A peer-reviewed version of this preprint was published in PeerJ on 21 July 2017.

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.

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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.

3

1 Introduction

2

3 Classical theory predicts extensive bottom-up control in detritus-based food webs. However,

4 accumulating empirical findings and modeling research suggest that bottom-up control may not

5 be as strong and pervasive as hypothesized, and that a mixture of bottom-up and top-down

6 control processes characterizes soil food webs (e.g. Bardgett & Wardle 2010; McCann 2012;

7 Moore & deRuiter 2012; Pimm 2002; Wardle 2002). Debates over the strength of bottom-up and

8 top-down control in food webs with many generalist predators (a characteristic of soil

9 communities) intensified in parallel with increasing reliance on controlled field experiments to

10 test theory (e.g. Hairston 1989; Hairston & Hairston 1993; McCann 2012; Menge 2000; Moore

11 et al. 2004; Moore & deRuiter 2012; Polis & Strong 1996; Polis 1996; Resetarits 1998).

12   Making inferences about population control processes from field experiments is not

13 straightforward (Raffaelli & Moller 2000). Two major challenges are space and time. Species

14 interactions occur over a spectrum of spatial scales. Finding an appropriate size for experimental

15 units is difficult, especially given opposing constraints imposed by the desire for realism, the

16 requirement of sufficient replication for adequate statistical power, and the frequent need to

17 impose barriers to migration by using cages or fencing (Gardner et al. 2004; Hurlbert 1984;

18 Raffaelli & Moller 2000; Resetarits 1998). Perhaps an even greater challenge is time. Short-term

19 experiments often fail to capture the spectrum of responses caused by temporal variation in

20 abiotic factors such as rainfall. Furthermore, short-term experiments are unlikely to reveal new

21 equilibria because detecting the consequences of time lags within chains of indirect effects

22 requires many generations of interacting organisms (Bender et al. 1984; Osenberg & Mittelbach

23 1996; Yodzis 1988).

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24   The most direct way to uncover the strength of bottom-up control and its pervasiveness

25   across trophic levels is to observe how adding energy- and/or nutrient-rich detritus to replicated

26   plots in a field experiment alters densities of major taxa of primary and secondary consumers.

27   Such experiments in terrestrial ecosystems have been conducted in prairies and grasslands

28   (Fountain et al. 2008; Hoekman et al. 2011; Oelbermann et al. 2008; Patrick et al. 2012) and

29   forests (Chen & Wise 1999; David et al. 1991; Lessard et al. 2011; Maraun et al. 2001; Raub et

30   al. 2014; Salamon et al. 2006; Scheu & Schaefer 1998; Yang 2006). Most experiments

31   uncovered some evidence for bottom-up control, but the strength and pervasiveness across

32   trophic levels of the responses varied substantially. In some studies, supplementing detrital input

33   resulted in increased populations of primary consumers and their predators. In other experiments the

34   predators showed no response. Sometimes effects occurred across many taxa, sometimes they were

35   limited to a few, and in some instances effects of detrital supplementation were negative. Such

36   variability in outcomes likely reflects differences between experiments in many factors, both

37   environmental and logistical: levels of limiting abiotic factors (i.e. rainfall and temperature) during

38   the experiment; type, quality, and amount of added detritus; taxonomic resolution of the response

39   variables; plot size; number of replicates; whether the plots were open or fenced; and duration of the

40   experiment.

41   Long-term experiments are more likely to capture the influence of variation in abiotic factors

42   and also are more likely to reveal indirect effects that propagate at different rates through a complex

43   food web. Among experiments conducted to date, densities of some trophic groups occasionally

44   responded negatively to addition of detritus. Do these negative effects reflect differential responses

45   by predators to resource-addition combined with intensification of top-down control processes

46   along a subset of trophic pathways due to the indirect effects of trophic-level omnivory in a

47   detritus-based food web (Polis & Strong 1996, Halaj & Wise 2002, Oelbermann et al. 2008)?

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48   Were different pathways of top-down control processes modulating the strength of bottom-up

49   control, producing different responses among trophic levels as the system moved towards a new

50   equilibrium state? Direct manipulation of predator densities in similar detritus-based food webs

51   has revealed top-down control, including trophic cascades affecting decomposition rates (Kajak

52   1997; Kajak & Jakubczyk 1977; Lawrence & Wise 2004; Lensing & Wise 2006; Wardle 2002;

53   Wise 2004). However, negative effects of detrital enhancement on densities of primary

54   consumers and predators were only infrequently observed in previous experiments. A caveat is

55   needed, though, as most resource-enhancement experiments have been relatively brief compared

56   to the generation times of species in the community [one exception is the 4-yr manipulation of

57   nutrients in a grassland (Patrick et al. 2012)]. Furthermore, no experiments of both short-and

58   long-term duration have been conducted with the same system, so the question remains

59   unanswered of whether short-term resource enhancement produces patterns predictive of longer-

60   term resource-enhancement experiments.

61   Detrital-enhancement experiments have been conducted with both fenced and open plots.

62   Fencing, which can limit confounding effects of emigration and immigration on responses of the

63   target taxa to resource enhancement, is potentially most critical for smaller experimental units.

64   This is especially true if the experiment is conducted over many generations of the affected

65   organisms. Positive responses in open plots possibly underestimate the actual strength of bottom-

66   up control because populations that increased in response to detrital supplementation can decline

67   as emigrants leave for areas outside the plots where densities are lower. Similarly, unexpected

68   decreases in density in supplemented unfenced plots might be masked by augmentation of

69   densities due to immigration from outside. Thus, we hypothesized that fencing the plots would

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70   produce more realistic estimates of the strength of bottom-up control, or conversely, would more

71   likely reveal population declines resulting from cascading indirect effects.

72   Despite the perceived need to impose barriers to migration, possible impacts of fencing

73   on results are difficult to interpret because some animals can cross the barrier, whereas others

74   cannot. In a 1.5-yr predator-reduction experiment conducted with 2x2-m plots in the same forest

75   as the current research, fencing had no impact upon densities of potential prey (families of

76   Collembola) in non-manipulated plots (Wise 2004), which implies that the results obtained in

77   fenced predator-reduction plots reflected processes occurring on the open forest floor. However,

78   this conclusion is not entirely without reservations because it was not possible to achieve

79   persistent predator-reductions without fencing. Therefore, in that experiment it was not possible

80   to establish a completely balanced design [predator treatment (2 levels) x fencing treatment (2

81   levels)]. In the current research, however, we could evaluate the impact of fencing directly and

82   unambiguously because the detrital-enhancement treatment was imposed equally in open and

83   fenced plots.

84   Here we report results of a 3-year detrital-addition experiment in a secondary oak-maple-

85   hickory forest, with a few scattered pine trees, in Madison Co., Kentucky, USA. Our experiment

86   was conducted within ~0.5 km of the sites of a previous similar, but short-term (3.5-months),

87   experiment that utilized open (unfenced) forest-floor plots (Chen & Wise 1999) — referred to as

88   "CW99" from now on. The earlier experiment in this forest produced clear evidence of detrital

89   resource *limitation* [*sensu* Osenberg & Mittelbach (1996)] i.e. relatively rapid elevation of

90   population densities of both primary and secondary consumers in response to addition of high-

91   quality detritus. Major groups of primary consumers, the microbi-detritivores (grazers of fungi

92   and consumers of organic debris), were at least 2-3x more abundant in supplemented than

4

93   control plots. Major arthropod predators were ~ 2x as abundant. No taxa were less abundant in

94   the resource-supplemented treatment. Because the plots were not fenced, emigration of some

95   taxa that responded positively to resource supplementation might have weakened the observed

96   magnitude of bottom-up control. Similarly, immigration of taxa that had actually declined in

97   density might have erased the negative treatment response. Our experiment expanded the design

98   of CW99 to answer two questions (the first, logistical; the second, conceptual): (1) How would a

99   barrier to emigration/immigration of some groups of ground arthropods affect conclusions about

100   bottom-up control? (2) Would a longer-term experiment reveal inconsistences in responses that

101   would suggest either tempering of bottom-up control by variation in abiotic factors and/or

102   movement of the perturbed community in the direction of a new equilibrium?

