-way interaction > .15), the design was collapsed...
Open and Fenced plots were pooled, yielding twice as many replicates per Resource level) to one involving only Resource and Year. If Fencing possibly influenced the Resource x Year interaction, further analyses were done separately for Open and Fenced plots. Use of \( P > .15 \) (instead of the conventional \( P > .05 \) criterion) for inferring no interaction with Fencing made it less likely to ignore a weak effect of fencing that could have influenced interpretation of the response patterns.

Multivariate analyses

Using all 18 response variables, we calculated a distance matrix using Gower’s similarity index [S15 of Legendre and Legendre (2012)]. Gower’s index was employed because it is designed to accommodate different types of variables (Kempson, sifting, and sticky-trap samples; Fig. 1). We implemented S15 because this version of Gower’s measure is a symmetrical index that gives equal weight to double zeroes (absence/absence) and ++ (presence/presence), which is the type of distance measure philosophically appropriate for analyzing results of a field experiment [unlike the more commonly employed “Bray-Curtis” measure, which is less suited to the assumptions behind controlled manipulative experiments (Legendre & Legendre 2012)]. Further details are in Appendix S2.

Permutational multivariate analysis of variance (perMANOVA) (Anderson et al. 2008) was then used to assess the multivariate Resource x Year interaction. Because our initial analysis revealed a Resource x Year interaction for both summer and fall (detailed in the Results section), we then assessed the changing impact of Resource on arthropod community structure over the experiment in two ways. First, we plotted the location of each experimental unit (i.e. 2x2-m plot) on the first two axes of the Principal Coordinates Ordination (PCO) for each year along with the
P value for the Resource effect each year. Multivariate effect size each year was defined as the proportion of variance explained by adding detritus to the system (Anderson et al. 2008).

Secondly, we evaluated how different response variables contributed to the change in community structure by plotting both simple and multiple correlation vectors on constrained PCO ordinations (CAP; constrained by Resource and Fencing treatments) for each year.

**Univariate analyses**

We plotted yearly means ± SE of each response variable and then used permutational univariate analysis of variance (permANOVA) (Anderson et al. 2008) to help evaluate the change over time in density differences between Supplemented and Ambient treatments. Possible interactions between [Resource x Year] and Fencing for single response variables were relatively infrequent (P for interaction < .15 for 7 out of 36 permANOVA’s; Appendix S6), but are noted and discussed when present. We used permANOVA after attempting to model the univariate variables with a mixed-effects generalized linear model [GLMM; functions “glmer” and “glmer.nb” in the R package “lme4” (R Core Team 2014)] using the Poisson and negative binomial families. The GLMM was not an appropriate statistical model for our data because for most response variables the residuals were poorly behaved (Zuur et al. 2009) and most GLMM models failed to converge properly.

**Overall interpretation of response patterns**

Interpretation of how the system responded was based upon evaluating the results of multivariate and univariate analyses together as a whole. Emphasis was placed upon using the statistical analyses to aid in interpreting the overall patterns of the ordinations and univariate plots. We
avoided a completely NHST (Null Hypothesis Significance Testing) approach as much as possible. Thus, we made no corrections for “multiple comparisons” in the univariate analyses, primarily because multivariate effects were clear; and we did not conclude that $P$ values close to .05, but slightly greater, indicated the absence of a response. Instead, we relied on $P$ values as a measure of strength of evidence (Cumming 2012; Hector 2015; Nakagawa & Cuthill 2007). Our overall evaluation of the impact of resource enhancement on the food web was a melding of (1) changes in community structure as indicated by perMANOVA and PCO, (2) patterns of correlation-vector overlays on constrained ordinations (CAP), (3) univariate effect sizes estimated from temporal plots of mean density for Resource and Ambient treatments, and (4) the $P$ value of the appropriate permANOVA statistic [Resource x Year interaction or simple Resource effect if there was no change over time in the Resource effect].

Results

Fungal density

Fungal hyphae, as measured by concentrations of ergosterol, were 3x denser in Supplemented than Ambient plots [Appendix S1].

Relative abundance of taxa
The most abundant taxa were six families of microbi-detritivores (Collembola) collected by Kempson extraction, with the Hypogastruridae, Onychiuridae, and Entomobryidae being the three most numerous (Fig. 1A). Remaining response variables were similar in value to each other, differing by less than 50%. Centipedes (Chilopoda) were the exception. This predatory taxon had the fewest individuals sampled of all response variables (Fig. 1B).

Response of arthropods to detrital supplementation

Results of multivariate analyses are presented first because they constituted the critical first step in the analysis. If detrital supplementation had no effect upon overall community structure, analyzing the 18 response variables separately would not have been justified. In each section below (both multivariate and univariate analyses), results of testing for interactions with Fencing are presented first, followed by the evidence for changes in the presence and strength of bottom-up control processes over the three years of the experiment.

