Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2011, **80**, 947–957 doi: 10.1111/j.1365-2656.2011.01853.x

Facilitation and predation structure a grassland detrital food web: the responses of soil nematodes to isopod processing of litter

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Summary

1. Detritus can support successive consumers, whose interactions may be structured by changes in the condition of their shared resource. One model of such species interactions is a processing chain, in which consumers feeding on the resource in a less processed state change the resource condition for subsequent consumers.

2. In a series of experiments, the hypothesis was tested that a common detritivore, the terrestrial isopod *Porcellio scaber*, affects soil nematodes through the processing of plant litter. Different detrital resources were added to soil from a California coastal prairie in order to simulate litter processing by the detritivore. Treatments that included only whole grass litter corresponded to detrital food webs lacking detritivores, while treatments that included mixtures of *P. scaber* faeces and grass litter corresponded to different densities or feeding rates of *P. scaber*.

3. Simulated litter processing by *P. scaber* increased the abundance of bacterivorous nematodes by between 32% and 202% after 24–44 days in laboratory experiments, but had no effect on fungivorous or predaceous nematodes.

4. In a subsequent field experiment, however, fungivorous nematodes were suppressed by isopod litter processing while bacterivores showed no response. Instead, *P. scaber* processing of litter increased the abundance of predaceous nematodes in the field experiment by 176%.

5. When simulated litter processing of litter was crossed in laboratory experiments with predaceous nematode addition (comparable to the response of predators in the field experiment), the abundance of bacterivores was increased by isopod processing of litter (by an average of 122%), but suppressed by elevated densities of predaceous nematodes (by an average of 41%).

6. This suggests that litter processing by *P. scaber* facilitates the bacterial channel of the soil food web, but that predaceous nematodes suppress the response of bacterivores in the field. Processing chain interactions may, therefore, be important in understanding the relative importance of bacterial and fungal channels in the soil food web, while top-down effects of predators determine the resulting changes in population abundance and biomass.

Key-words: detrital succession, processing chain, resource processing, soil food web, top-down effect

Introduction

Decomposition is one of the fundamental ecosystem processes and is the process through which nutrients in dead biomass are recycled. Dead biomass, or detritus, is broken down by detritivores and decomposers, which feed on the detritus, assimilate a fraction of what they ingest, and modify the quality and condition of the unassimilated fraction (Hunter *et al.* 2003). From the point of view of consumers, one of the distinctive characteristics of detritus is that its resource quality and condition are continually changing as a result of other consumers in the community. It is therefore not surprising that the assemblage of consumers feeding on detritus undergoes succession as the basal resource decomposes. Carrion feeding insects (Payne 1965), wood-degrading fungi (Renvall 1995), dung beetles (Gittings & Giller 1998) and consumers of whale carcasses (Smith & Baco 2003) are just a few examples of the species assemblages for which such succession on a resource is well documented.

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Such systems, in which a resource is shared by successive consumers that feed on the resource in different conditions, have been termed 'processing chains' (Heard 1994a, 1995). Consumers in a processing chain may positively or negatively affect later successional consumers by altering the rate or efficiency with which the resource is processed. Thus, processing chain interactions occur when early successional consumers of a resource alter the rate with which the resource becomes available to subsequent consumers (Heard 1995) or the total quantity of resource which becomes available to them (Heard 1994a). Resource processing is, therefore, one mechanism through which species in a community may have positive interactions with other species, although facilitation is by no means the inevitable outcome of a processing chain interaction.

