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Responses of forest-floor fungivores to experimental food enhancement

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Summary. We conducted a field experiment to test the hypothesis that populations of fungivorous arthropods in forest litter are food limited. The experiment was carried out in a secondary mixed forest in Madison County, Kentucky, USA. Sliced mushrooms and potatoes, and dry instant *Drosophila* medium were added to the litter layer of four 1 – m² open plots for 2 months starting in April, 1995. Eight similar open plots served as controls. Mites and Collembola were the two most abundant microarthropods. Mite density was more than 1.5× higher in the food-enhancement plots. Total Collembola density was 3–4 times higher. Most collembolan families showed density increases. A major factor contributing to the increase in density of Entomobryidae was apparently higher rates of reproduction and/or juvenile survival in the treatment plots. The relative activity of most collembolan families was lower in the food-enhancement plots. Sticky trap samples revealed that the relative density of adult fruit flies and fungus gnats just above the litter layer also increased in response to enhanced food levels. These responses support the hypothesis that many populations of fungivorous arthropods in the detrital food web of forest litter are food limited.

Key words: Population density, food limitation, leaf litter, field experiment, Collembola, mites, Diptera

Introduction

Theoretical arguments suggest that in general, detrital food webs are strongly donor-controlled (e.g. Hairston et al. 1960; Pimm 1982). If this hypothesis is true, populations of lower trophic levels of the forest-litter detrital food web should be food limited; in particular, fungivore populations should increase in response to enhancement of their resource base. Several lines of indirect evidence that fungivorous arthropods experience food shortages support the hypothesis that a scarcity of food often limits their population densities.

Data on the feeding behavior and distribution patterns of Collembola constitute one type of evidence that forest-floor fungivores are food-limited. Although Collembola can feed on a wide range of foods, their main food is fungal material (Peterson 1971; Chen et al. 1996). Laboratory feeding experiments indicate that Collembola prefer fungi over plant materials, yet field-collected Collembola contain a high proportion of leaf materials, which suggests a scarcity of preferred fungal food in the field (Knight and Angel 1967). Plant debris in col-

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lembolan guts may have been ingested by accident or may serve as a secondary food source (Chen et al. 1996). Collembolans aggregate around food sources (Usher et al. 1982), and apparently suffer temporary starvation as indicated by a high percentage of field-collected individuals with empty guts (Joosse and Testerink 1977).

The majority of mites in the litter layer are fungivorous (Luxton 1982). Food availability affects mite survival, suggesting that food is an important factor limiting population densities of mites (Stefaniak and Seniczak 1981). A tight coupling between the distribution of fungi and fungivorous mites is found in some agroecosystems, which also suggests food limitation (Mueller et al. 1990). Many Diptera not only feed on, but also breed in, fleshy fungi (Buxton 1960; Hackman and Meinander 1979). At natural densities, mushroom-inhabiting dipteran larvae can experience a shortage of food, since food supplementation increases pupal size (Grimaldi and Jaenike 1984).

We added readily accessible, high-quality food to field plots to uncover direct responses that would support the hypothesis that populations of fungivorous arthropods in forest litter are food limited.

Materials and Methods

The experiment was conducted in Madison County, Kentucky, USA, in a secondary mixed forest dominated by oak, hickory and maple, with a few scattered pine trees. Experimental units were 12 open, circular 1-m^2 plots separated from each other by at least 15 m. There were four Food Enhancement and eight Control plots arranged in a completely randomized design. The number of controls was 2× the number of manipulated plots because an intended treatment – water addition – was eliminated due to higher-than-average rainfall. Starting 11 April 1995 and continuing at two-week intervals, the Food Enhancement plots received 100 g sliced mushrooms, 100 g chopped potatoes and 20 g dry, instant *Drosophila* medium (Carolina Biological Supply; Burlington, North Carolina, USA; Formula 4-24). Preliminary field and laboratory observations showed that a wide range of collembolan species readily fed on these foods.

Densities of Collembola and mites were determined by collecting one 180-cm^2 sample of litter (top and fragmented, but not humus, layers) from each plot, and extracting microarthropods for 7 days in a modified Kempson-Macfadyen apparatus (Kempson et al. 1963; Schauermann 1982). Animals were extracted into 50 % ethylene glycol and washed in 95 % ethyl alcohol prior to identification. Plots were first sampled 4 weeks after the start of the experiment (6 May), and again on 23 June. Mites were not identified further, but Collembola were identified to family level according to Christiansen and Bellinger (1981). Entomobryidae were further identified to Entomobryinae and Tomocerinae; springtails in these subfamilies were further separated as adults or immatures. After animals were extracted, the litter was dried at 60 °C for 3 d and then weighed.