Multivariate analyses

**Fencing** – Permutational multivariate analysis of variance (perMANOVA) uncovered no evidence of an interaction between the openness of a plot and the overall community response to the addition of detritus. In the full perMANOVA model (Appendix S3), $P[(\text{Resource} \times \text{Year}) \times \text{Season} \times \text{Fencing}] = 0.67$ and $P[(\text{Resource} \times \text{Year}) \times \text{Fencing}] = 0.22$ (Table S3.1, Appendix S3). Therefore, Open and Fenced plots were pooled for the multivariate analyses of the Resource $\times$ Year interaction, which were performed separately for summer and fall samples.
because $P \ [(\text{Resource} \times \text{Year}) \times \text{Season}] = 0.039$ (Table S3.2, Appendix S3), and because of logistical and biological considerations explained in the Methods section.

**Bottom-up Control** – Increasing the detrital resource base clearly altered arthropod community structure and the magnitude of the response (i.e. separation of plots by treatment in ordination space) increased over time (Fig. 2; Tables S3.3A and S3.3B, Appendix S3). Divergence between Ambient and Supplemented plots was greater in fall than summer (Fig. 2; Table S3.3 in Appendix S3). In summer, percentages of total variation explained by the Resource treatment for Years 1-3 were 12%, 26%, and 28%, respectively. Percentages for fall samples were 24%, 41%, and 32%. Divergence in community structure over time was due primarily to increasing separation of centroid locations (Fig. 2). However, on the last sampling date of the experiment (fall of Year 3), the Supplemented sites were also more dispersed in ordination space than the Ambient sites [Pseudo-$F_{1,18} = 8.85$, $P = .007$, PERMDISP test (Anderson et al. 2008)].

Community structure differed between Ambient and Supplemented plots less in Year 1 than in the last two years of the experiment (Fig. 2; Table S3.3, Appendix S3). Although the degree of divergence between Ambient and Resource plots in Years 2 and 3 appears similar, the impact of the resource treatment on arthropod community structure in Year 3 differed from that of Year 2 [$P(\text{Pseudo-}F_{1,71}(\text{Resource} \times \text{Year})) = .014$, perMANOVA; Appendix S4]. It is likely that the lower dispersion among Ambient plots in the fall of Year 3 (Fig. 2) is the major cause of the Resource x Year interaction.

The identity of the response variables that were most highly correlated with the divergence in community structure changed over time. The pattern of these correlations also differed between seasons. Comparing simple Spearman and multiple (“partial”) correlation
coefficients gives some additional insight into which taxa were the primary drivers of the divergence in community structure.

**Simple Spearman Correlation Coefficients**

*Summer* -- In the summer of Year 1, the plots were not clearly separated according to detritus treatment, so the vector for isotomid Collembola does not reflect effects of detritus addition (Fig. 3A, Summer, Year 1). In the following two summers, vector patterns reveal bottom-up control of several primary consumers that only weakly reached the secondary-consumer level (Fig. 3A, Summer, Years 2, 3). In the last two summers, all response variables with coefficients ≥ .50 were positively associated with the first axis, which is strongly linked to the detritus-addition treatment. Seven of the ten vectors for Years 2 and 3 represent microbi-detritivores [three for Diptera and four for Collembola (Hypogastruridae, Sminthuridae, and Entomobryidae)]. The remaining three vectors represent simple correlations with larval and adult Coleoptera, which include both predators and microbi-detritivores.

*Fall* -- The pattern for fall samples is more complex (Fig. 3A, Fall). Years 1 and 2 exhibited a pattern broadly similar to that of summer samples for Years 2 and 3, although the total number of responding taxa was greater in fall than summer (16 vectors versus 10, respectively). All vectors were positively correlated with CAP Axis 1 except for Thysanoptera, a consumer of detritus/fungi. Among the other microbi-detritivores, all six Collembola families showed increased densities in the Supplemented treatment in Year 1 and/or Year 2, as did larval and adult Diptera. In the fall, more predatory groups had responded to detritus addition than in the summer. Vectors for both cursorial and web-building spiders in litter-sifting samples were positively associated with the first axis in Year 1 but not Year 2. In Year 3, larval and adult Coleoptera, many of which are predators, responded positively to detritus addition. The pattern
for Year 3 in fall samples is strikingly different. Only two microbi-detritivore groups displayed positive vectors, and one group, larval Lepidoptera, had a weak negative correlation with Axis 1. The strongest correlation in Year 3 was that for web-building spiders. However, the relationship with detrital addition was negative, not positive as was the case in Year 1 (Fig. 3A, Fall).

**Multiple (Partial) Correlation Coefficients**

The multiple (partial) coefficient removes correlations with other response variables (Anderson et al. 2008). Thus, it is not surprising that fewer show a relationship with Axis 1, even with a lower $R^2$ threshold, than do vectors representing the simple Spearman statistic (11 vs. 31 vectors, respectively; Fig. 3B vs. Fig. 3A [ignoring Summer of Year 1, when arthropod community structure showed no clear response to adding detritus]). The pattern over time of vectors for the multiple correlation coefficient is complex (Fig. 3B). Among the nine vectors exhibiting a component positively correlated with Axis 1, only one includes some predatory taxa (larval Coleoptera). Among the four vectors that indicate a negative response to detrital supplementation, one is that of a microbi-detritivore (tomocerid Collembola). The other three negative vectors are strictly predatory taxa: pseudoscorpions and total spiders (Ara) in Kempson samples, and web-building spiders (Web) in litter-sifting samples (Fig. 3B, Years 2 and 3).