Heard's processing chain model has primarily been applied to aquatic container communities, including pitcher plants (Heard 1994b; Hoekman, Winston & Mitchell 2009), bromeliad tanks (Starzomski, Suen & Srivastava 2010) and tree holes (Paradise 1999; Daugherty & Juliano 2003). These studies have shown that litter processing by aquatic detritivores can have facilitative effects on particle-feeding insects (Heard 1994b; Daugherty & Juliano 2003; Starzomski, Suen & Srivastava 2010) and bacteria (Hoekman, Winston & Mitchell 2009), but that resource availability (Paradise 1999) and predation (Hoekman, Winston & Mitchell 2009; Starzomski, Suen & Srivastava 2010) are important in understanding how processing chain interactions are manifest in real food webs. Although resource processing is believed to be a general feature of detrital food webs (Moore *et al*. 2004), processing chains have been difficult to demonstrate in more open aquatic systems (Heard & Buchanan 2004) and have rarely been invoked to explain species interactions in terrestrial or marine systems (but see Tiunov & Scheu 2005 for an exception). There are, however, a number of apparently facilitative interactions among terrestrial detritivores and decomposers that appear to be structured by the processing of detritus, including the facilitation of soil microbes by invertebrate detritivores (Hättenschwiler & Bretscher 2001; Zimmer, Kautz & Topp 2005), sugar fungi by lignin-degrading fungi (Osono & Takeda 2001), and nitrifying bacteria by ammonifying bacteria (Torres, Abril & Bucher 2005).

I tested the hypothesis that an abundant detritivore in California coastal prairie, the isopod *Porcellio scaber*, positively affects soil-dwelling nematodes through its processing of grass litter. Terrestrial isopods often increase litter decomposition rates (Kautz & Topp 2000; Hättenschwiler & Bretscher 2001; Zimmer, Kautz & Topp 2005; Bastow, Preisser & Strong 2008) and soil microbial abundance or activity (Hanlon & Anderson 1980; Hassall, Turner & Rands 1987; Kayang, Sharma & Mishra 1996; Kautz & Topp 2000; Hättenschwiler & Bretscher 2001; Zimmer, Kautz & Topp 2005), but their interactions with microbivorous soil fauna have not previously been studied. Nematodes were chosen as focal soil fauna because of their importance in nutrient cycling and ubiquity in soils (Bongers & Bongers 1998). Because the nematode assemblage includes bacterivores, fungivores, herbivores and predators of other nematodes, its structure provides information about the importance of detrital and rhizal energy sources, bacterial and fungal channels, and higher trophic levels in the soil food web (Neher 2001).

As a detritivore feeding at the soil surface, isopods likely act as early successional consumers (upstream consumers, sensu Heard 1994a) in a litter-processing chain. By increasing decomposition rates, isopod processing of litter may increase the rate at which organic matter is incorporated into the soil, thus having short-term facilitative effects on soil microbes (i.e. bacteria and fungi) as well as microbivorous soil fauna (downstream consumers). Fungi are generally better able to utilize litter on the soil surface than bacteria, because of their hyphal growth form and ability to translocate water and nutrients (Beare *et al*. 1992). Bacteria and bacterivores are therefore likely to be more strongly facilitated by isopod processing of litter than fungi and fungivores, because in addition to making organic matter available to fungi in the soil, isopods likely compete with fungi for surface litter. Comparing the responses of bacteria and fungi to isopod processing of litter may provide insights into the ecosystem consequences of detritivores; the bacterial channel of the soil food web is generally associated with rapid decomposition and nutrient turnover and the fungal channel with slower decomposition and greater nutrient retention (Moore & Hunt 1988; Wardle 2002).

Responses of nematode populations to simulated litter processing by isopods were measured in laboratory and field microcosm experiments. In these experiments, I added grass litter and *P. scaber* faeces (grass litter that was consumed but not assimilated) to soil microcosms to simulate different activity levels (i.e. different densities or feeding rates) of isopods. These experiments isolated the effects of litter processing by *P. scaber* from other effects the isopod may have on soil fauna (e.g. through soil turbation) in order to clarify the importance of this particular mechanism through which detritivores may affect soil food webs. In two of the experiments, isopod litter processing was crossed with different densities of predaceous nematodes, which are known to exert strong top-down control of microbivorous nematodes (Allen-Morley & Coleman 1989; Mikola & Setälä 1998). The following hypotheses were tested: (i) litter processing by *P. scaber* increases the abundance of microbivorous nematodes, (ii) because fungi are better able to utilize litter on the soil surface than bacteria, bacterivorous nematodes are more strongly facilitated by *P. scaber* than fungivorous nematodes, and (iii) predaceous nematodes suppress the positive response of microbivores to isopod processing of litter.