103

104   # Methods

105

106   ## Experimental design

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108   The experiment started two years after CW99 and ran from 1997 through 1999 (hereon

109   designated Years 1, 2, and 3). Each experimental unit (20 in total) was a 2 x 2-m area of forest

110   floor, separated from each other by at least 10 m. Experimental units were randomly assigned to

111   one of two levels of a resource treatment and one of two levels of a fencing treatment, yielding

112   five replicates of each of the four combinations of treatment levels. Thus, half of the units

113   received a detrital supplement (Supplemented), the others none (Ambient), and half of the plots

114   in each resource treatment were open to emigration and immigration (Open), while the others

5

115   were enclosed with 35-cm aluminum flashing inserted 8 cm into the ground (Fenced). The fence

116   was topped with a 15-cm horizontal strip of flashing that formed two lips coated on the underside

117   with a tree-banding compound (Tanglefoot®, Grand Rapids, Michigan) to further retard

118   movement of epigeic (ground-active) arthropods across the barrier. This design is more complex

119   than that of CW99, which had no fenced plots but employed the same total number of

120   experimental units: twenty 2 x 5-m open plots, half of which received a detrital supplement.

121   We employed the detritus-supplementation protocol of CW99, which has also been used

122   in other experiments (Chen & Wise 1997; Raub et al. 2014). Our goal was not to determine

123   which components of the resource base (bacteria, fungi, and organic debris) were possibly

124   limiting densities of microbivores and detritivores, as was the aim of Salamon et al. (2006).

125   Rather, our goal was to follow the community response to long-term enhancement of a broadly

126   defined resource base. This experimental approach, including that of Salamon et al. (2006) and

127   others, involves adding artificial forms of organic matter and nutrients. Every two weeks from

128   April through September we added chopped "fresh" (i.e. not dried) mushrooms and potatoes, and

129   dry flakes of *Drosophila* medium (Carolina Biological Supply; Burlington, North Carolina,

130   USA; Formula 4-24) to the Supplemented plots.

131   We decided initially to supplement at a rate approximately 1/3 that of CW99 because we

132   hypothesized that the strong responses exhibited in the earlier experiment were due to a high

133   level of detrital enhancement. We planned to continue this rate of supplementation in the

134   following years, but decided to increase the rate because the increase in densities of most taxa in

135   response to the detrital enhancement in Year 1 was much less (including no responses) than that

136   observed by CW99. Therefore, in Years 2 and 3 we increased the rate of supplementation to a

137   level similar to CW99. In Year 1 each Supplemented plot received 195 g (dry wt.) m^{-2} of detritus

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138   (26 g m^{-2}, 79 g m^{-2} and 90 g m^{-2} of mushrooms, potatoes, and *Drosophila* medium, respectively).

139   In Years 2 and 3 the rate of detritus supplementation was increased ca. 4x (to 770 g m^{-2} and 874

140   g m^{-2} total dry wt., respectively). The slightly larger amount of detritus added during Year 3

141   reflects a slightly longer period of detrital addition than in Year 2. Biweekly rates were the same

142   in Years 2 and 3.

143   Adding artificial detritus can influence the structure of the leaf-litter layer, so it is

144   instructive to compare amounts added with litter standing crops. In Year 1 the average (± SE)

145   standing crop of litter (dry wt. m^{-2}) in Ambient plots was 671 ± 43 g (n = 10). Thus, the dry

146   weight of detritus added throughout Year 1 was ~ 30% of the average standing crop of detritus,

147   compared to an addition rate of ~100% of the litter standing crop in CW99. In Years 2 and 3

148   each Supplemented plot received ~136% and ~122% of that year's average standing crop of

149   litter, respectively. By the end of Year 3 litter weight was only 13% higher in Supplemented than

150   Ambient plots ($F_{1, 16}$ = 4.93, P = .04), compared to a ~30% increase at the end of CW99.

151   Due to our decision to increase the supplementation rate in Years 2 and 3 to ~4x the rate

152   of Year 1, differences in response patterns between Year 1 and the following two years can be

153   attributed not only to differences in abiotic factors between years and time lags in the appearance

154   of direct and indirect effects, but also to markedly different rates of detrital supplementation. In

155   contrast, differences between Years 2 and 3 must have been due primarily to factors other than a

156   difference in the rate of resource addition, since biweekly rates of supplementation in Years 2

157   and 3 were the same.

158

159   Fungal biomass

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7

161   Differences in fungal abundance between Supplemented and Ambient plots at the end of the

162   experiment were estimated by assaying leaf litter for ergosterol (Appendix S1), a common sterol

163   in fungal hyphae that is nearly absent from plants (Weete & Weber 1980). The amount of

164   ergosterol is correlated with both total hyphal mass and membrane content and likely assayed

165   both living and dead hyphae (Mille-Lindblom et al. 2004; Ruzicka et al. 2000; Zhao et al. 2005).

166

167   ## Arthropods

168

169   Selected taxa of arthropods active within and on the surface of leaf litter were sampled three

170   times in Year 1 (18 July, 15 August, 13 October), twice in Year 2 (20 June, 23 September) and

171   twice in Year 3 (3 June, 5 September). Values for the first two dates in Year 1 were averaged,

172   yielding two values (Summer and Fall) for each year. Densities of most taxa were estimated by

173   litter extraction and/or litter sifting. Sticky traps were used to measure activity-densities of adult

174   flies (Diptera) just above the litter layer.

175

176   *Litter extraction*

177   Densities (measured as number per .05-m^2 of forest floor) of 15 taxonomic groupings [six

178   families of springtails (Collembola), thrips (Thysanoptera), larval moths (Lepidoptera), larval

179   and adult beetles (Coleoptera), larval and adult flies (Diptera), pseudoscorpions

180   (Pseudoscorpiones), centipedes (Chilopoda) and spiders (Araneae)] were estimated by taking

181   litter from .05-m^2 of forest floor per plot and using a temperature/humidity gradient in a modified

182   Kempson-McFadyen apparatus (Kempson et al. 1963; Schauermann 1982) to extract animals

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183   into 50% ethylene glycol over 10 days. Extracted arthropods were washed and stored in 70%

184   ethyl alcohol until identified.

185

186   *Litter sifting*

187   Litter extraction is not the best way to sample densities of active, larger spiders that often are less

188   abundant than smaller life stages and species (Chen & Wise 1999). Therefore, densities of

189   cursorial spiders (primarily Corinnidae, Clubionidae, Gnaphosidae, and Lycosidae) and web-

190   weaving spiders (primarily Linyphiidae and Dictynidae) were assessed by carefully sifting and

191   searching, in the field, one 0.2-m^2 sample of litter per plot (different from the .05- m^2 sample).

192

193   *Sticky traps*

194   Densities (number per .05-m^2) of larval and adult Diptera within the litter were determined by

195   Kempson extractions. In addition, activity-densities (combined result of density and activity;

196   number captured per trap) of selected families of adult Diptera were assessed with aerial traps

197   placed just above the litter layer. Two 10 x 10-cm vertical pieces of metal insect screening

198   attached to thin steel rods were coated with Tanglefoot® and placed 0.5m apart and

199   perpendicular to each other in each plot for 24 hours.

200

201   *Taxonomic resolution of response variables*

202   Several criteria dictated the taxonomic resolution of the response variables: (1) a close-as-

203   feasible match to the degree of resolution reported in CW99; (2) logistical constraints (e.g. time

204   and technical help) related to sorting and identifying the number of arthropods collected; (3) the

205   overall pattern of relative abundance (i.e. numbers of each family of Collembola were greater

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206 than numbers for each of the other categories, all of which were orders or selected families

207 within orders); and (4) the fact that trophic position (i.e. predator or detritivore) was broadly

208 similar for organisms within orders, with the exception of Coleoptera [CW99 reported total

209 Coleoptera and Staphylinidae, but did not distinguish other families; results were similar in

210 CW99 for total Coleoptera and Staphylinidae)]. Diptera in the litter were fungivorous families.

211 Only fungivorous familes (Mycetophilidae, Sciaridae, and Phoridae) are included in the Diptera

212 numbers from the sticky traps. Note that Diptera adults and spiders each are represented in

213 Kempson samples and also in a different response variable, either sticky traps (Diptera) or litter-

214 sifting (cursorial and web-building spiders). Cursorial and web-building families utilize very

215 different foraging modes (Wise 1993) and could easily be distinguished in sifting samples. They

216 were pooled for Kempson samples due to the challenge of correctly identifying small specimens

217 to family. Logistical constraints forced us to exclude mites (Acarina), a group that is abundant in

218 leaf litter and was sampled in CW99.

219

220 Statistical analyses

221

222   The core structure of the experiment is a repeated-measures 2 x 2 x 3 design [Resource

223 (Ambient, Supplemented) x Fencing (Open, Fenced) x Year (1, 2, and 3)] analyzed separately for

224 summer and fall samples (rationale for separating seasons is explained below). Methodological

225 details of statistical analyses appear in Appendix S2. The complete arthropod data set is

226 described in Appendix S7 and presented in Supplemental Data S8. Below we present an

227 overview of our approach to data analysis.