**Univariate analyses**

We analyzed each of the 18 response variables separately for summer and fall samples. Plots over time of those variables that exhibited either a Resource x Year interaction or a simple Resource effect appear in Figs. S5.1 – S5.5 in Appendix S5. The full permANOVA results for all analyses, including a comparison with the vector patterns in Fig. 3, appear in Tables S6.1 and
S6.2 in Appendix S6. These analyses yield a complex pattern of responses that is best summarized pictorially (Fig. 4A).

**Fencing** — Although the multivariate analyses uncovered no interactions with Fencing, ~20% of the univariate tests (7/36; 2 for summer, 5 for fall samples) exhibited some evidence for an interaction with the Fencing treatment ($P \leq .15$; Figs. S5.4, S5.5 in Appendix S5; Appendix S6). All but one interaction (summer samples of Lepidoptera larvae in Year 1) were due to a larger effect of detrital addition on densities in the Fenced treatment.

In terms of magnitude of effect, the presence of fencing was most pronounced for two families of Collembola (Tomoceridae and Hypogastruridae). Plot openness altered the effect of adding detritus for tomocerid Collembola in the fall of Year 1 ($P = .003$), when densities were 3x higher in Supplemented than Ambient plots in the Fenced treatment, but did not differ between Resource treatments in Open plots (Fig. S5.5). Fall samples showed a roughly similar pattern for isotomid Collembola – a Resource effect in only one year (Year 2 instead of Year 1) and only in Fenced plots – but evidence for the interaction was not as strong ($P = .15$, Fig. S5.5, Appendix S5). The pattern for hypogastrurid Collembola is more complex. In the summer, Hypogastruridae were absent or very rare in all plots for the first two years, then increased to high numbers in Year 3. Fencing had a strong effect on the Year 3 pattern ($P = .003$). Hypogastrurids were very abundant in Fenced Supplemented plots (~750/sample/plot), but were still extremely rare in Fenced Ambient plots [$P$(Resource) = .008; Fig. S4.4, Appendix S5)]. In contrast, in Open plots the mean density was ~4x higher in Ambient than Supplemented plots, but this difference was due to high densities in only two plots (five replicates were 3000, 1760, 24, 21 and 0; Supplemental Data S8) and likely not the result of adding detritus [$P$(Resource) = .44 in Open
plots in Year 3; S5.4, Appendix 5). In the fall, hypogastrurids were absent or extremely rare in all Ambient plots in all years, but in Supplemented plots (Open and Fenced) densities started to increase in Year 2 and were extremely abundant by Year 3 [the weak interaction term (P = .10), possibly reflecting an earlier and greater increase in the Fenced plots (Fig. S5.5)].

The only other taxa showing an interaction term with Fencing were Lepidoptera larvae [P = .055 (summer), P = .10 (fall)] and pseudoscorpions [P = .036 (fall)]. Patterns of response of these two taxa are discussed in more detail in the following section. Overall distribution of the Fencing interaction among univariate analyses can be seen most clearly in Fig. 4A.

**Bottom-Up Control** – The overall pattern of univariate responses (Fig. 4A) is broadly congruent with that of the multivariate analyses (Figs. 2, 3). First, effects of detrital supplementation tended to be stronger and more widespread across taxa in fall samples, particularly in Year 1 (Fig. 4A). Secondly, the pattern of response changed over the three years. Evidence of bottom-up control (i.e. a positive response to adding detritus) by the fall of Year 1 was transformed the following two years into a mixture of continued positive responses to detrital addition, disappearance of the early positive responses, appearance of new positive responses, and appearance of negative effects of adding detritus (Fig. 4A). Individual patterns are presented below by trophic categories.

**Detritivores / Fungivores**

The pattern among Collembola families is complicated (first six entries of Fig. 4A). Hypogastrurids and sminthurids exhibited strong positive responses in both summer and fall, but only in one year, and in different years. Onychurids showed a moderately strong positive response in the fall of the first two years. The positive effect on isotomid densities was limited to
fenced plots in the fall of Year 2. The most diverse pattern is that of tomocerid Collembola: a positive response in the fall of Year 1 (Fenced plots), no response in Year 2, and a negative response in the summer of Year 3. By the fall of Year 3 tomocerid densities were close to zero in all plots, as were densities of onychurids and isotomids. Entomobryidae was the only Collembola family that exhibited evidence of bottom-up control throughout the experiment, with a consistently strong response each fall and weaker but positive responses to detrital addition in the summers of the last two years.