Materials and methods

STUDY SITE

All of the soil, litter and animals used in these experiments came from the University of California Bodega Marine Reserve which was also the site of the field experiment. The Bodega Marine Reserve is a 146-

ha reserve in Sonoma Co., CA, USA (38° 19′ N, 123° 4′ W). The reserve has a coastal Mediterranean climate, with a cool, rainy winter (November–March, average precipitation of 71 cm per season, Bodega Ocean Observing Node 2008) and a dry, but foggy, summer (average precipitation 14 cm per season). The coastal prairie of the Bodega Marine Reserve is an annual-dominated grassland with loamy sand soil. The vegetation comprises both native Californian and introduced European grasses and forbs. *Porcellio scaber* (Latreille), a terrestrial isopod native to Europe (Harding & Sutton 1985), is the most abundant macrodetritivore at the Bodega Marine Reserve. Pitfall trap data suggest that *P. scaber* is relatively inactive during the winter at the Bodega Marine Reserve, but that their numbers and activity increase steadily through the spring and summer (J.L. Bastow unpublished data). Fall densities average 350 *P. scaber* per m^2 (based on trapping isopods out of enclosed 0·25 m^2 plots, $N = 8$). Similarly, *P. scaber* has little effect on litter decomposition in the winter, but accounts for most of the litter lost from litterbags during the summer (Bastow, Preisser & Strong 2008). Overall, *P. scaber* increases litter mass loss at the Bodega Marine Reserve by *c.* 29% (Bastow, Preisser & Strong 2008), consuming between 90 and 126 g m^{-2} of grass litter and producing between 45 and 63 g m^{-2} of faeces (based on laboratory measurements of consumption and assimilation rates, Bastow 2007 and J.L. Bastow unpublished data).

LABORATORY MICROCOSM EXPERIMENTS

The responses of microbivorous nematodes (i.e. bacterivores and fungivores) to detrital resources were measured in four laboratory microcosm experiments. In the first two of these experiments (Processing Experiments 1 and 2), the response of nematodes to four different levels of litter processing by isopods was measured at multiple points in time (10–59 days). In the next two experiments (Predation Experiments 1 and 2), the response of nematodes to two different levels of litter processing at two different densities of predaceous nematodes was measured.

In the two processing experiments, microcosms received one of five resource treatments, although only four of the treatments were included in each of the two experiments. Both experiments included a treatment in which the soil received no added resource ('soil control') and a treatment that received 0·18 g of grass litter (dry mass, 'grass addition'). Each experiment also included two treatments of simulated isopod processing of litter. These treatments simulated the conversion of 25%, 50% or 100% of the grass litter to isopod faeces with a 0·50 assimilation efficiency, assuming that uneaten litter is unaltered by isopods. These treatments correspond to different densities or feeding rates of isopods. The 0·50 assimilation efficiency was determined gravimetrically in a preliminary experiment (Bastow 2007) and is within the range of values reported for terrestrial isopods (Zimmer 2002). These treatments included the following: 0·135-g grass litter and 0·0225-g isopod faeces ('25% processing'); 0·09-g grass litter and 0·045-g faeces ('50% processing'); and 0·09-g faeces ('100% processing') (all masses expressed in dry mass). Processing Experiment 1 included the 25% and 50% processing treatments, while Processing Experiment 2 included the 50% and 100% processing treatments.

The grass litter used in each experiment is listed in Table 1. Isopod faeces were produced in the laboratory by feeding *P. scaber* on 1·5-mm mesh screen and collecting the faeces that fell through the screen. The species of grass litter used differed between experiments because of the limited availability of grass litters of particular species in certain seasons, but all species were of similar resource quality (i.e. carbon : nitrogen ratio) and all were common species at the Bodega Marine Reserve. Within each experiment, all grass litter and isopod faeces were derived from the same batch of grass litter, collected from the field on the same date.

The two predation experiments included grass addition and 100% processing treatments but, due to limited growth chamber capacity and processing time constraints, omitted the intermediate levels of isopod processing. These two resource treatments were crossed in the predation experiments with two different levels of predaceous nematodes: ambient (no predators added) and elevated (10 Mononchida predators added). The density of additional predators (1 per g dry soil) was based on the response of predaceous nematodes in the field experiment (see below). Predaceous nematodes were extracted from raw soil using Baermann funnels (Coleman *et al.* 1999), removed from samples using a pipette and stored individually at 8 °C in vials until experimental set-up (less than a week).