The activity of surface-dwelling Collembola was assessed with 8.5-cm diameter live pitfall traps. Four traps were installed 20 cm inside the edge of each plot. Animals were returned to the plots after being identified. To minimize predation on Collembola in the traps, the inner cup was separated into two levels by a fine screen, which allowed collembolans to fall through to the lower level, but excluded the larger predacious arthropods (mainly spiders, beetles and centipedes). Three days before the first food addition, traps were opened twice (24 hrs. each time) to assess the initial activity of Collembola. During the experiment traps were opened for five additional 24-h periods. An index of relative activity was calculated for the date corresponding to each litter extraction sample by dividing the numbers trapped by the numbers extracted from the litter sample from each plot. Since we did not have trap data for the 6 May litter-extraction sample, the means of the two adjacent pitfall-sampling dates (30 April and 12 May) were used for the calculation.

Relative densities of Diptera were estimated by sticky traps. Two vertically oriented 10-by-10 cm pieces of metal screening, coated on both sides with Tanglefoot (The Tanglefoot Co.; Grand Rapids, Michigan, USA.) were placed 20 cm apart just above the litter layer at the center of each plot. Plots were sampled for 24 h 6–7 May and 23–24 June. Treatment effects were analyzed by repeated-measures ANOVA (SAS Institute 1990). When necessary, data were square-root or log-transformed to make variances homogenous. Because we predicted that food enhancement should increase fungivore densities and reduce Collembola activity, one-tailed tests were used. For each sampling method, there were several variables tested simultaneously in comparison of Food Enhancement and Control plots. We used the sequential Bonferroni method to control the table-wide type-I error rate (Rice 1989).

Results

Mites and Collembola were the two most abundant arthropods extracted from the litter samples, representing 81 % and 13 %, respectively, of total arthropods for Control plots. Adding food significantly increased densities of both groups (Figs. 1; Table 1). Mite density in the Food Enhancement plots was more than 1.5× higher than Control plots in both May and June (Fig. 1A). The Food Enhancement treatment elevated total Collembola density 3–4 times (Fig. 1B).

Densities of several Collembola families – Entomobryidae, Isotomidae and Hypogastruridae – were higher in the Food Enhancement plots. Although densities of Onychiuridae, Sminthuridae and Neelidae were also higher in experimental plots, differences between Food Enhancement and Control plots were not statistically significant. Density increases for both Entomobryinae and Tomocerinae were due mainly to elevated numbers of immature individuals (Figs. 2; Table 1).

Numbers from pitfall-trap samples did not differ significantly between Control and Food Enhancement plots for any collembolan group ($P > 0.05$, sequential Bonferroni correction). Sampling by pitfall traps yielded different proportions of collembolan families compared to the litter-extraction samples. Hypogastrurids were the most abundant Collembola in the pitfall samples, accounting for more than 80 % of total Collembola from Control plots. Sometimes several thousand hypogastrurids were found in a single pitfall trap. Onychiurids were the least abundant, accounting for less than 0.5 % of total Collembola from Control plots.