10

228   The central **conceptual** question addressed by our field experiment is: *How does the*

229   *response of the system to resource supplementation change over time?* The focus of our analyses

230   is the statistic that directly addresses this question, the Resource x Year interaction. We

231   evaluated this interaction by relying on a combination of multivariate and univariate statistical

232   techniques. We first used multivariate analyses to determine how detrital supplementation

233   changed arthropod community structure over time and which response variables were most

234   closely linked to these changes. Multivariate analyses were performed first because if there is no

235   multivariate effect, there is no justification for doing separate univariate analyses. Because

236   multivariate effects were present we then conducted independent univariate analyses and

237   compared patterns of change over time of individual response variables with the multivariate

238   patterns.

239   We postulated that the system would respond differently in summer and fall because

240   summer samples had been exposed to detrital enhancement for fewer months than fall samples

241   and because life histories of many taxa show pronounced seasonal patterns. Multivariate analysis

242   of the community distance matrix based on the entire data set confirmed this expectation, as

243   there was an interaction between [Resource x Year] and Season (Tables S3.1, S3.2 in Appendix

244   S3). Thus, we divided the community distance matrix into summer and fall subsets, yielding one

245   distance matrix for each season. All subsequent multivariate and univariate analyses were done

246   separately for summer and fall samples.

247   The central **logistical** question addressed by our field experiment is: *How does the*

248   *openness of the plots affect the observed pattern of responses to detrital supplementation?*

249   Thus, we first tested for an interaction between [Resource x Year] and Fencing. If there was no

250   evidence for an interaction (P value of the 3-way interaction > .15), the design was collapsed

11

251   (Open and Fenced plots were pooled, yielding twice as many replicates per Resource level) to

252   one involving only Resource and Year. If Fencing possibly influenced the Resource x Year

253   interaction, further analyses were done separately for Open and Fenced plots. Use of $P > .15$

254   (instead of the conventional $P > .05$ criterion) for inferring no interaction with Fencing made it

255   less likely to ignore a weak effect of fencing that could have influenced interpretation of the

256   response patterns.

257

258   *Multivariate analyses*

259   Using all 18 response variables, we calculated a distance matrix using Gower's similarity index

260   [S15 of Legendre and Legendre (2012)]. Gower's index was employed because it is designed to

261   accommodate different types of variables (Kempson, sifting, and sticky-trap samples; Fig. 1).

262   We implemented S15 because this version of Gower's measure is a symmetrical index that gives

263   equal weight to double zeroes (absence/absence) and ++ (presence/presence), which is the type

264   of distance measure philosophically appropriate for analyzing results of a field experiment

265   [unlike the more commonly employed "Bray-Curtis" measure, which is less suited to the

266   assumptions behind controlled manipulative experiments (Legendre & Legendre 2012)]. Further

267   details are in Appendix S2.

268   Permutational multivariate analysis of variance (perMANOVA) (Anderson et al. 2008)

269   was then used to assess the multivariate Resource x Year interaction. Because our initial analysis

270   revealed a Resource x Year interaction for both summer and fall (detailed in the Results section),

271   we then assessed the changing impact of Resource on arthropod community structure over the

272   experiment in two ways. First, we plotted the location of each experimental unit (i.e. 2x2-m plot)

273   on the first two axes of the Principal Coordinates Ordination (PCO) for each year along with the

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274   *P* value for the Resource effect each year. Multivariate effect size each year was defined as the

275   proportion of variance explained by adding detritus to the system (Anderson et al. 2008).

276   Secondly, we evaluated how different response variables contributed to the change in community

277   structure by plotting both simple and multiple correlation vectors on constrained PCO

278   ordinations (CAP; constrained by Resource and Fencing treatments) for each year.

279

280   *Univariate analyses*

281   We plotted yearly means ± SE of each response variable and then used permutational univariate

282   analysis of variance (permANOVA) (Anderson et al. 2008) to help evaluate the change over time

283   in density differences between Supplemented and Ambient treatments. Possible interactions

284   between [Resource x Year] and Fencing for single response variables were relatively infrequent

285   (*P* for interaction < .15 for 7 out of 36 permANOVA's; Appendix S6), but are noted and

286   discussed when present. We used permANOVA after attempting to model the univariate

287   variables with a mixed-effects generalized linear model [GLMM; functions "glmer" and

288   "glmer.nb" in the R package "lme4" (R Core Team 2014)] using the Poisson and negative

289   binomial families. The GLMM was not an appropriate statistical model for our data because for

290   most response variables the residuals were poorly behaved (Zuur et al. 2009) and most GLMM

291   models failed to converge properly.

292

293   *Overall interpretation of response patterns*

294   Interpretation of how the system responded was based upon evaluating the results of multivariate

295   and univariate analyses together as a whole. Emphasis was placed upon using the statistical

296   analyses to aid in interpreting the overall patterns of the ordinations and univariate plots. We

13

297 avoided a completely NHST (Null Hypothesis Significance Testing) approach as much as

298 possible. Thus, we made no corrections for "multiple comparisons" in the univariate analyses,

299 primarily because multivariate effects were clear; and we did not conclude that P values close to

300 .05, but slightly greater, indicated the absence of a response. Instead, we relied on P values as a

301 measure of strength of evidence (Cumming 2012; Hector 2015; Nakagawa & Cuthill 2007). Our

302 overall evaluation of the impact of resource enhancement on the food web was a melding of (1)

303 changes in community structure as indicated by perMANOVA and PCO, (2) patterns of

304 correlation-vector overlays on constrained ordinations (CAP), (3) univariate effect sizes

305 estimated from temporal plots of mean density for Resource and Ambient treatments, and (4) the

306 P value of the appropriate permANOVA statistic [Resource x Year interaction or simple

307 Resource effect if there was no change over time in the Resource effect].

308

309 ## Results

310

311 ## Fungal density

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313 Fungal hyphae, as measured by concentrations of ergosterol, were 3x denser in Supplemented

314 than Ambient plots [Appendix S1].

315

316 ## Relative abundance of taxa

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318   The most abundant taxa were six families of microbi-detritivores (Collembola) collected by

319   Kempson extraction, with the Hypogastruridae, Onychiuridae, and Entomobryidae being the

320   three most numerous (Fig. 1A). Remaining response variables were similar in value to each

321   other, differing by less than 50%. Centipedes (Chilopoda) were the exception. This predatory

322   taxon had the fewest individuals sampled of all response variables (Fig. 1B).

323

324   Response of arthropods to detrital supplementation

325

326   Results of multivariate analyses are presented first because they constituted the critical first step

327   in the analysis. If detrital supplementation had no effect upon overall community structure,

328   analyzing the 18 response variables separately would not have been justified. In each section

329   below (both multivariate and univariate analyses), results of testing for interactions with Fencing

330   are presented first, followed by the evidence for changes in the presence and strength of bottom-

331   up control processes over the three years of the experiment.

332

333   *Multivariate analyses*

334

335   **Fencing –** Permutational multivariate analysis of variance (perMANOVA) uncovered no

336   evidence of an interaction between the openness of a plot and the overall community response to

337   the addition of detritus. In the full perMANOVA model (Appendix S3), P[(Resource x Year) x

338   Season x Fencing] = 0.67 and P[(Resource x Year) x Fencing] = 0.22 (Table S3.1, Appendix

339   S3). Therefore, Open and Fenced plots were pooled for the multivariate analyses of the

340   Resource x Year interaction, which were performed separately for summer and fall samples

15

341   because P [(Resource x Year) x Season] = 0.039 (Table S3.2, Appendix S3), and because of

342   logistical and biological considerations explained in the Methods section.

343

344   **Bottom-up Control –**   Increasing the detrital resource base clearly altered arthropod

345   community structure and the magnitude of the response (i.e. separation of plots by treatment in

346   ordination space) increased over time (Fig. 2; Tables S3.3A and S3.3B, Appendix S3).

347   Divergence between Ambient and Supplemented plots was greater in fall than summer (Fig. 2;

348   Table S3.3 in Appendix S3). In summer, percentages of total variation explained by the Resource

349   treatment for Years 1-3 were 12%, 26%, and 28%, respectively. Percentages for fall samples

350   were 24%, 41%, and 32%. Divergence in community structure over time was due primarily to

351   increasing separation of centroid locations (Fig. 2). However, on the last sampling date of the

352   experiment (fall of Year 3), the Supplemented sites were also more dispersed in ordination space

353   than the Ambient sites [Pseudo-$F_{1,18}$ = 8.85, P = .007, PERMDISP test (Anderson et al. 2008)].