Soil for all laboratory experiments was collected to a depth of 20 cm and stored at room temperature until microcosm construction (Table 1). Soil was passed through a sieve (1·6 mm) immediately prior to microcosm construction and wetted to 0·19 gravimetric water content (g water per g dry weight soil, SD 0·017). Each microcosm consisted of a polystyrene sample vial (79 mm height × 27 mm diameter) to which was added 12·00 g of soil (wet weight, ±0·20 g). Microcosms were randomly arranged in a growth chamber, which cycled between 11 and 15 °C on a 24-h cycle (12 h light, 12 h dark), approximating field conditions at the Bodega Marine Reserve in the spring (Bastow 2007). Microcosms were watered every 5–10 days in an effort to maintain constant soil moisture. Soil moisture nonetheless declined over the course of the experiments, to a mean gravimetric water content of 0·14 (SD 0·064).

MICROCOSM SAMPLING AND PROCESSING

There were six replicate microcosms of each treatment at each sampling point within each experiment. Processing Experiments 1 and 2 were destructively sampled four times, first at 10 or 12 days, then at 26 or 24 days, at 44 or 39 days, and finally at 58 or 59 days. Predation Experiments 1 and 2 were sampled once, at 24 and 23 days,

Table 1. Litter resources and sampling schedule of microcosm experiments

Experiment	Grass litter	C : N grass litter	C : N isopod faeces	Soil collected	Start date	Duration (days)
Processing 1	*Bromus diandrus*	47·2	22·0	27/9/2005	19/10/2005	58
Processing 2	Mixed annuals	47·4	24·0	20/4/2005	29/4/2005	59
Field	Mixed annuals	56·3	25·6	6/2/2006	13/2/2006	111
Predation 1	*Calamagrostis nutkaensis*	52·6	27·4	8/6/2008	13/6/2008	24
Predation 2	*Bromus diandrus*	45·5	25·6	22/6/2008	2/7/2008	23

C : N, carbon-to-nitrogen ratio by mass.

respectively. Sampling dates differed slightly between experiments because of access to the growth chambers. Nematodes were extracted from six soil samples for day 0 data in each experiment. In addition to microcosms sampled for nematodes, four microcosms were used at each sampling time to measure gravimetric water content of the soil.

Microcosms were destructively sampled for nematodes by placing all soil and litter into a Baermann funnel. Nematodes were extracted for 2 days at 22 °C. The total numbers of nematodes were then counted, and a subsample of nematodes (10% of the total) was identified to functional group on the basis of stylet and oesophagus features (Freckman & Baldwin 1990; Yeates *et al.* 1993). The functional groups identified were bacterivore, fungivore, predator (i.e. consuming nematodes, enchytraeids, protists, and rotifers), omnivore, plant parasite, and 'tylenchus type' (i.e. Tylenchida of ambiguous feeding habit, most likely feeding on roots and fungal hyphae). Plant parasitic, tylenchus type, and omnivorous nematodes did not respond to treatments in any experiment and were generally at low abundance in laboratory microcosms; only the data on microbivorous and predaceous nematodes are presented here.

FIELD MICROCOSM EXPERIMENT

The field microcosm experiment was similar in design to the processing experiments, but measured the response of nematodes to simulated processing of litter in the field rather than the laboratory. Each microcosm consisted of a cylinder of 0·5-mm mesh nylon screen (12 cm height × 4 cm diameter), rolled up at the bottom and stapled shut, to which 55 g (wet weight, ± 5 g) of soil was added. The soil had an initial gravimetric water content of 0·20 (SD 0·005), and no additional water was added before microcosm construction. Resource treatments were the same as in the processing experiments, scaled to the larger microcosm size: 0·5 g grass litter ('grass addition'); 0·375 g grass litter and 0·0675 g faeces ('25% processing'); 0·25 g grass litter and 0·125 g faeces ('50% processing'); 0·25 g faeces ('100% processing') (all masses expressed in dry mass). Resources were placed on the soil surfaces.