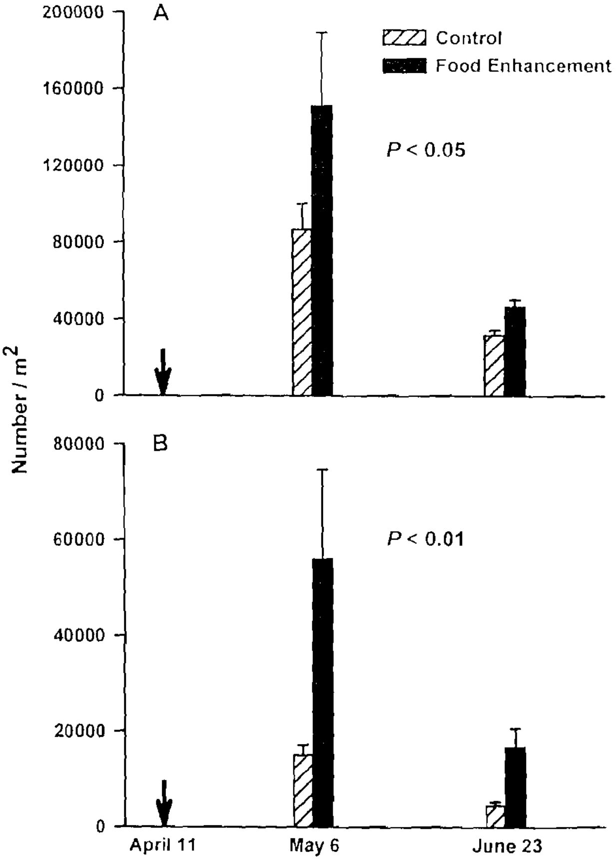

Fig. 1. Microarthropod densities (mean ± standard error) from litter extractions. Arrow indicates the date food additions were started. P value represents significance of treatment effect of repeated-measures ANOVA, adjusted by the sequential Bonferroni method. A: Mites; B: Collembola

Table 1. Density (mean number/m^2 ± standard error) of microarthropods and litter weight (mean g/m^2 ± standard error). Significance of between-subjects (treatment) effect determined by repeated-measures ANOVA for the litter-extraction samples

	Control		Food Enhancement		P (one-tail: non-adjusted)	Adjusted P value, sequential Bonferroni method
	6 May	*23 June*	*6 May*	*23 June*		
Total Collembola	14,900 ± 2,070	4,310 ± 800	55,900 ± 18,900	16,500 ± 4,060	0.0001	**
Entomobryidae	3,240 ± 700	3,250 ± 640	5,500 ± 1,050	9,710 ± 1,430	0.0001	**
Entomobryinae	2,910 ± 610	2,940 ± 610	4,710 ± 1,150	7,000 ± 750	0.0004	**
Adult	160 ± 70	120 ± 70	220 ± 40	180 ± 50	0.1343	NS
Immature	2,750 ± 550	2,820 ± 540	4,490 ± 1,130	6,820 ± 720	0.0003	**
Tomocerinae	330 ± 110	300 ± 90	790 ± 220	2,710 ± 1,550	0.0062	*
Adult	70 ± 30	100 ± 40	140 ± 50	200 ± 40	0.0199	NS
Immature	260 ± 90	200 ± 60	650 ± 200	2,510 ± 1,490	0.0013	*
Isotomidae	960 ± 220	150 ± 50	2,610 ± 570	1,380 ± 790	0.0005	**
Hypogastruridae	780 ± 230	70 ± 30	21,310 ± 20,100	640 ± 190	0.0045	*
Sminthuridae	680 ± 200	210 ± 60	1,260 ± 310	790 ± 470	0.0655	NS
Onychiuridae	9,190 ± 1,430	600 ± 220	24,920 ± 11,390	3,610 ± 1,570	0.0213	NS
Neelidae	60 ± 40	30 ± 20	260 ± 250	380 ± 230	0.0204	NS
Mites	86,530 ± 13,450	31,320 ± 2,720	150,920 ± 38,230	46,110 ± 3,790	0.0051	*
Litter Weight	560 ± 50	470 ± 40	620 ± 30	490 ± 50	0.4599	NS

The Date x Treatment interaction was not significant in any of the tests; d.f. = 1 for treatment effect; d.f. = 10 for error; **: $P < 0.01$; *: $P < 0.05$; NS: $P \geq 0.05$