Adult Diptera showed a similarly strong response, as they were trapped more frequently in Supplemented plots throughout the experiment (except for the first summer). In contrast, larval and adult Diptera within the litter layer (Kempson samples) never differed between Supplemented and Ambient treatments. Thysanoptera also never exhibited evidence of bottom-up control. In marked contrast, larval Lepidoptera displayed a negative, not positive, response to detrital enhancement in the Fenced plots of fall samples in both Years 2 and 3 (the weak negative effect in the summer of Year 1 is most prudently interpreted as a random effect).

Mixed Trophic Levels

Coleoptera, the most trophically diverse of all response variables, exhibited higher densities in the Supplemented treatment in two-thirds of the sampling periods (middle section of Fig. 4A). Adult beetles showed the most consistent response. The lag in appearance of larvae (Years 2 and Years 3) is consistent with beetle life histories.

Predators

Supplementing detrital input produced evidence of weak, non-persistent or no bottom-up control among the strictly predaceous taxa (bottom section of Fig. 4A). In the litter-extraction samples, densities of centipedes and total spiders (Ara) were similar in Supplemented and
Ambient treatments over all three years. Pseudoscorpions showed a weak response to detrital enhancement, but in the direction opposite to that of bottom-up control. In the last two years pseudoscorpions tended to be less abundant in the Supplemented treatment. Only spiders were sampled in the litter-sifting samples and they were divided into web-building and cursorial categories. Cursorial spiders exhibited a consistent but weak positive response to detritus addition in all summer samples, but never in fall samples. Web-building spiders exhibited a positive response in the fall of Year 1 that gradually disappeared over the experiment.

Patterns opposite to bottom-up control – Patterns of univariate responses that are opposite to bottom-up control are largely congruent with the occurrence of negative correlations with CAP Axis 1 (Fig 4A compared with Fig. 3). All univariate variables that exhibited one to three instances of a negative response to detrital addition among the permANOVAs also exhibited a negative correlation vector in one of the samples (tomocerid Collembola, larval Lepidoptera, and pseudoscorpions). The initially positive impact of detritus addition on fall densities of web-building spiders declined in intensity throughout the experiment, as mentioned above. The multivariate analyses suggest that this decline reflects a possibly negative impact of detrital addition after three years. The Spearman correlation vector was positive, absent, and negative in the fall of Years 1-3, respectively (Fig. 3A, Fall). The multiple correlation coefficient in Year 3 (Fig. 3B, Fall) was also negative.

Discussion
Many ecologists have interpreted CW99 as evidence of strong bottom-up control in terrestrial detritus-based food webs. The consistently positive response to detrital enhancement of primary consumers and their predators reported by CW99 has been cited frequently (224 citations as of December 2016 according to Google Scholar; 26 citations in 2015-2016). The results of our long-term experiment suggest that inferences based solely upon CW99 must be re-examined.

Fourteen of our 18 response variables are shared with CW99. The mixture of outcomes for these shared response variables in our 3-yr experiment contrasts markedly with the strong, pervasive bottom-up control observed for all 14 variables in the same forest just a few years earlier in the shorter-term (3.5 mos.) experiment (Fig. 4B vs. Fig. 4A). Which pattern — the one we observed or that of CW99 — is closer to the pattern of results obtained in other resource-addition experiments with terrestrial detrital food webs? In what ways do our results resemble, and differ from, the pattern of pervasive bottom-up control discovered by CW99? Variation in which factors has most likely affected conclusions about bottom-up control obtained from detrital-supplementation experiments conducted to date?

First, we will examine results and the experimental design of similar detrital addition experiments other than CW99. Then we will discuss possible explanations for why our results are more complex than those of CW99. Finally, we will conclude by examining the broader implications of the results obtained to date from all these diverse experiments. It will become clear that variation in outcomes most likely has been caused by differences between studies in uncontrolled abiotic environmental factors, the influence of earthworms on other taxa, plot size and openness, amount and nature of the added detrital resource, taxonomic resolution of the response variables, and duration of the experiment.
Other Experiments Testing for Bottom-up Control in Terrestrial Detritus-Based Food Webs

Nutrient and/or energy-enhancement experiments in grasslands and forests have exhibited a wide range of results, from increased densities of a few or many taxa on the lower and/or higher trophic levels to a mixture of responses (i.e. positive, zero and negative effects) by primary and secondary consumers.

**Grasslands** – After adding nitrogen and lime to 12 x 20-m unfenced plots for four years, Fountain et al. (2008) found that densities of isotomid Collembola and three spider families had increased, but densities of two spider families had decreased, in response to nutrient enhancement. Patrick et al. (2012) also added nutrients (NPK) to large (314 sq. m) open plots for four years, but observed only positive responses by several families of web-building and cursorial spiders, though some responses were delayed. However, in both studies some spiders may have been responding to changes in both the belowground detrital food web and the aboveground green web. In a clear perturbation of the detrital web, Hoekman et al. (2011) added midge (Diptera: Chironomidae) carcasses to small (1x1-m) open plots for two years or over a single year starting at different times. Collembola, larval Diptera, and Coleoptera exhibited varying positive responses, but spiders showed no treatment effect, most likely because the plots were small and open to migration. Oelbermann et al. (2008) directly manipulated energy input to the detrital web in fenced 5-m² plots for five months. Many Collembola families responded positively as did total spider numbers, which were ca. 2x higher in the detritus-enhanced plots.
Some spiders, though, exhibited no numerical response even though stable-isotope analysis revealed that all sampled spiders relied more heavily on the decomposer food web in the detritus-addition plots. Oelbermann et al. (2008) suggested that even though the secondary-consumer trophic level was strongly linked to the detritus base, individual groups of predators showed inconsistent evidence of bottom-up control due to increased cannibalism and intraguild predation in the plots with additional detritus.