The microcosms were placed in the field and the experiment began in February 2006. There were six replicate microcosms for each resource treatment at each of five sampling times (16, 31, 62, 87 and 111 days). The microcosms were arranged in a fully randomized 10 × 12 grid in the field with 0·5 m of undisturbed soil between adjacent rows and columns. The microcosms were placed in holes, so that the soil surface within the sleeve was flush with the surrounding soil, and the entire experiment was watered immediately after set up so that water films in the soil cores would be reconnected to those in the surrounding soil. The microcosms were not watered again for the remainder of the study. Six microcosms were collected for initial (day 0) data. Beginning on the second sampling time (day 31), six soil samples were collected from the prairie surrounding the experimental grid at the same time that microcosms were collected ('ambient' samples, from within 1 m of the edge of the grid). Microcosms and ambient soil samples were processed within twelve hours of collection. Two subsamples were removed from each of the microcosms and ambient soil samples. One subsample was used to measure nematode abundances, as in the laboratory experiments, and the other was used to measure gravimetric moisture content. Although it would have been possible for *P. scaber* to climb into microcosms, none were found during microcosm processing.

Soil temperature was measured from day 31 to 62 and from day 68 to 111 of the experiment using a HOBO temperature data logger (Onset Computer Corporation, Bourne, MA, USA) buried at a depth of 10 cm. Daily minimum and maximum soil temperatures between day 31 and 62 were 10·5 ± 1·3° and 15·7 ± 2·5 °C (mean ± SD) and rose to 14·4 ± 1·4° and 22·1 ± 2·3 °C between day 68 and 111. Precipitation was measured by the Bodega Ocean Observing Node (2008). Soil moisture increased from 0·20 ± 0·002 to 0·43 ± 0·013 g water per g dry soil during the first half of the experiment due to frequent rains (Appendix S1, Supporting information), but subsequently declined to less than 0·10 g water per g dry soil.

DATA ANALYSIS

The responses of nematode abundance (per g dry soil) to treatments and sampling time were analysed in factorial ANOVAs. The initial nematode abundances (day 0) were not included in the analyses, because the initial sampling was not crossed with treatment. In the processing experiments, treatment and sampling time were included as fixed factors, along with their interaction. Time was regarded as a fully crossed factor because experimental units were destructively sampled. In the predation experiments, resource treatment and predator treatment were included as fixed factors, along with their interaction. The abundances of nematodes in the field experiment were analysed using ANCOVAs with treatment and time as fixed factors and soil moisture content as a covariate. Because ambient soil for nematode extraction was not collected at the first sampling time (day 16), treatment and time were not fully crossed, and the analysis of the full data set could not test for an interaction between the two factors. An initial analysis was performed excluding the ambient soil treatment to see whether the interaction between time and treatment was significant for the other treatments. The interaction term was not significant for any functional group of nematodes. The results of analysis of the full data set, without the interaction term in the model, are reported here. Separate ANOVAs were used for each functional group of nematodes (bacterivores, fungivores and predators) in each experiment and Bonferroni corrected for performing three ANOVAs (i.e. $\alpha = 0{\cdot}016$). Tukey tests were used to separate means when factors were significant in the ANOVA and had more than two levels. Nematode abundances were log transformed to meet ANOVA assumptions (normally distributed residuals and homogeneity of variances). In the case of predaceous nematodes, which were absent from some replicates, a constant was added to all data points prior to transformation. All means and standard errors presented in text and on figures are of raw data. Analyses were performed in JMP IN 4.0.3.

Results

PROCESSING EXPERIMENTS

Bacterivorous nematodes were the most abundant functional group of nematodes in all experiments and accounted for two-thirds of all nematodes recovered from laboratory microcosm experiments. In Processing Experiment 1, bacterivore abundances increased in the grass addition treatment while remaining low in the soil control (Fig. 1a). Bacterivore abundances increased more rapidly, however, in the two isopod processing treatments than they had in the grass addition treatment (Fig. 1a, time × treatment interaction, Table 2). Although overall nematode abundances were lower in Processing Experiment 2, the response of bacterivores to treatments was similar; bacterivore abundances in the 50% and 100% processing treatments increased to between 110 and