354   Community structure differed between Ambient and Supplemented plots less in Year 1

355   than in the last two years of the experiment (Fig. 2; Table S3.3, Appendix S3). Although the

356   degree of divergence between Ambient and Resource plots in Years 2 and 3 appears similar, the

357   impact of the resource treatment on arthropod community structure in Year 3 differed from that

358   of Year 2 [P(Pseudo-$F_{1,71}$(Resource x Year)] = .014, perMANOVA; Appendix S4]. It is likely

359   that the lower dispersion among Ambient plots in the fall of Year 3 (Fig. 2) is the major cause of

360   the Resource x Year interaction.

361   The identity of the response variables that were most highly correlated with the

362   divergence in community structure changed over time. The pattern of these correlations also

363   differed between seasons. Comparing simple Spearman and multiple ("partial") correlation

16

364 coefficients gives some additional insight into which taxa were the primary drivers of the

365 divergence in community structure.

Simple Spearman Correlation Coefficients

367 *Summer* -- In the summer of Year 1, the plots were not clearly separated according to

368 detritus treatment, so the vector for isotomid Collembola does not reflect effects of detritus

369 addition (Fig. 3A, Summer, Year 1). In the following two summers, vector patterns reveal

370 bottom-up control of several primary consumers that only weakly reached the secondary-

371 consumer level (Fig. 3A, Summer, Years 2, 3). In the last two summers, all response variables

372 with coefficients ≥ .50 were positively associated with the first axis, which is strongly linked to

373 the detritus-addition treatment. Seven of the ten vectors for Years 2 and 3 represent microbi-

374 detritivores [three for Diptera and four for Collembola (Hypogastruridae, Sminthuridae, and

375 Entomobryidae)]. The remaining three vectors represent simple correlations with larval and adult

376 Coleoptera, which include both predators and microbi-detritivores.

377 *Fall* -- The pattern for fall samples is more complex (Fig. 3A, Fall). Years 1 and 2

378 exhibited a pattern broadly similar to that of summer samples for Years 2 and 3, although the

379 total number of responding taxa was greater in fall than summer (16 vectors versus 10,

380 respectively). All vectors were positively correlated with CAP Axis 1 except for Thysanoptera, a

381 consumer of detritus/fungi. Among the other microbi-detritivores, all six Collembola families

382 showed increased densities in the Supplemented treatment in Year 1 and/or Year 2, as did larval

383 and adult Diptera. In the fall, more predatory groups had responded to detritus addition than in

384 the summer. Vectors for both cursorial and web-building spiders in litter-sifting samples were

385 positively associated with the first axis in Year 1 but not Year 2. In Year 3, larval and adult

386 Coleoptera, many of which are predators, responded positively to detritus addition. The pattern

17

387   for Year 3 in fall samples is strikingly different. Only two microbi-detritivore groups displayed

388   positive vectors, and one group, larval Lepidoptera, had a weak negative correlation with Axis 1.

389   The strongest correlation in Year 3 was that for web-building spiders. However, the relationship

390   with detrital addition was negative, not positive as was the case in Year 1 (Fig. 3A, Fall).

391   *Multiple (Partial) Correlation Coefficients*

392   The multiple (partial) coefficient removes correlations with other response variables

393   (Anderson et al. 2008). Thus, it is not surprising that fewer show a relationship with Axis 1, even

394   with a lower R^2 threshold, than do vectors representing the simple Spearman statistic (11 vs. 31

395   vectors, respectively; Fig. 3B vs. Fig. 3A [ignoring Summer of Year 1, when arthropod

396   community structure showed no clear response to adding detritus]). The pattern over time of

397   vectors for the multiple correlation coefficient is complex (Fig. 3B). Among the nine vectors

398   exhibiting a component positively correlated with Axis 1, only one includes some predatory taxa

399   (larval Coleoptera). Among the four vectors that indicate a negative response to detrital

400   supplementation, one is that of a microbi-detritivore (tomocerid Collembola). The other three

401   negative vectors are strictly predatory taxa: pseudoscorpions and total spiders (Ara) in Kempson

402   samples, and web-building spiders (Web) in litter-sifting samples (Fig. 3B, Years 2 and 3).

403

Univariate analyses

405   We analyzed each of the 18 response variables separately for summer and fall samples. Plots

406   over time of those variables that exhibited either a Resource x Year interaction or a simple

407   Resource effect appear in Figs. S5.1 – S5.5 in Appendix S5. The full permANOVA results for all

408   analyses, including a comparison with the vector patterns in Fig. 3, appear in Tables S6.1 and

18

409   S6.2 in Appendix S6. These analyses yield a complex pattern of responses that is best

410   summarized pictorially (Fig. 4A).

411

412   **Fencing –** Although the multivariate analyses uncovered no interactions with Fencing, ~20%

413   of the univariate tests (7/36; 2 for summer, 5 for fall samples) exhibited some evidence for an

414   interaction with the Fencing treatment ($P \leq .15$; Figs. S5.4, S5.5 in Appendix S5; Appendix S6).

415   All but one interaction (summer samples of Lepidoptera larvae in Year 1) were due to a larger

416   effect of detrital addition on densities in the Fenced treatment.

417   In terms of magnitude of effect, the presence of fencing was most pronounced for two

418   families of Collembola (Tomoceridae and Hypogastruridae). Plot openness altered the effect of

419   adding detritus for tomocerid Collembola in the fall of Year 1 ($P = .003$), when densities were 3x

420   higher in Supplemented than Ambient plots in the Fenced treatment, but did not differ between

421   Resource treatments in Open plots (Fig. S5.5). Fall samples showed a roughly similar pattern for

422   isotomid Collembola – a Resource effect in only one year (Year 2 instead of Year 1) and only in

423   Fenced plots – but evidence for the interaction was not as strong ($P = .15$, Fig. S5.5, Appendix

424   S5). The pattern for hypogastrurid Collembola is more complex. In the summer, Hypogastruridae

425   were absent or very rare in all plots for the first two years, then increased to high numbers in

426   Year 3. Fencing had a strong effect on the Year 3 pattern ($P = .003$). Hypogastrurids were very

427   abundant in Fenced Supplemented plots (~750/sample/plot), but were still extremely rare in

428   Fenced Ambient plots [P(Resource) = .008; Fig. S4.4, Appendix S5)]. In contrast, in Open plots

429   the mean density was ~4x higher in Ambient than Supplemented plots, but this difference was

430   due to high densities in only two plots (five replicates were 3000, 1760, 24, 21 and 0;

431   Supplemental Data S8) and likely not the result of adding detritus [P(Resource) = .44 in Open

19

432   plots in Year 3; S5.4, Appendix 5). In the fall, hypogastrurids were absent or extremely rare in

433   all Ambient plots in all years, but in Supplemented plots (Open and Fenced) densities started to

434   increase in Year 2 and were extremely abundant by Year 3 [the weak interaction term ($P = .10$),

435   possibly reflecting an earlier and greater increase in the Fenced plots (Fig. S5.5)].

436   The only other taxa showing an interaction term with Fencing were Lepidoptera larvae [P

437     $= .055$ (summer), $P = .10$ (fall)] and pseudoscorpions [$P = .036$ (fall)]. Patterns of response of

438   these two taxa are discussed in more detail in the following section. Overall distribution of the

439   Fencing interaction among univariate analyses can be seen most clearly in Fig. 4A.

440

441   **Bottom-Up Control –** The overall pattern of univariate responses (Fig. 4A) is broadly

442   congruent with that of the multivariate analyses (Figs. 2, 3). First, effects of detrital

443   supplementation tended to be stronger and more widespread across taxa in fall samples,

444   particularly in Year 1 (Fig. 4A). Secondly, the pattern of response changed over the three years.

445   Evidence of bottom-up control (i.e. a positive response to adding detritus) by the fall of Year 1

446   was transformed the following two years into a mixture of continued positive responses to

447   detrital addition, disappearance of the early positive responses, appearance of new positive

448   responses, and appearance of negative effects of adding detritus (Fig. 4A). Individual patterns are

449   presented below by trophic categories.

                                  Detritivores / Fungivores

451   The pattern among Collembola families is complicated (first six entries of Fig. 4A).

452   Hypogastrurids and sminthurids exhibited strong positive responses in both summer and fall, but

453   only in one year, and in different years. Onychurids showed a moderately strong positive

454   response in the fall of the first two years. The positive effect on isotomid densities was limited to

20

455   fenced plots in the fall of Year 2. The most diverse pattern is that of tomocerid Collembola: a

456   positive response in the fall of Year 1 (Fenced plots), no response in Year 2, and a negative

457   response in the summer of Year 3. By the fall of Year 3 tomocerid densities were close to zero in

458   all plots, as were densities of onychurids and isotomids. Entomobryidae was the only

459   Collembola family that exhibited evidence of bottom-up control throughout the experiment, with

460   a consistently strong response each fall and weaker but positive responses to detrital addition in

461   the summers of the last two years.