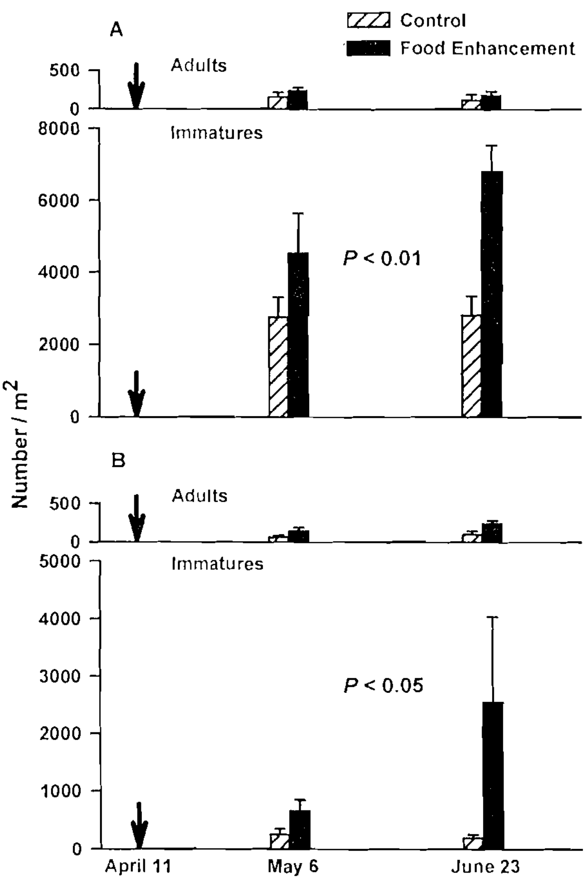

Fig. 2. Densities of some surface-dwelling Collembola (mean ± standard error) from litter extractions. Arrow indicates the date food additions were started. P value as Fig. 1.
A: Entomobryinae; B: Tomocerinae

Relative activity of all collembolan groups except Sminthuridae was significantly lower in the Food Enhancement plots (Figs. 3, 4; Table 2). Both adult and immature Entomobryinae and Tomocerinae had a lower relative activity in Food Enhancement plots (Figs. 4; Table 2).

Fruit flies (mainly Drosophilidae) and fungus gnats (Mycetophilidae and Sciaridae) were the two major dipteran groups caught on the sticky traps. Numbers of fruit flies were 20× higher in Food Enhancement than Control plots in May, and 5× higher in June (Fig. 5A). Fungus gnats did not differ between treatments in May, but in June were twice as high in Food Enhancement plots (Fig. 5B).

During the experiment we added a total (dry weight) of 53 g mushrooms, 184 g potatoes and 80 g *Drosophila* medium into each Food Enhancement plot. We did not remove food remnants from litter samples when we weighed them. Differences in litter weight between the treatments were never statistically significant (Table 1).

Discussion

The experiment uncovered direct responses to food enhancement, which support the hypothesis that fungivore populations in the detrital food web of the leaf-litter community are food limited. Enhancing the resource base increased densities of entomobryid, hypogastrurid and

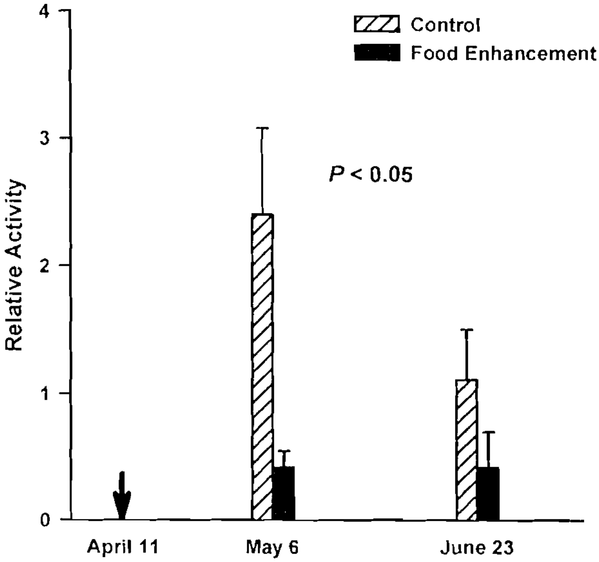

Fig. 3. Relative activity of total Collembola (mean ± standard error). Arrow indicates the date food additions were started. P value as Fig. 1

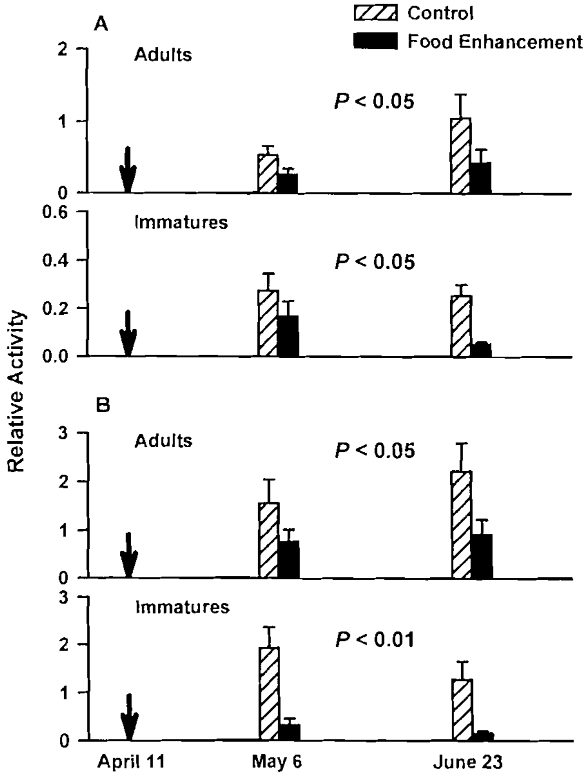

Fig. 4. Relative activity of some surface-dwelling Collembola (mean ± standard error). Arrow indicates the date food additions were started. P value as Fig. 1.
A: Entomobryinae; B: Tomocerinae