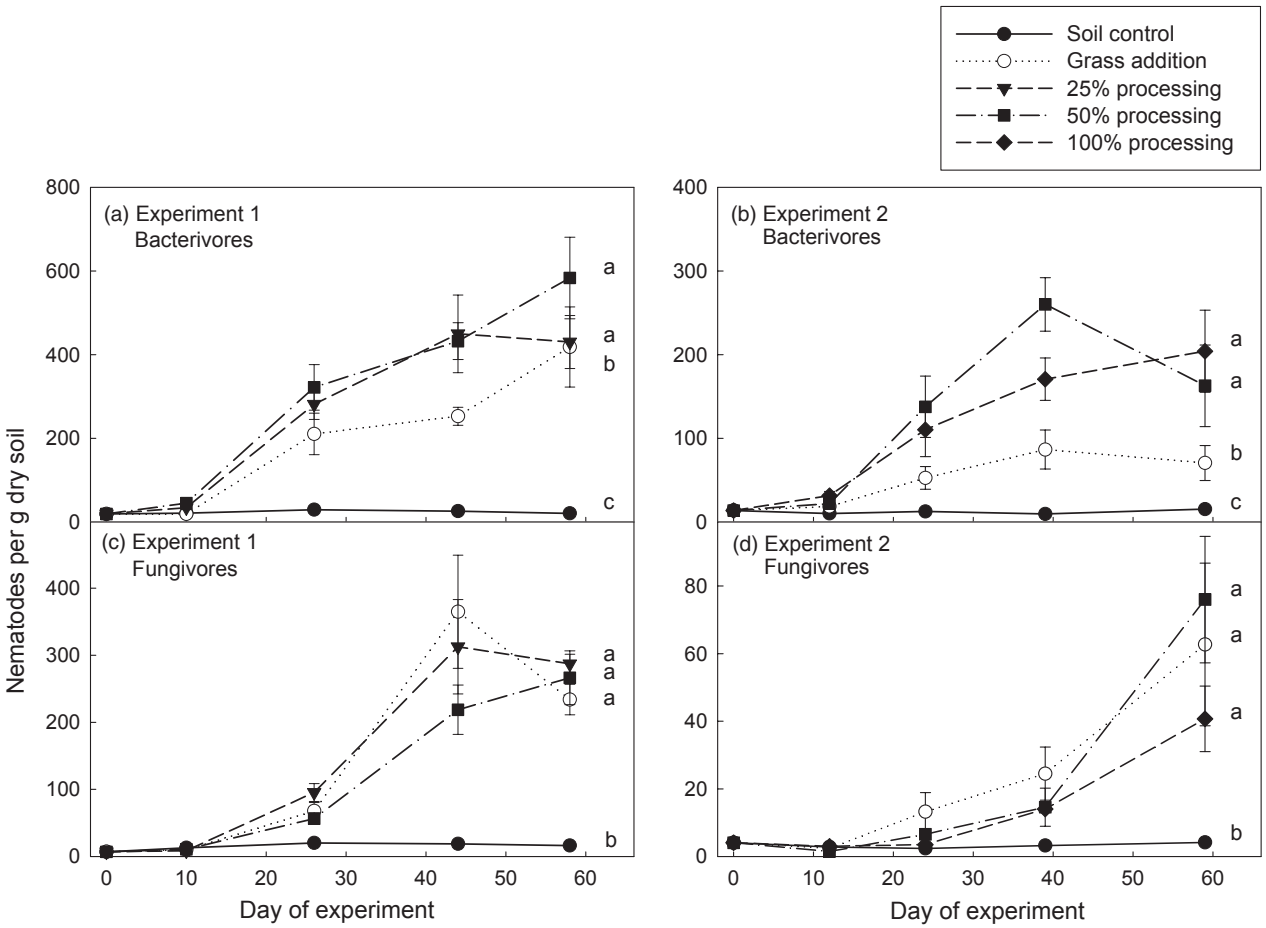

Fig. 1. The responses of bacterivorous (a, b) and fungivorous (c, d) nematode density (per g dry soil, mean ± SE) to simulated isopod processing of litter in Processing Experiments 1 (a, c) and 2 (b, d). The grass addition treatment simulates the absence of terrestrial isopods, while the 25%, 50% and 100% processing treatments simulate different densities or feeding rates of isopods. Only four of the five treatments were included in each of the experiments. Different letters indicate treatments that are significantly different according to Tukey post-hoc test. Bacterivores increased in density in response to simulated isopod processing of litter.