**Forests** – Because of differences between grasslands and forests in rates of litter production, litter quality, and litter decomposition, experiments in forests are more comparable to ours. Scheu and Schaefer (1998) and Maraun et al. (2001) increased microbial growth in the litter layer of fenced 1-m² plots by adding glucose and nitrogen for 15 months with no effect on millipedes, isopods, Collembola, or centipedes of the litter layer. In contrast, Collembola and centipedes of the lower soil horizon responded negatively, most likely due to indirect effects of increased earthworm densities (Scheu & Schaefer 1998; Maraun et al. 2001). We did not sample lower soil layers and in our forest earthworms appear to be much less abundant than in the German beech forest on limestone (Göttinger Wald) where these studies were conducted (pers. obs., Kentucky and German sites). Salamon et al. (2006) also uncovered possible indirect negative effects of increased earthworm activity on centipede densities in a 17-month field experiment with fenced 1-sq m plots. Several Collembola families did respond positively to an enhanced resource base, with effect sizes similar to those observed by CW99. In contrast, pseudoscorpions and spiders did not respond. Thus, in the experiment of Salamon et al. (2006) bottom-up control was not pervasive because it did not propagate to the next trophic level. Raub et al. (2014) also concluded that bottom-up control, although present, was weak and not
pervasive. Every two weeks they added the same type of artificial detritus used by CW99 and in this experiment to 1.5 x 1.5-m unfenced plots for 3 months. Collembola numbers displayed a clear positive response to resource enhancement, but total predators (spiders, pseudoscorpions, and centipedes combined) did not increase. Lessard et al. (2011) found evidence of even weaker bottom-up control in a 3-month press perturbation with 4-sq m open plots spaced 2-m apart. This was possibly due to increased densities of predaceous ants in the resource-addition treatment (Lessard et al. 2011) and perhaps also because migration swamped treatment effects because the open plots were close together.

Comparison with experiment of Chen and Wise 1999 (CW99)

None of the above experiments produced evidence of bottom-up control as strong and pervasive as the bottom-up limitation [sensu Osenberg & Mittelbach (1996)] of both primary and secondary consumers found in the short-term experiment upon which the current study was based (CW99) (Fig. 4B). Why do the results of our experiment differ from those of CW99? The difference is not due to differences in statistical power, which was similar (20 experimental units in both experiments). Because statistical interactions with fencing were infrequent in our experiment, most tests for the effect of detrital supplementation were based upon 10 replicates per Resource level, the same as CW99. Most critical is the need to explain why our study did not reveal continued bottom-up control over three years by the same taxonomic groups that showed such a clear response after 3.5 months of detrital addition in CW99 (Fig. 4A, B). Below we evaluate the possible influence of several factors.
Fencing – This factor was one of the experimental treatments, so its possible influence can be evaluated most directly. Effects of fencing on the Resource treatment were fewer than expected and did not produce a pattern opposite to that of CW99. The relatively few effects of fencing did confirm the expectation that fencing can increase the evidence for strong bottom-up control. In the multivariate analyses of community structure there was no evidence of an interaction between Fencing and (Resource x Year) and the interaction was relatively infrequent in the univariate analyses (ca. 20% of the analyses, using a liberal criterion of $P \leq .15$). Most effects of the barrier (6/7) were due to detrital supplementation having produced a response only in the Fenced plots. For the three examples involving Collembola (Tomoceridae, Isotomidae, and Hypogastruridae), the fence may have yielded a greater positive response than in Open plots by preventing emigration. However, the absence of similar fencing effects for the other three Collembola families, which also had higher densities in the Supplemented plots in two to five of the sampling periods, suggests that fencing did not alter the overall pattern for Collembola. The other fencing effects involved Lepidoptera larvae, which were not sampled in CW99, and pseudoscorpions at the very end of the experiment (Fig. 4A). Hence the effects of fencing were sporadic, and for Collembola (all of which showed strong responses to detrital addition in CW99) fencing brought the overall pattern of Collembola responses in our experiment closer to those of CW99, which solely employed open plots.

Plot size – Plot area was 2.5 larger in CW99 than in our experiment (10 m$^2$ versus 4 m$^2$) but the effect of this difference on the possible swamping effect of migration is smaller than the 2.5 ratio might suggest, for three reasons: (1) the rectangular plot shape of CW99 (2 x 5 m) means that the perimeter-to-area ratio of our plots is only 1.4x greater than that of CW99 [(8/4) / (14/10)]; (2)
microbi-detritivores showed a strong response to resource supplementation in open 1-m² plots in an earlier experiment in the same forest (Chen & Wise 1997); and (3) the absence of consistent and strong Fencing x (Resource x Year) interactions suggests that migration across open plot boundaries did not strongly dilute or increase the responses of most taxa to effects of detrital supplementation.