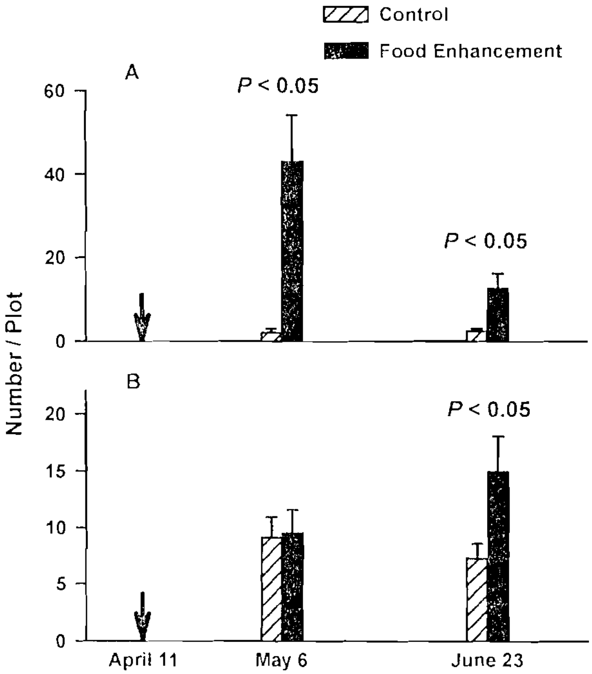

Fig. 5. Flying insects (mean ± standard error) from sticky traps. Arrow indicates the date food additions were started. The Date x Treatment interaction was significant for both fruit flies and fungus gnats. P value represents significance of t-test for individual sample date, adjusted by the sequential Bonferroni method.
A: Fruit flies; B: Fungus gnats

Table 2. Significance of the between-subjects (treatment) effect determined by repeated-measures ANOVA for relative activity of Collembola

	P (one-tail; non-adjusted)	Adjusted P value, sequential Bonferroni method
Total Collembola	0.0047	*
Entomobryidae	0.0028	*
Entomobryinae	0.0023	*
Adult	0.0123	*
Immature	0.0035	*
Tomocerinae	0.0018	*
Adult	0.0200	*
Immature	0.0007	**
Isotomidae	0.0011	*
Hypogastruridae	0.0002	**
Sminthuridae	0.2032	NS

The Date x Treatment interaction was not significant in any of the tests; ** P < 0.01; * P < 0.05; NS: P ≥ 0.05; d. f. = 1 for treatment effect; d. f. = 10 for error

isotomid Collembola at least twofold during the 2.5-month experimental period; some exhibited a tenfold increase. Densities of Onychiuridae, Sminthuridae and Neelidae were not significantly affected, though numbers were also higher. The experimental design may not have had enough power to detect differences for these families because of their high variances. We simultaneously conducted many statistical tests and used the sequential Bonferroni test to adjust our P values, which further reduces the power to detect differences. Detrital food webs are based primarily on dead plant materials (Swift et al. 1979). In decomposition food webs, fungi and bacteria provide most of the energy and nutrition to microarthropods (Moore et al. 1988). These microbes are not always available and/or accessible to the fungivorous and bacterivorous arthropods (Seastedt 1984). Not all of these microorganisms are suitable food for arthropods; some are even toxic to collembolans. Most collembolan species show strong food preferences in laboratory studies (Shaw 1985; Visser and Whittaker 1977), and have different rates of growth and reproduction when fed on different foods (Chen et al. 1995; Usher 1985; Walsh and Bolger 1990). Although we did not compare the palatability of the foods used in this experiment with litter fungi, preliminary field and laboratory observations showed that a wide range of collembolan species readily feed on these foods. The preferred fungi for collembolans usually are also non-toxic to humans and other animals (Shaw 1988). These findings and our experimental results strongly suggest that both the quantity and quality of food in the field have a significant impact on collembolan densities. Seastedt et al. (1988) reported an increase of microarthropod density in response to adding carbon or nitrogen to the tallgrass prairie; they did not measure which food resources were enhanced.