260 nematodes per g soil at the second and third sampling times, while increasing more slowly in the grass addition and remaining unchanged in the soil control (Fig. 1b, Table 2).

Fungivorous nematodes increased in abundance in the grass addition and 25%, 50% and 100% processing treatments, but there were no differences in fungivore abundance between these treatments in either experiment (Fig. 1c,d; Table 2). Fungivore abundances were considerably higher in all treatments in Processing Experiment 1 than in Processing Experiment 2. Predaceous nematodes were scarce in both processing experiments (0·026 ± 0·016 and 0·21 ± 0·043 per g soil in processing experiments 1 and 2, respectively) and did not respond to treatments (Table 2).

FIELD EXPERIMENT

Although, still the most abundant functional group of nematodes, bacterivorous nematodes were much less abundant in the field experiment than in the Processing Experiments. Bacterivore abundances declined during the first 16 days of the experiment and then fluctuated between 6 and 14 per g soil (Fig. 2a, Table 2). There was no effect of treatment on bacterivore abundance (Fig. 3a, Table 2). Fungivorous nematodes generally increased in abundance throughout the field experiment (Fig. 2b, Table 2). The highest level of isopod processing (100% processing treatment) suppressed the abundance of fungivores relative to the 25% and 50% processing and grass addition treatments (Fig. 3b, Table 2).

In contrast to bacterivores and fungivores, predaceous nematodes were more abundant in the field experiment (0·87 ± 0·11 per g soil) than they had been in the processing experiments (0·12 ± 0·024 per g soil), although their abundances declined throughout the experiment (Fig. 2c). The highest level of isopod processing increased the abundance of predators relative to ambient soil and the grass addition and 25% processing treatments (Fig. 3c, Table 2).

PREDATION EXPERIMENTS

The addition of ten predaceous Mononchid nematodes, obtained from field soil, to microcosms in the elevated predator treatment significantly increased the number of such nem-

Table 2. Results of ANOVAS on nematode abundance in the five experiments. Separate ANOVAS were performed on each of the three functional groups of nematodes (bacterivores, fungivores and predators) and an α of 0·016 was used to determine statistical significance (i.e. $\alpha = 0{\cdot}05$ Bonferroni corrected for performing three ANOVAS on each experiment)

			Bacterivorous nematodes			Fungivorous nematodes			Predaceous nematodes		
Experiment	Source	d.f.	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Processing Experiment 1	Treatment	3	21·21	123·91	< 0·0001*	14·75	68·75	< 0·0001*	0·017	1·46	0·23
	Time	3	26·35	153·97	< 0·0001*	37·56	175·09	< 0·0001*	0·0046	0·39	0·76
	Treatment × Time	9	2·26	13·21	< 0·0001*	3·37	15·71	< 0·0001*	0·0096	0·82	0·60
	Error	79	0·17			0·21			0·012		
Processing Experiment 2	Treatment	3	25·31	65·84	< 0·0001*	6·51	15·58	< 0·0001*	0·14	1·74	0·17
	Time	3	9·79	25·47	< 0·0001*	20·80	49·78	< 0·0001*	0·074	0·92	0·44
	Treatment × Time	9	1·39	3·62	0·0008*	1·98	4·73	0·0008*	0·075	0·93	0·51
	Error	80	0·38			0·42			0·080		
Field experiment	Treatment	4	0·23	0·46	0·77	2·16	5·01	0·0009*	1·07	5·44	0·0004*
	Time	4	2·12	4·26	0·0028*	7·21	16·71	< 0·0001*	1·35	6·86	< 0·0001*
	Soil moisture	1	2·13	4·29	0·04	2·89	6·71	0·011*	0·79	4·02	0·047
	Error	133	0·50			0·43			0·20		
Predation Experiment 1	Resource	1	14·68	22·55	< 0·0001*	0·68	1·47	0·24	1·05	7·37	0·013*
	Predator	1	5·17	7·95	0·011*	3·08	6·63	0·018	6·18	43·51	< 0·0001*
	Resource × Predator	1	2·30	3·52	0·075	2·71	5·83	0·025	0·030	0·21	0·65
	Error	20	0·65			0·46			0·14		
Predation Experiment 2	Resource	1	2·92	13·78	0·0014*	0·42	2·15	0·16	0·12	0·49	0·49
	Predator	1	1·72	8·11	0·0099*	0·37	1·91	0·18	3·16	13·37	0·0016*
	Resource × Predator	1	0·12	0·54	0·47	0·34	1·71	0·21	0·0034	0·015	0·91
	Error	20	0·21			0·20			0·24		