Rates of detrital supplementation – The rate of detritus addition in Year 1 was approximately one-fourth that employed by CW99. This difference correlates well with the fewer number of positive responses in the fall of Year 1 compared with the fall of CW99 (6 versus 14, respectively; Fig. 4A versus Fig. 4B) and with the increased intensity of positive responses in our experiment across summer and fall of Year 2, after we had increased our supplementation rate 4x to match CW99 more closely. Biweekly rates of detrital supplementation were the same in Years 2 and 3 and were similar to CW99, yet the patterns of response in both years differed markedly from each other and also from CW99. One factor that likely contributes to these differences is variation in rainfall between experiments and between years 2 and 3 of our experiment.

Variation in rainfall – Rainfall was 35% above the long-term average during CW99, in contrast to close-to-normal levels during Years 1 and 2 of our experiment (Lawrence 2000). Year 3 rainfall was markedly less, ca. 50% lower than the first two years. Higher rainfall may have accelerated fungal growth in the leaf litter in the short-term experiment of CW99, intensifying the effect of the detrital subsidy compared to all three years of our experiment. Lower rainfall in Year 3 could explain why densities of three Collembola families — Onychiuridae, Isotomidae,
and Tomoceridae — had declined to near zero in both Ambient and Supplemented plots by the fall of Year 3; and why Sminthuridae showed no response to additional detritus, in contrast to its positive response the previous year (Christiansen 1964; Hopkin 1997; Petersen 2002). In contrast to this pattern, however, hypogastrurid Collembola responded strongly and positively to Resource supplementation throughout Year 3 — and only in Year 3. This response may have been due to release from competition with the Collembola families that had declined in the Supplemented plots by the end of Year 3. Several long-term studies suggest that strong biotic interactions influence Collembola densities, particularly in forests (Chernova & Kuznetsova 2000; Kampichler & Geissen 2005; Kuznetsova 2006; Takeda 1987; van Straalen 1985; Vegter 1987; Wolters 1998). However, direct experimental evidence is lacking for resource competition or apparent competition due to shifting predation pressures between Collembola families.

A long-term experiment is more likely than a short-term study to reveal effects of temporal variation in abiotic factors on bottom-up control processes. The variability in responses to the addition of detritus during our 3-year experiment reflects the range of outcomes across the entire set of similar previously published experiments. CW99 uncovered strong bottom-up control of all sampled primary consumers accompanied by increased densities of the major predatory taxa. This pattern is not typical. The strong responses in CW99, consistently positive and pervasive across trophic levels, were likely due to the higher-than-average rainfall that year and an amount of high-quality detritus that could serve as a substrate for extensive fungal growth. The fact that the experiment lasted only 3.5 months instead of several years increased the probability that a simple pattern of responses would be detected.

The entire body of evidence, however, is not consistent with the interpretation that all examples of weak, intermittent or no bottom-up in our long-term experiment were caused solely
by changes in abiotic conditions that retard fungal growth. Fungal hyphae in the leaf litter were 3x more abundant in Supplemented than Ambient plots at the end of the experiment, when rainfall was the lowest, (though data are not available for fungal densities the first two years)

More importantly, responses of several taxa clearly were opposite to bottom-up control. Variation in rainfall cannot explain these patterns.

**Approach to a differently configured equilibrium state?** – It is possible that long-term resource supplementation leads to a community configuration that cannot be predicted from initial short-term population responses. In other experiments populations sometimes declined in response to resource supplementation, e.g. two spider families in a grassland (Fountain et al. 2008), and Collembola and centipedes at lower soil depths in two forest experiments (Maraun et al. 2001; Scheu & Schaefer 1998). Negative effects in the cited forest experiments likely were caused by disturbances caused by increased earthworm densities. In grasslands some negative responses, and also the failure of some populations to increase in response to detrital addition, could have been caused by shifting strengths of intra-guild predation and cannibalism among generalist predators that altered the strength of top-down control of selected taxa at lower trophic levels (Oelbermann et al. 2008). Such shifting predation pressure could explain some of our results, such as lower numbers of Lepidoptera larvae in response to higher numbers of carabid beetles, and lower densities of web spiders and pseudoscorpions in Supplemented plots at the end of the experiment due to increased predation from elevated numbers of carabid beetles and cursorial spiders. Other interpretations are also possible. An alternative explanation for the latter two examples would be declining numbers of high-quality prey (Tomoceridae) (Toft & Wise 1999b) and increased densities of possibly toxic isotomid (Toft & Wise 1999a; Toft & Wise
Towards a deeper understanding of bottom-up control in detrital food webs

Clearly variation in abiotic factors and biotic interactions can alter the strength and pervasiveness of bottom-up control among different trophic groupings. In detrital food webs a weak positive and/or no response to resource addition is expected if drought impedes fungal growth. It is the negative responses that are more difficult to interpret. Do they reflect the play of top-down control processes expressed differentially along a subset of interaction pathways and if so, do the negative responses signal an approach to a new equilibrium community? One would predict that such compensatory responses are more likely to appear in experiments of longer duration. However, could relatively uncommon negative responses in long-term experiments simply be random vagaries emerging from the low replication in most field experiments? Or might they be the surprising results that ecologists often fail to report (Doak et al. 2008) — the unexpected observations that can help build stronger theory? More long-term experiments will help resolve this dilemma.