Although the total dry weight of food added to the plots was more than half of the litter weight, litter weights never differed between treatments. Some of the food was consumed by the fungivores, and some likely leached into humus and mineral layers. The rapid disappearance of the food suggests that the food addition did not substantially change litter structure in the Food Enhancement plots.

Because our plots were open, increased densities in the Food Enhancement treatment could have resulted from higher immigration rates, and/or lower rates of emigration, rather than or in addition to higher rates of survival and/or reproduction. If the density increase were due primarily to increased colonization of the experimental plots, we would expect that any increase in adult numbers in the Food Enhancement plots would be at least the same as, or more than, the increase in immatures. However, numbers of adult Entomobryinae did not differ between treatments, but immatures were significantly more abundant in the Food Enhancement plots. For Tomocerinae, adult density was 2× higher in the experimental plots, but immature density increased more than 6× in response to additional food. These results suggest that the density increase in Food Enhancement plots was due mainly to higher reproductive rates and/or higher immature survival rates. Laboratory studies have shown that Collembola fed high nutritional foods display elevated reproductive rates (Booth and Anderson 1979). Most entomobryids have only 1–2 generations per year under stable environments like forests (Huhta and Mikkonen 1982; Leinaas and Bleken 1983; Vegter 1988). Under field conditions the juvenile stage lasts about 3 months (Joosse 1969). Our experiment did not last long enough to detect the consequence of elevated immature numbers. A longer experiment likely would have detected a significant increase in adult density.

Some collembolans, such as isotomids and onychiurids, can move between litter, humus and mineral layers (Macfadyen 1962; Usher 1970). The density of isotomids and onychiurids increased in response to food enhancement in our experiment. The density increase in the litter layer could have been due to higher survival and reproductive rates in the litter layer, and/or increased rates of migration from the humus and mineral soil layers into the litter layer. We cannot evaluate this possibility because we did not sample the humus and mineral soil, although we expect that food added to the litter would leach into humus and mineral layers and increase the densities of collembolans in these layers. It would be worthwhile to investigate further the effects of enhanced food on the dynamics of Collembola populations in the humus and mineral soil.

McNamara and Houston (1994) predict that under high food availability, animals will reduce their activity if mortality from predation increases with increased activity. A wide range of animals in the forest floor, including spiders, centipedes, pseudoscorpions, predacious beetles and mites, prey upon collembolans. Joosse (1981) reported that higher activity of Collembola leads to increased mortality from predation. Consistent with these theoretical predictions and the known increased predation risk from increased activity, all groups of Collembola except Sminthuridae reduced their relative activity in the Food Enhancement plots.

Sminthuridae is the only collembolan group that did not increase in density or reduce its activity. Possibly this group was not food limited. Also, the possibility exists that for Sminthuridae, risk of predation is independent of activity, so it might not reduce its activity in response to the food increase. Some sminthurid species even have increased their density in litter-removal experiments (Betsch 1991; Ponge et al. 1993).

A wide range of flying insects in the forest are fungal feeders (Hammond and Lawrence 1989). These fungivores are generally very polyphagous (Hanski 1989). Competition for resources may occur among dipteran larvae (Russell-Smith 1979), leading to reduced pupal and adult size, and hence reduced female fecundity (Grimaldi and Jaenike 1984). Fruit flies and fungus gnats were major fungal feeders in our samples. When the local food level increased, these flying insects, particularly the fruit flies, likely aggregated in the high-food location to either feed and/or reproduce. It is also possible that food enhancement increased rates of larval survival and growth, leading to increased numbers of adults in the next generation. This may be particularly true for fungus gnats, which were not more abundant in the Food Enhancement plots 4 weeks after food additions started, but were 2× higher in experimental than control plots at the end of the experiment.

The majority of the mites in our samples were oribatids, which can be categorized as macrophytophages, microphytophages and panphytophages (Luxton 1972). The majority of oribatid mites can feed and reproduce well on fungal materials (Norton 1990). It is reasonable to conclude from our results that as a group, populations of these mites in the litter layer are food-limited. Some predacious mesostigmatid and prostigmatid mites also occurred in our samples. These mites can prey upon other small invertebrates, including nematodes, collembolans and other mites. Predacious mites may also have increased in response to increases in their prey, though this possibility was not tested.