462   Adult Diptera showed a similarly strong response, as they were trapped more frequently

463   in Supplemented plots throughout the experiment (except for the first summer). In contrast,

464   larval and adult Diptera within the litter layer (Kempson samples) never differed between

465   Supplemented and Ambient treatments. Thysanoptera also never exhibited evidence of bottom-

466   up control. In marked contrast, larval Lepidoptera displayed a negative, not positive, response to

467   detrital enhancement in the Fenced plots of fall samples in both Years 2 and 3 (the weak negative

468   effect in the summer of Year 1 is most prudently interpreted as a random effect).

469   *Mixed Trophic Levels*

470   Coleoptera, the most trophically diverse of all response variables, exhibited higher

471   densities in the Supplemented treatment in two-thirds of the sampling periods (middle section of

472   Fig. 4A). Adult beetles showed the most consistent response. The lag in appearance of larvae

473   (Years 2 and Years 3) is consistent with beetle life histories.

474   *Predators*

475   Supplementing detrital input produced evidence of weak, non-persistent or no bottom-up

476   control among the strictly predaceous taxa (bottom section of Fig. 4A). In the litter-extraction

477   samples, densities of centipedes and total spiders (Ara) were similar in Supplemented and

21

478   Ambient treatments over all three years. Pseudoscorpions showed a weak response to detrital

479   enhancement, but in the direction opposite to that of bottom-up control. In the last two years

480   pseudoscorpions tended to be less abundant in the Supplemented treatment. Only spiders were

481   sampled in the litter-sifting samples and they were divided into web-building and cursorial

482   categories. Cursorial spiders exhibited a consistent but weak positive response to detritus

483   addition in all summer samples, but never in fall samples. Web-building spiders exhibited a

484   positive response in the fall of Year 1 that gradually disappeared over the experiment.

485

486   **Patterns opposite to bottom-up control –** Patterns of univariate responses that are

487   opposite to bottom-up control are largely congruent with the occurrence of negative correlations

488   with CAP Axis 1 (Fig 4A compared with Fig. 3). All univariate variables that exhibited one to

489   three instances of a negative response to detrital addition among the permANOVAs also

490   exhibited a negative correlation vector in one of the samples (tomocerid Collembola, larval

491   Lepidoptera, and pseudoscorpions). The initially positive impact of detritus addition on fall

492   densities of web-building spiders declined in intensity throughout the experiment, as mentioned

493   above. The multivariate analyses suggest that this decline reflects a possibly negative impact of

494   detrital addition after three years. The Spearman correlation vector was positive, absent, and

495   negative in the fall of Years 1-3, respectively (Fig. 3A, Fall). The multiple correlation coefficient

496   in Year 3 (Fig. 3B, Fall) was also negative.

497

498   # Discussion

499

500   Many ecologists have interpreted CW99 as evidence of strong bottom-up control in

501   terrestrial detritus-based food webs. The consistently positive response to detrital enhancement

502   of primary consumers and their predators reported by CW99 has been cited frequently (224

503   citations as of December 2016 according to Google Scholar; 26 citations in 2015-2016). The

504   results of our long-term experiment suggest that inferences based solely upon CW99 must be re-

505   examined.

506   Fourteen of our 18 response variables are shared with CW99. The mixture of outcomes

507   for these shared response variables in our 3-yr experiment contrasts markedly with the strong,

508   pervasive bottom-up control observed for all 14 variables in the same forest just a few years

509   earlier in the shorter-term (3.5 mos.) experiment (Fig. 4B vs. Fig. 4A). Which pattern — the one

510   we observed or that of CW99 — is closer to the pattern of results obtained in other resource-

511   addition experiments with terrestrial detrital food webs? In what ways do our results resemble,

512   and differ from, the pattern of pervasive bottom-up control discovered by CW99? Variation in

513   which factors has most likely affected conclusions about bottom-up control obtained from

514   detrital-supplementation experiments conducted to date?

515   First, we will examine results and the experimental design of similar detrital addition

516   experiments other than CW99. Then we will discuss possible explanations for why our results

517   are more complex than those of CW99. Finally, we will conclude by examining the broader

518   implications of the results obtained to date from all these diverse experiments. It will become

519   clear that variation in outcomes most likely has been caused by differences between studies in

520   uncontrolled abiotic environmental factors, the influence of earthworms on other taxa, plot size

521   and openness, amount and nature of the added detrital resource, taxonomic resolution of the

522   response variables, and duration of the experiment.

523

Other Experiments Testing for Bottom-up Control in Terrestrial

Detritus-Based Food Webs

526

527 Nutrient and/or energy-enhancement experiments in grasslands and forests have exhibited a wide

528 range of results, from increased densities of a few or many taxa on the lower and/or higher

529 trophic levels to a mixture of responses (i.e. positive, zero and negative effects) by primary and

530 secondary consumers.

531

532 **Grasslands –** After adding nitrogen and lime to 12 x 20-m unfenced plots for four years,

533 Fountain et al. (2008) found that densities of isotomid Collembola and three spider families had

534 increased, but densities of two spider families had decreased, in response to nutrient

535 enhancement. Patrick et al. (2012) also added nutrients (NPK) to large (314 sq. m) open plots for

536 four years, but observed only positive responses by several families of web-building and

537 cursorial spiders, though some responses were delayed. However, in both studies some spiders

538 may have been responding to changes in both the belowground detrital food web and the

539 aboveground green web. In a clear perturbation of the detrital web, Hoekman et al. (2011) added

540 midge (Diptera: Chironomidae) carcasses to small (1x1-m) open plots for two years or over a

541 single year starting at different times. Collembola, larval Diptera, and Coleoptera exhibited

542 varying positive responses, but spiders showed no treatment effect, most likely because the plots

543 were small and open to migration. Oelbermann et al. (2008) directly manipulated energy input to

544 the detrital web in fenced 5-m^2 plots for five months. Many Collembola families responded

545 positively as did total spider numbers, which were ca. 2x higher in the detritus-enhanced plots.

24

546   Some spiders, though, exhibited no numerical response even though stable-isotope analysis

547   revealed that all sampled spiders relied more heavily on the decomposer food web in the detritus-

548   addition plots. Oelbermann et al. (2008) suggested that even though the secondary-consumer

549   trophic level was strongly linked to the detritus base, individual groups of predators showed

550   inconsistent evidence of bottom-up control due to increased cannibalism and intraguild predation

551   in the plots with additional detritus.

552

553   **Forests –** Because of differences between grasslands and forests in rates of litter production,

554   litter quality, and litter decomposition, experiments in forests are more comparable to ours.

555   Scheu and Schaefer (1998) and Maraun et al. (2001) increased microbial growth in the litter

556   layer of fenced 1-m^2 plots by adding glucose and nitrogen for 15 months with no effect on

557   millipedes, isopods, Collembola, or centipedes of the litter layer. In contrast, Collembola and

558   centipedes of the lower soil horizon responded negatively, most likely due to indirect effects of

559   increased earthworm densities (Scheu & Schaefer 1998; Maraun et al. 2001). We did not sample

560   lower soil layers and in our forest earthworms appear to be much less abundant than in the

561   German beech forest on limestone (Göttinger Wald) where these studies were conducted (pers.

562   obs., Kentucky and German sites). Salamon et al. (2006) also uncovered possible indirect

563   negative effects of increased earthworm activity on centipede densities in a 17-month field

564   experiment with fenced 1-sq m plots. Several Collembola families did respond positively to an

565   enhanced resource base, with effect sizes similar to those observed by CW99. In contrast,

566   pseudoscorpions and spiders did not respond. Thus, in the experiment of Salamon et al. (2006)

567   bottom-up control was not pervasive because it did not propagate to the next trophic level. Raub

568   et al. (2014) also concluded that bottom-up control, although present, was weak and not

25

569   pervasive. Every two weeks they added the same type of artificial detritus used by CW99 and in

570   this experiment to 1.5 x 1.5-m unfenced plots for 3 months. Collembola numbers displayed a

571   clear positive response to resource enhancement, but total predators (spiders, pseudoscorpions,

572   and centipedes combined) did not increase. Lessard et al. (2011) found evidence of even weaker

573   bottom-up control in a 3-month press perturbation with 4-sq m open plots spaced 2-m apart. This

574   was possibly due to increased densities of predaceous ants in the resource-addition treatment

575   (Lessard et al. 2011) and perhaps also because migration swamped treatment effects because the

576   open plots were close together.