How long is long enough? The behavior of mathematical models of long-term press perturbations suggests that many generations will be required to reach a new equilibrium (Bender et al. 1984; Raffaelli & Moller 2000; Yodzis 1988), which coupled with environmental noise might make the prospects of a “long-enough” field experiment seem hopeless. However, after reviewing short- and long-term experiments (2 to 31 mos.) in the intertidal, Menge (1997)
concluded that “. . . community dynamics may be more predictable than expected . . .” because most indirect effects had appeared half-way through the experiment. “Long enough” is at least the number of generations sufficient to reveal indirect effects. An even longer time would reveal how close the community may be to a new equilibrium. This longer time will never be achieved with certainty, but snapshots yielded by short-term experiments cannot answer the question.

Simply advocating experiments of longer duration is not enough. Even in long-term experiments we need to reduce the impact of unpredictable and unknown variation in other factors. Furthermore, we must have a deeper understanding of which interaction pathways were altered, and how much, in response to resource supplementation. How might these two challenges be met?

The first challenge can be addressed by expanding the experimental design. A critical design element lacking in field experiments to date is the initiation of resource additions in new sets of experimental units in each subsequent year after the first perturbation. Phased temporal replication of the experimental perturbation offers the surest way of clearly separating effects due to time lags from those due to changing levels of unknown but influential abiotic and biotic factors. Hoekman et al. (2011) employed a preliminary but elegant version of this approach by combining two yearly pulse treatments of detritus addition with a two-year press treatment.

The second challenge can be met in several ways. One is the use of path analysis and structural equation modeling to help separate direct and indirect effects among interaction pathways between taxa in major trophic groupings in the food web (Grace 2006; Wootton 1994). However, this statistical modeling approach requires numerous replicates, more than are possible with most types of detrital enhancement experiments performed to date. Tradeoffs between too-many response variables, too-few replicates, and experimental units too small to be realistic
present daunting challenges. The other approach is to measure more variables than just the
densities of primary consumers and their predators. Molecular techniques are available to
measure different functional categories of fungi (Nguyen et al. 2016; Shokralla et al. 2012).
Shifts in major trophic pathways can be revealed by techniques such as stable isotopes and fatty
acid analysis (Halaj & Wise 2002; Ruess et al. 2004), and PCR of prey DNA in guts of predators
such as spiders and carabids (Harper et al. 2005; Symondson 2002).

Some of the above suggestions already have been incorporated into short-term field
experiments testing for bottom-up control in detritus-based terrestrial food webs. Utilizing all of
them in a single study is a challenge. Nevertheless, paying heed to their advantages when
planning future long-term research would help reveal likely causes of the type of variability
found in our 3-yr experiment.

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Figure 1. **N** (ordinate) = total number extracted, encountered in litter sifting, or trapped during the experiment. Response variables (combinations of taxa and sampling methods) pooled across treatments, seasons, and years. (A) All response variables (*N* = 18); (B) Non-Collembola response variables (*N* = 12). Variables are arranged in descending order of abundance. Abbreviations are grouped below according to the three different sampling techniques. **KEMPSON**: Collembola (springtails) -- **Hyp** = Hypogastruridae, **Ony** = Onychiuridae, **Ent** = Entomobryidae, **Iso** = Isotomidae, **Tom** = Tomoceridae, **Smi** = Sminthuridae; **Thy** = Thysanoptera (thrips); **Llep** = larval Lepidoptera (moths); **Lcol** = larval Coleoptera (beetles); **Ara** = Araneae (total spiders); **Ldip** = larval Diptera (flies); **Pse** = Pseudoscorpiones; **Acol** = adult Coleoptera (beetles); **Adip** = adult Diptera (flies); **Chi** = Chilopoda (centipedes). **LITTER SIFTING**: **Cur** = cursorial spider families (primarily Corinnidae, Clubionidae, Gnaphosidae and Lycosidae); **Web** = web-weaving spider families (primarily Linyphiidae and Dictynidae). **STICKY TRAPS**: **TrpDip** = adult fungivorous Diptera (flies). Note that estimates of spider densities and adult Diptera numbers (density and activity-density) come from two different sampling methods.
Figure 2. Changing impact over time of detritus addition upon arthropod community structure. Principal Coordinates Ordinations (PCO on Gower’s distance measure; Appendix S2) presented separately for (A) SUMMER and (B) FALL because $P((\text{Resource} \times \text{Year}) \times \text{Season}) = .039$ (Table A3.2 in Appendix S3). Open and Fenced plots have been pooled for perMANOVA because there were no interactions involving (Resource x Year) and Fencing (Table S3.1 in Appendix S3). Because each season exhibited a (Resource x Year) interaction (Table S3.3 in Appendix S3), $P$-values for the Resource treatment are given for each Year.
Figure 3. (A) Constrained ordination (CAP; Resource and Fencing are the constraining factors) with vector overlays representing simple Spearman correlations between response variables and the two axes (Appendix S2). Except for Summer of Year 1, separation of communities along axis 1 (CAP1) is strongly related to the impact of the Supplemented resource treatment on community structure. Thus, the extent to which a vector is parallel with CAP1 reflects the extent of the negative (to the left) or positive (to the right) correlation of densities of that taxon with the resource treatment. The length of each vector represents the joint correlation of the response variable with both axes of the ordination, with the circle representing a correlation of 1. Vectors shown have Spearman coefficients with CAP1 ≥ .50 or ≤ -.50. To prevent clutter on the graph, arrow heads of the vectors are not drawn. Key to abbreviations is in Fig. 1. (B) Constrained ordination (CAP) with vector overlays representing multiple correlation coefficients (analogous to univariate partial correlation coefficients).
**Trophic Category:**