Behavioral responses that occur across the boundaries of open field plots, such as decreased emigration or increased immigration, do not constitute direct evidence that food shortage affect population density. Changes in population density that result from increased survival and/or reproduction constitute direct evidence of food limitation. In this experiment the pattern of results for entomobryid Collembola and fungus gnats is consistent with increased survival and/or reproduction being a major cause of the increased density exhibited in the Food Enhancement plots. The small size and short generation time of mites suggest a similar interpretation for their response to food enhancement.

Biotic control processes in terrestrial decomposition systems are poorly understood (Schaefer 1991, 1995). If bottom-up control processes are strong in the system we studied, we would expect the effects of food enhancement to propagate upwards to higher trophic levels, causing predacious arthropods which prey upon the fungivores to increase. So far there is no direct experimental evidence to confirm the hypothesis of such propagating bottom-up control in forest-floor litter communities. By investigating such multi-trophic level interactions we can improve our understanding of control processes in terrestrial decomposition systems.

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References

Betsch, J. M. (1991) Effets de la privation des apports annuels de litière sur les Collemboles Symphypléones épigés d'une forêt sur rendzine. Rev. Ecol. Biol. Sol **28**, 41–49.

Booth, R. G., Anderson, J. M. (1979) The influence of fungal food quality on the growth and fecundity of *Folsomia candida* (Collembola: Isotomidae). Oecologia **38**, 317–323.

Buxton, P. A. (1960) British Diptera associated with fungi. III. Flies of all families reared from about 150 species of fungi. Entomol. Mon. Mag. **96**, 61–94.

Chen, B., Snider, R. J., Snider, R. M. (1995) Food preference and effects of food type on the life history of some soil Collembola. Pedobiologia **39**, 496–505.

Chen, B., Snider, R. J., Snider, R. M. (1996) Food consumption by Collembola from northern Michigan deciduous forest. Pedobiologia **40**, 149–161.

Christiansen, K., Bellinger, P. (1981) Collembola of North America. Grinnell College, Grinnell, Iowa.

Grimaldi, D., Jaenike, J. (1984) Competition in natural populations of mycophagous *Drosophila*. Ecology **65**, 1113–1120.

Hackman, W., Meinander, M. (1979) Diptera feeding as larvae on macrofungi in Finland. Ann. Zool. Fenn. **16**, 50–83.

Hairston, N. G., Smith, F. E., Slobodkin, L. B. (1960) Community structure, population control, and competition. Am. Nat. **94**, 421–425.

Hammond, P. M., Lawrence, J. F. (1989) Appendix: Mycophagy in insects: a summary. In: Wilding, N., N. M. Collins, P. M. Hammond and J. F. Webber (eds.) Insect-fungus interactions. Academic Press. London. pp. 275–324.

Hanski, I. (1989) Fungivory: Fungi, insects and ecology. In: Wilding, N., Collins, N. M., Hammond, P. M., Webber, J. F. (eds.) Insect-fungus interactions. Academic Press. London. pp. 26–68.

Huhta, V., Mikkonen, M. (1982) Population structure of Entomobryidae (Collembola) in a mature spruce stand and in a clear-cut reforested areas in Finland. Pedobiologia **24**, 231–240.

Joosse, E. N. G., Testerink, G. J. (1977) The role of food in the population dynamics of *Orchesella cincta* (Linne) (Collembola). Oecologia **29**, 189–204.

Joosse, E. N. G. (1981) Ecological strategies and population regulation of Collembola in heterogenous environments. Pedobiologia **21**, 346–356.

Kempson, D., Lloyd, M., Ghelardi, R. (1963) A new extractor for woodland litter. Pedobiologia **3**, 1–21.

Knight, C. B., Angel, R. A. (1967) A preliminary study of the dietary requirements of *Tomocerus* (Collembola). Am. Midl. Nat. **77**, 510–517.

Leinaas, H. P., Bleken, E. (1983) Egg diapause and demographic strategy in *Lepidocyrtus lignorum* Fabricius (Collembola: Entomobryidae). Oecologia **58**, 194–199.

Luxton, M. (1972) Studies on the oribatid mites of a Danish beech wood soil. Pedobiologia **12**, 434–463.

Luxton, M. (1982) The biology of mites from beech woodland soil. Pedobiologia **23**, 1–8.

Macfadyen, A. (1962) Soil arthropod sampling. Adv. Ecol. Res. **1**, 1–34.

McNamara, J. M., Houston, A. I. (1994) The effect of a change in foraging options on intake rate and predation rate. Am. Nat. **144**, 978–1000.