577

578   ## Comparison with experiment of Chen and Wise 1999 (CW99)

579

580   None of the above experiments produced evidence of bottom-up control as strong and pervasive

581   as the bottom-up *limitation* [*sensu* Osenberg & Mittelbach (1996)] of both primary and

582   secondary consumers found in the short-term experiment upon which the current study was

583   based (CW99) (Fig. 4B). Why do the results of our experiment differ from those of CW99? The

584   difference is not due to differences in statistical power, which was similar (20 experimental units

585   in both experiments). Because statistical interactions with fencing were infrequent in our

586   experiment, most tests for the effect of detrital supplementation were based upon 10 replicates

587   per Resource level, the same as CW99. Most critical is the need to explain why our study did not

588   reveal continued bottom-up control over three years by the same taxonomic groups that showed

589   such a clear response after 3.5 months of detrital addition in CW99 (Fig. 4A, B). Below we

590   evaluate the possible influence of several factors.

591

26

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)

27

615   microbi-detritivores showed a strong response to resource supplementation in open 1-m^2 plots in

616   an earlier experiment in the same forest (Chen & Wise 1997); and (3) the absence of consistent

617   and strong Fencing x (Resource x Year) interactions suggests that migration across open plot

618   boundaries did not strongly dilute or increase the responses of most taxa to effects of detrital

619   supplementation.

620

621   **Rates of detrital supplementation –** The rate of detritus addition in Year 1 was

622   approximately one-fourth that employed by CW99. This difference correlates well with the

623   fewer number of positive responses in the fall of Year 1 compared with the fall of CW99 (6

624   versus 14, respectively; Fig. 4A versus Fig. 4B) and with the increased intensity of positive

625   responses in our experiment across summer and fall of Year 2, after we had increased our

626   supplementation rate 4x to match CW99 more closely. Biweekly rates of detrital

627   supplementation were the same in Years 2 and 3 and were similar to CW99, yet the patterns of

628   response in both years differed markedly from each other and also from CW99. One factor that

629   likely contributes to these differences is variation in rainfall between experiments and between

630   years 2 and 3 of our experiment.

631

632   **Variation in rainfall –** Rainfall was 35% above the long-term average during CW99, in

633   contrast to close-to-normal levels during Years 1 and 2 of our experiment (Lawrence 2000). Year

634   3 rainfall was markedly less, ca. 50% lower than the first two years. Higher rainfall may have

635   accelerated fungal growth in the leaf litter in the short-term experiment of CW99, intensifying

636   the effect of the detrital subsidy compared to all three years of our experiment. Lower rainfall in

637   Year 3 could explain why densities of three Collembola families — Onychiuridae, Isotomidae,

28

638 and Tomoceridae — had declined to near zero in both Ambient and Supplemented plots by the

639 fall of Year 3; and why Sminthuridae showed no response to additional detritus, in contrast to its

640 positive response the previous year (Christiansen 1964; Hopkin 1997; Petersen 2002). In contrast

641 to this pattern, however, hypogastrurid Collembola responded strongly and positively to

642 Resource supplementation throughout Year 3 — and only in Year 3. This response may have

643 been due to release from competition with the Collembola families that had declined in the

644 Supplemented plots by the end of Year 3. Several long-term studies suggest that strong biotic

645 interactions influence Collembola densities, particularly in forests (Chernova & Kuznetsova

646 2000; Kampichler & Geissen 2005; Kuznetsova 2006; Takeda 1987; van Straalen 1985; Vegter

647 1987; Wolters 1998). However, direct experimental evidence is lacking for resource competition

648 or apparent competition due to shifting predation pressures between Collembola families.

649 A long-term experiment is more likely than a short-term study to reveal effects of

650 temporal variation in abiotic factors on bottom-up control processes. The variability in responses

651 to the addition of detritus during our 3-year experiment reflects the range of outcomes across the

652 entire set of similar previously published experiments. CW99 uncovered strong bottom-up

653 control of all sampled primary consumers accompanied by increased densities of the major

654 predatory taxa. This pattern is not typical. The strong responses in CW99, consistently positive

655 and pervasive across trophic levels, were likely due to the higher-than-average rainfall that year

656 and an amount of high-quality detritus that could serve as a substrate for extensive fungal

657 growth. The fact that the experiment lasted only 3.5 months instead of several years increased

658 the probability that a simple pattern of responses would be detected.

659 The entire body of evidence, however, is not consistent with the interpretation that all

660 examples of weak, intermittent or no bottom-up in our long-term experiment were caused solely

29

661   by changes in abiotic conditions that retard fungal growth. Fungal hyphae in the leaf litter were

662   3x more abundant in Supplemented than Ambient plots at the end of the experiment, when

663   rainfall was the lowest, (though data are not available for fungal densities the first two years)

664   More importantly, responses of several taxa clearly were opposite to bottom-up control.

665   Variation in rainfall cannot explain these patterns.

666

667   **Approach to a differently configured equilibrium state? –** It is possible that long-term

668   resource supplementation leads to a community configuration that cannot be predicted from

669   initial short-term population responses. In other experiments populations sometimes declined in

670   response to resource supplementation, e.g. two spider families in a grassland (Fountain et al.

671   2008), and Collembola and centipedes at lower soil depths in two forest experiments (Maraun et

672   al. 2001; Scheu & Schaefer 1998). Negative effects in the cited forest experiments likely were

673   caused by disturbances caused by increased earthworm densities. In grasslands some negative

674   responses, and also the failure of some populations to increase in response to detrital addition,

675   could have been caused by shifting strengths of intra-guild predation and cannibalism among

676   generalist predators that altered the strength of top-down control of selected taxa at lower trophic

677   levels (Oelbermann et al. 2008). Such shifting predation pressure could explain some of our

678   results, such as lower numbers of Lepidoptera larvae in response to higher numbers of carabid

679   beetles, and lower densities of web spiders and pseudoscorpions in Supplemented plots at the

680   end of the experiment due to increased predation from elevated numbers of carabid beetles and

681   cursorial spiders. Other interpretations are also possible. An alternative explanation for the latter

682   two examples would be declining numbers of high-quality prey (Tomoceridae) (Toft & Wise

683   1999b) and increased densities of possibly toxic isotomid (Toft & Wise 1999a; Toft & Wise

30

684   1999b) and hypogastrurid prey (Messer et al. 2000; Negri 2004) in Years 2 and/or 3 in the

685   Supplemented plots. It is difficult to evaluate the solidity of such post-hoc theorizing without

686   additional information.

687

688   ## Towards a deeper understanding of bottom-up control in detrital food webs

689

690   Clearly variation in abiotic factors and biotic interactions can alter the strength and

691   pervasiveness of bottom-up control among different trophic groupings. In detrital food webs a

692   weak positive and/or no response to resource addition is expected if drought impedes fungal

693   growth. It is the negative responses that at more difficult to interpret. Do they reflect the play of

694   top-down control processes expressed differentially along a subset of interaction pathways and if

695   so, do the negative responses signal an approach to a new equilibrium community? One would

696   predict that such compensatory responses are more likely to appear in experiments of longer

697   duration. However, could relatively uncommon negative responses in long-term experiments

698   simply be random vagaries emerging from the low replication in most field experiments? Or

699   might they be the surprising results that ecologists often fail to report (Doak et al. 2008) — the

700   unexpected observations that can help build stronger theory? More long-term experiments will

701   help resolve this dilemma.

702   How long is long enough? The behavior of mathematical models of long-term press

703   perturbations suggests that many generations will be required to reach a new equilibrium

704   (Bender et al. 1984; Raffaelli & Moller 2000; Yodzis 1988), which coupled with environmental

705   noise might make the prospects of a "long-enough" field experiment seem hopeless. However,

706   after reviewing short- and long-term experiments (2 to 31 mos.) in the intertidal, Menge (1997)

31

707 concluded that ". . . community dynamics may be more predictable than expected . . ." because

708 most indirect effects had appeared half-way through the experiment. "Long enough" is at least

709 the number of generations sufficient to reveal indirect effects. An even longer time would reveal

710 how close the community may be to a new equilibrium. This longer time will never be achieved

711 with certainty, but snapshots yielded by short-term experiments cannot answer the question.

712   Simply advocating experiments of longer duration is not enough. Even in long-term

713 experiments we need to reduce the impact of unpredictable and unknown variation in other

714 factors. Furthermore, we must have a deeper understanding of which interaction pathways were

715 altered, and how much, in response to resource supplementation. How might these two

716 challenges be met?