| Taxonomic Category | (A) Temporal Response Pattern: Size and Direction of ΔResource Effect |
|--------------------|---------------------------------------------------------------|
|                    | YEAR 1 | YEAR 2 | YEAR 3 |
| Detritivores/Fungivores: |        |        |         |
| Hypogastruridae (Hyp) |  |  |  |  |
| Onychuridae (Ony) |  |  |  |  |
| Entomobryidae (Ent) |  |  |  |  |
| Isotomidae (Iso) |  |  |  |  |
| Tomoceridae (Tom) |  |  |  |  |
| Sminthuridae (Smi) | | | |
| Diptera Larvae (Ldip) | | | |
| Diptera Adults (Adip) | | | |
| Diptera Adults (TrpDip) | | | |
| Lepidoptera Larvae (Llep) | | | |
| Thysanoptera (Thy) |  |  |  |  |
| Mixed Trophic Levels: |  |  |  |  |
| Coleoptera Larvae (Lcol) | | | |
| Coleoptera Adults (Acol) | | | |
| Predators: |  |  |  |  |
| Cursorial Spiders (Cur) | | | |
| Total Spiders (Ara) | | | |
| Pseudoscorpiones (Pse) | | | |
| Web Spiders (Web) |  |  |  |  |
| Chilopoda (Chi) |  |  |  |  |

**KEY:**

| Adjusted Effect Size (Suppl. / Control) | 1.5x | 2x | >3x | 0.75x | 0.5x |
|----------------------------------------|-----|----|-----|-------|------|
| Symbol           | ↑   | ↑  | ↑   | ↓     | ↓    |

Figure 4. (A) Temporal pattern of responses of all 18 response variables to supplementing the resource base, derived from plots of treatment means over time (Appendix S5) and permANOVA S6). Cont’d ...
**Figure. 4 (cont’d). . .** Arrow width reflects an **Adjusted Effect Size**: the simple effect size, based upon changes over time in the difference between means of Supplemented and Ambient treatments, modified by the $P$ value (a measure of strength of evidence) of the Resource x Year and/or Resource pseudo-$F$’s from the permANOVA. This was done by inspection, not by a single, simple rule. *Thus, widths and placement of these arrows do not precisely reflect statistical tests for each sampling date, but are meant to summarize the overall patterns.* For example, if the simple effect size is ~2x but the $P$ value of the pseudo-$F$ statistic is between .10 and .05 for both the interaction and overall resource effect, the smallest-width arrow is given for the Adjusted Effect Size (i.e. Adjusted Effect Size of 1.5x instead of 2x). Furthermore, if there is no Resource x Time interaction but there is an overall Resource effect, an arrow is present for each date even though the $P$ value of a test on that date might be higher than the overall $P$ value. Empty cells for all three years in a season means there was no Resource x Year interaction, nor was there a simple Resource effect over the three years (for that season). One or two blank cells across a season indicates the shape of the Resource x Year interaction for that season. A “zero” indicates that densities in both Supplemented and Resource treatments were $\approx 0$ that sampling period, although there was an overall Resource x Year interaction across the entire experiment. A simple arrow, i.e. one without a letter next to it, depicts analyses based upon pooled Open and Fenced plots ($N = 10$ / Resource treatment). If there was an interaction with Fencing, the arrow describes the fencing treatment that displayed a Resource x Year interaction or simple Resource effect, indicated by “O” or “F” to the right of the arrow for Open or Fenced plots, respectively. 

**(B)** Results for the study by CW99, which are based upon 3.5 months of adding detritus to open (unfenced) 2 x 5-m plots ($N = 10$ / Resource treatment). $P$ values for all test statistics were < .05, with most being < .01 or < .001 (Chen and Wise 1999). N/A = response variable not sampled.