Moore, J. C., Walter, D. E., Hunt, H. W. (1988) Arthropod regulation of microand mesobiota in belowground detrital food webs. Ann. Rev. Entomol. **33**, 419–439.

Mueller, B. R., Beare, M. H., Crossley, Jr. D. A. (1990) Soil mites in detrital food webs of conventional and no-tillage agroecosystems. Pedobiologia **34**, 389–401.

Norton, R. A. (1990) Acarina: Oribatida. In: Dindal, D. L. (ed.) Soil biology guide. John Wiley & Sons. pp. 779–803.

Peterson, H. (1971) The nutritional biology of Collembola and its ecological significance. A review of recent literature with a few original observations. Ent. Meddr. **39**, 97–118.

Pimm, S. L. (1982) Food webs. Chapman & Hall, London.

Ponge, J. E., Arpin, P., Vannier, G. (1993) Collembolan response to experimental perturbations of litter supply in a temperate forest ecosystem. Eur. J. Soil Biol. **29**, 141–153.

Rice, W. R. (1989) Analyzing tables of statistical tests. Evolution **43**, 223–225.

Russell-Smith, A. (1979) A study of fungus flies (Diptera: Mycetophilidae) in beech woodland. Ecol. Entomol. **4**, 355–364.

SAS Institute (1990) SAS/STAT user's guide, version 6.08, Fourth Edition. SAS Institute, Inc., Cary, North Carolina, USA.

Schaefer, M. (1991) The animal community: Diversity and resources. In: Röhrig, E., Ulrich, B. (eds.), Temperate deciduous forests (Ecosystems of the world). Elsevier, Amsterdam, London, New York, Tokyo. pp. 51–120.

Schaefer, M. (1995) Interspecific interactions in the soil community. Acta Zool. Fenn. **196**, 101–106.

Schauermann, J. (1982) Verbesserte Extraktion der terrestrischen Bodenfauna im Vielfachgeraet modifiziert nach Kempson und Macfadyen. Mitteilungen aus dem Sonderforschungsbereich 135 (Ökosysteme auf Kalkstein) **1**, 47–50.

Seastedt, T. R. (1984) The role of microarthropods in decomposition and mineralization processes. Ann. Rev. Entomol. **29**, 25–46.

Seastedt, T. R., James, S. W., Todd, T. C. (1988) Interactions among soil invertebrates, microbes and plant growth in the tallgrass prairie. Agric. Ecosyst. Environ. **24**, 219–228.

Shaw, P. J. A. (1985) Grazing preferences of *Onychiurus armatus* (Insecta: Collembola) for mycorrhizal and saprophytic fungi of pine plantations. In: Fitter, A. F., Atkinson, D., Read, D. J., Usher, M. B. (eds.), Ecological interactions in soil: plants, microbes and animals. Blackwell. pp. 333–337.

Shaw, P. J. A. (1988) A consistent hierarchy in the fungal feeding preferences of the Collembola *Onychiurus armatus*. Pedobiologia **31**, 179–187.

Stefaniak, O., Seniczak, S. (1981) The effect of fungal diet on the development of *Oppia nitens* (Acari, Oribatei) and on the microflora of its alimentary tract. Pedobiologia **21**, 202–210.

Swift, M. F., Heal, O. W., Anderson, J. M. (1979) Decomposition in terrestrial ecosystems. Berkeley: University of California Press.

Usher, M. B. (1970) Seasonal and vertical distribution of a population of soil arthropods: Collembola. Pedobiologia **10**, 224–236.

Usher, M. B., Booth, R. G., Sparkes, K. E. (1982) A review of progress in understanding the organization of communities of soil arthropods. Pedobiologia **23**, 126–144.

Usher, M. B. (1985) Population and community dynamics in the soil ecosystem. In: Fitter, A. F., Atkinson, D., Read, D. J., Usher, M. B. (eds.), Ecological interactions in soil: plants, microbes and animals. Blackwell. pp. 243–265.

Vegter, J. J. (1987) Phenology and seasonal resource partitioning in forest floor Collembola. Oikos **48**, 175–185.

Visser, S., Whittaker, J. B. (1977) Feeding preferences for certain litter fungi by *Onychiurus subtenius*. Oikos **29**, 320–325.

Walsh, M. I., Bolger, T. (1990) Effects of diet on the growth and reproduction of some Collembola in laboratory culture. Pedobiologia **34**, 161–172.