717   The first challenge can be addressed by expanding the experimental design. A critical

718 design element lacking in field experiments to date is the initiation of resource additions in new

719 sets of experimental units in each subsequent year after the first perturbation. Phased temporal

720 replication of the experimental perturbation offers the surest way of clearly separating effects

721 due to time lags from those due to changing levels of unknown but influential abiotic and biotic

722 factors. Hoekman et al. (2011) employed a preliminary but elegant version of this approach by

723 combining two yearly pulse treatments of detritus addition with a two-year press treatment.

724   The second challenge can be met in several ways. One is the use of path analysis and

725 structural equation modeling to help separate direct and indirect effects among interaction

726 pathways between taxa in major trophic groupings in the food web (Grace 2006; Wootton 1994).

727 However, this statistical modeling approach requires numerous replicates, more than are possible

728 with most types of detrital enhancement experiments performed to date. Tradeoffs between too-

729 many response variables, too-few replicates, and experimental units too small to be realistic

32

730   present daunting challenges. The other approach is to measure more variables than just the

731   densities of primary consumers and their predators. Molecular techniques are available to

732   measure different functional categories of fungi (Nguyen et al. 2016; Shokralla et al. 2012).

733   Shifts in major trophic pathways can be revealed by techniques such as stable isotopes and fatty

734   acid analysis (Halaj & Wise 2002; Ruess et al. 2004), and PCR of prey DNA in guts of predators

735   such as spiders and carabids (Harper et al. 2005; Symondson 2002).

736   Some of the above suggestions already have been incorporated into short-term field

737   experiments testing for bottom-up control in detritus-based terrestrial food webs. Utilizing all of

738   them in a single study is a challenge. Nevertheless, paying heed to their advantages when

739   planning future long-term research would help reveal likely causes of the type of variability

740   found in our 3-yr experiment.

741

742   ## Acknowledgements

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Figures 1-4
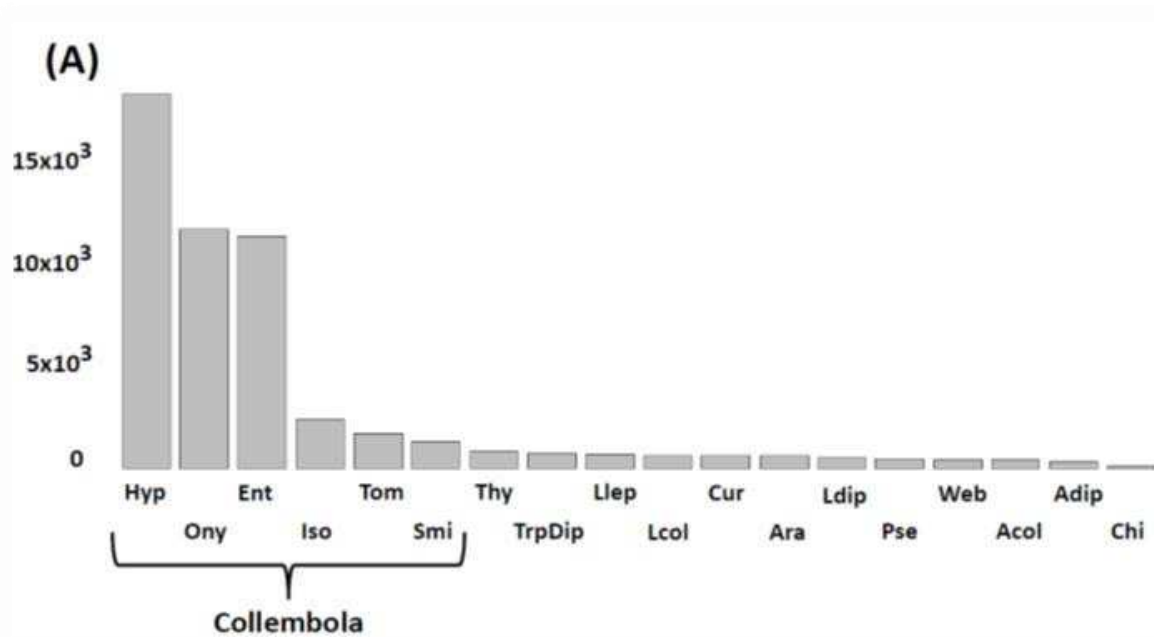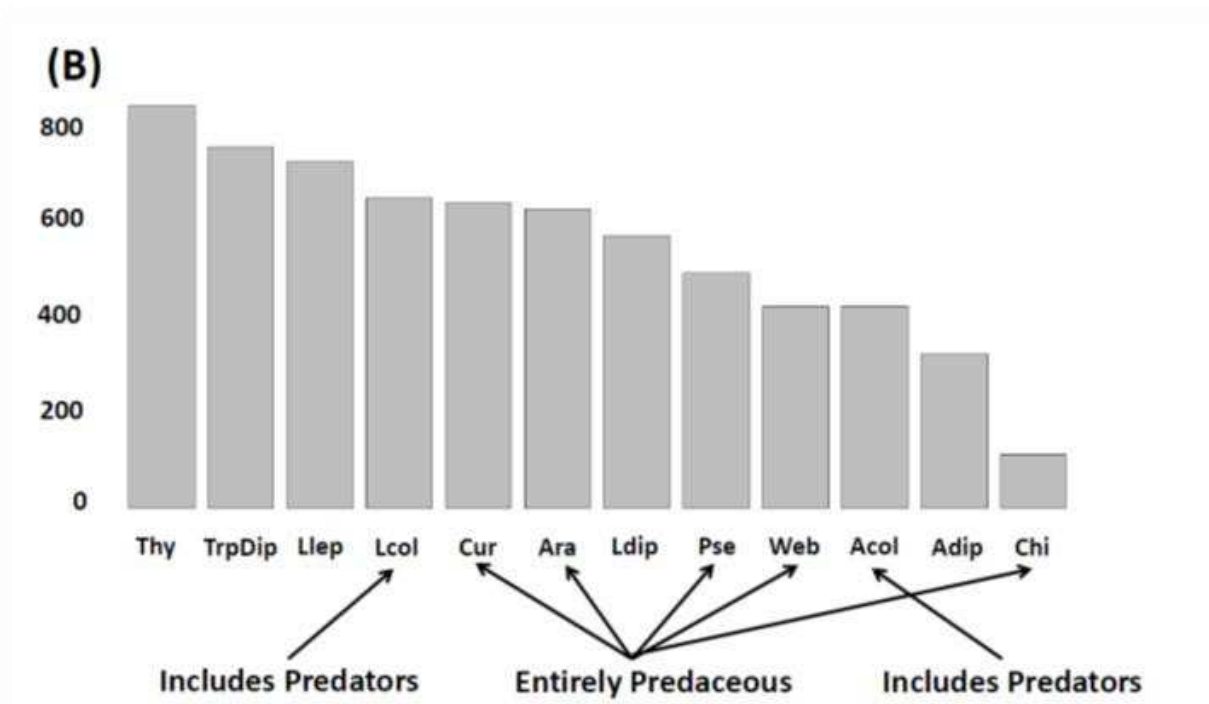
Figure 1. **N** (ordinate) = total number extracted, encountered in litter sifting, or trapped during the experiment. Response variables (combinations of taxa and sampling methods) pooled across treatments, seasons. and years. **(A)** All response variables ($N = 18$); **(B)** Non-Collembola response 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.
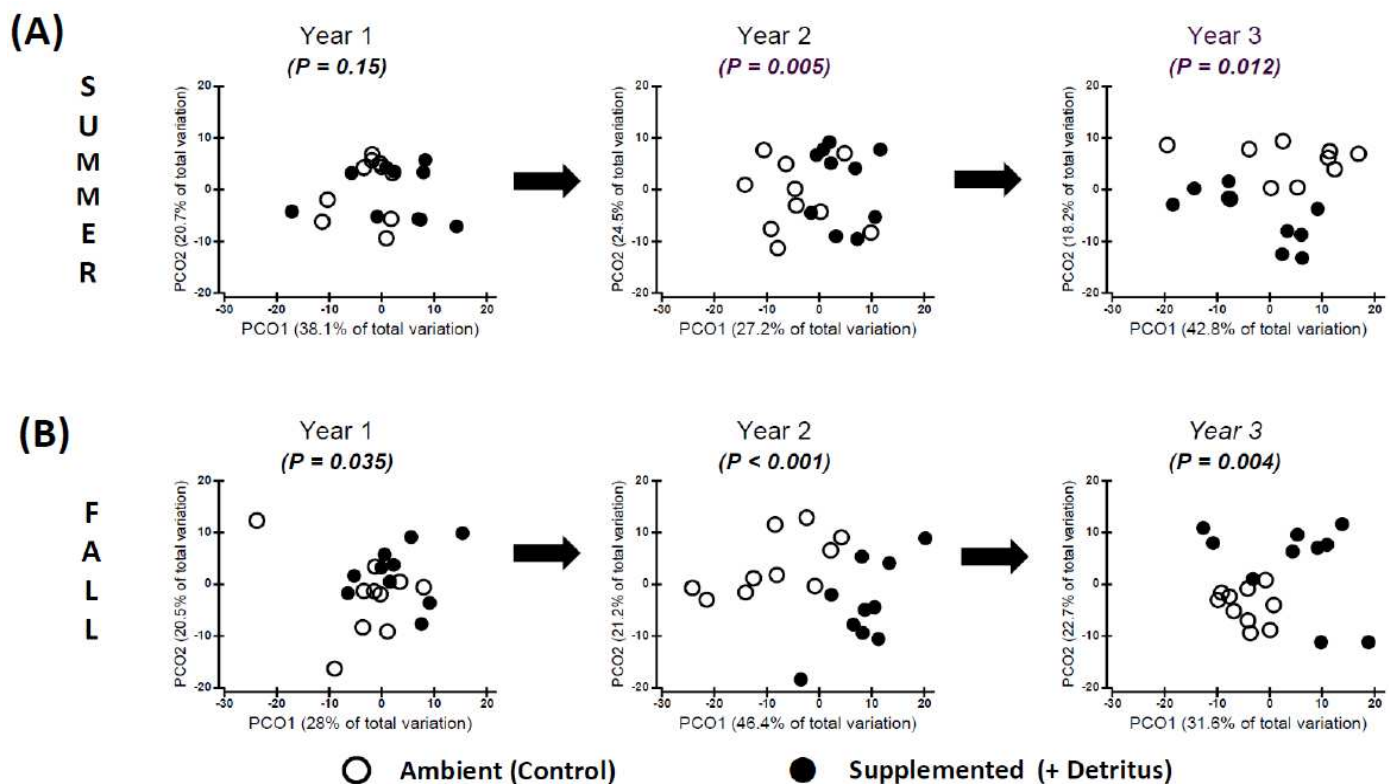
Figure 2. Changing impact over time of detritus addition upon arthropod community structure. Principal Coordinates Ordinations (PCO on Gower's distance measure; Appendix S2) presented separately for **(A)** SUMMER and **(B)** FALL because P[(Resource x Year) x Season] = .039 (Table A3.2 in Appendix S3). 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.
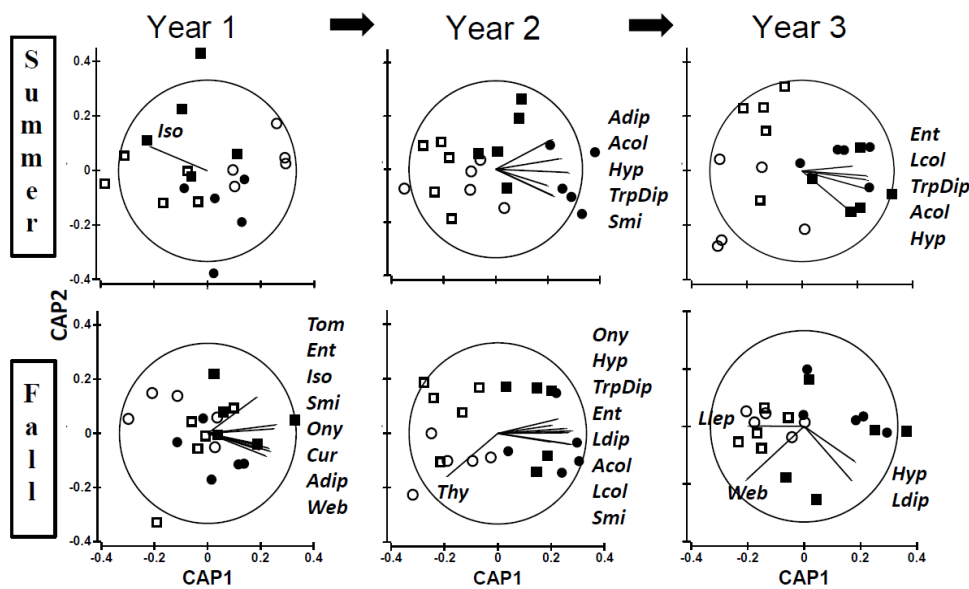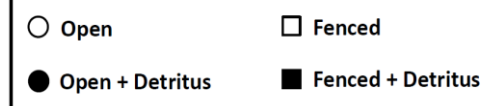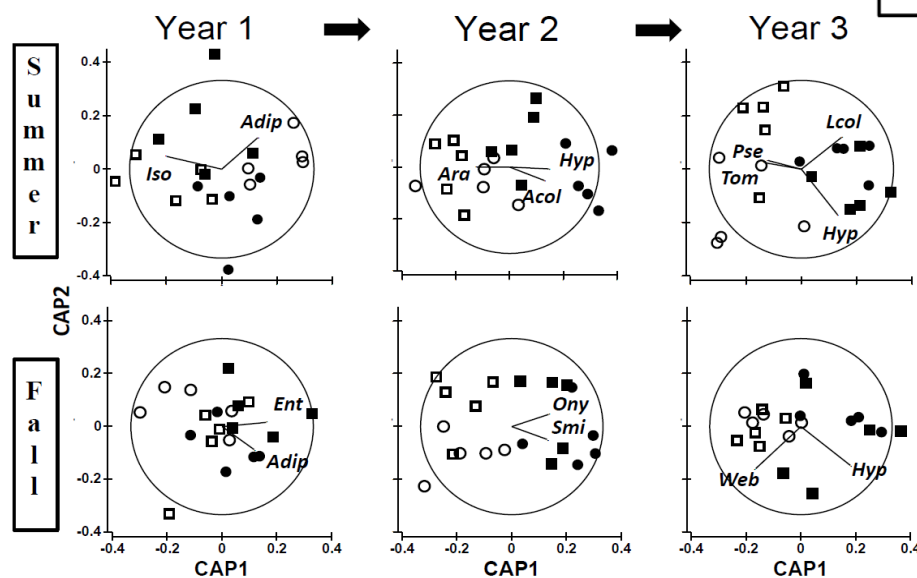
Figure 3. **(A)** Constrained ordination (CAP; Resource and Fencing are the constraining factors) with vector overlays representing simple ***Spearman correlations*** between response variables and the two axes (Appendix S2). Except for Summer of Year 1, separation of communities along axis 1 (CAP1) 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 $\geq$ .50 or $\leq$ -.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						(B) Chen and Wise (1999)
	YEAR 1		YEAR 2		YEAR 3		FALL
	Summer	FALL	Summer	FALL	Summer	FALL	FALL
Detritivores/Fungivores:							
Hypogastruridae (Hyp)					↑ (>3x) F	↑ (>3x)	↑ (>3x)
Onychuridae (Ony)		↑ (~2x)		↑ (~2x)		0	↑ (~2x)
Entomobryidae (Ent)		↑ (>3x)	↑ (~1.5x)	↑ (>3x)	↑ (~2x)	↑ (>3x)	↑ (>3x)
Isotomidae (Iso)				↑ (~2x) F		0	↑ (>3x)
Tomoceridae (Tom)		↑ (~2x) F			⇩ (~0.5x)	0	↑ (>3x)
Sminthuridae (Smi)			↑ (>3x)	↑ (~2x)			↑ (~2x)
Diptera Larvae (Ldip)							N/A
Diptera Adults (Adip)							N/A
Diptera Adults (TrpDip)		↑ (~1.5x)	↑ (~2x)	↓ (~0.75x)	↑ (~2x)	↓ (~0.75x)	↑ (~2x)
Lepidoptera Larvae (Llep)	⇩ (~0.5x) O			⇩ (~0.5x) F		⇩ (~0.5x) F	N/A
Thysanoptera (Thy)							N/A
Mixed Trophic Levels:							
Coleoptera Larvae (Lcol)			↑ (~1.5x)	↑ (>3x)	↑ (~2x)		↑ (~2x)
Coleoptera Adults (Acol)	↑ (~1.5x)	↑ (>3x)	↑ (~1.5x)	↑ (>3x)	↑ (~1.5x)		↑ (~2x)
Predators:							
Cursorial Spiders (Cur)	↑ (~1.5x)		↑ (~1.5x)		↑ (~1.5x)		↑ (~2x)
Total Spiders (Ara)							↑ (~2x)
Pseudoscorpiones (Pse)			⇩ (~0.5x)		⇩ (~0.5x)	⇩ (~0.5x) F	↑ (~2x)
Web Spiders (Web)		↑ (~2x)		↑ (~1.5x)			↑ (~2x)
Chilopoda (Chi)							↑ (~2x)

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 ≈ 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.