*Statistical significance after Bonferroni correction.
d.f., degrees of freedom; MS, mean square.

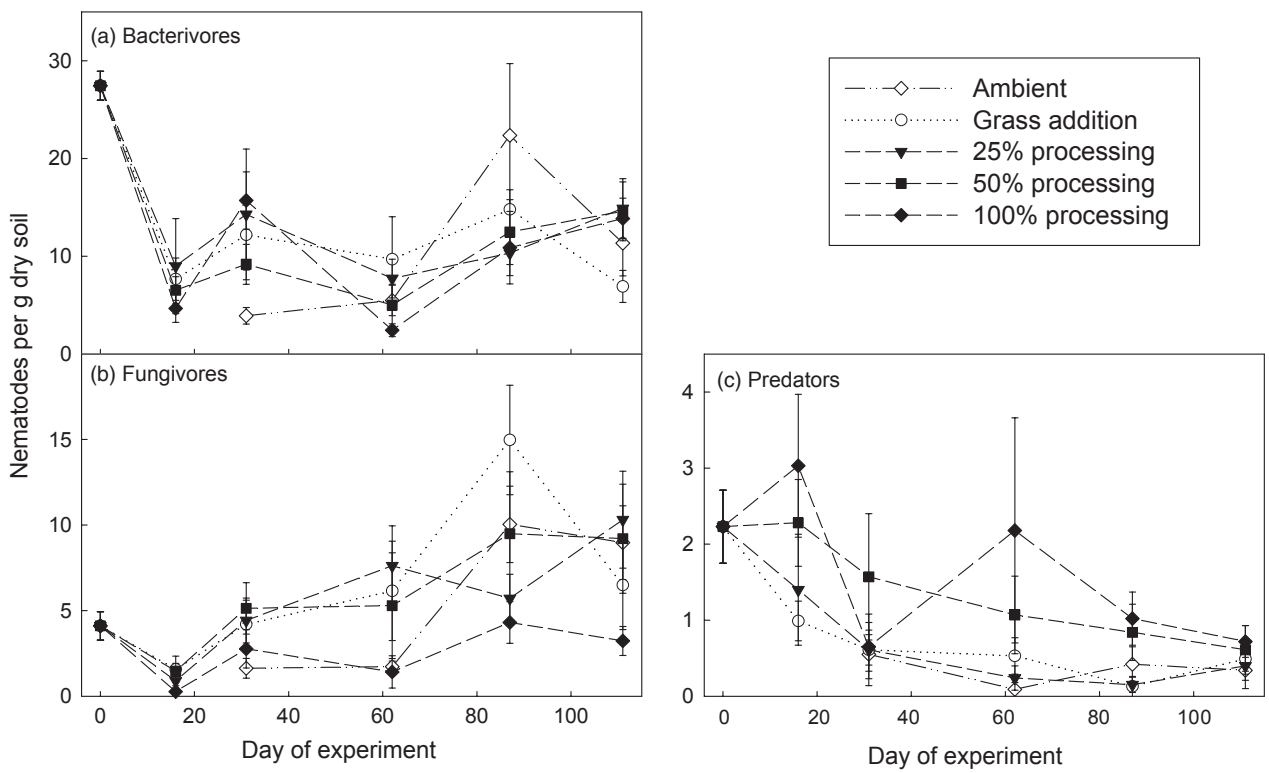

Fig. 2. The responses of bacterivorous (a), fungivorous (b), and predaceous (c) nematode density (per g dry soil, mean ± SE) to simulated isopod processing of litter in the field experiment over 111 days. Treatments are the same as in Fig. 1, except that ambient soil was used instead of a soil control.

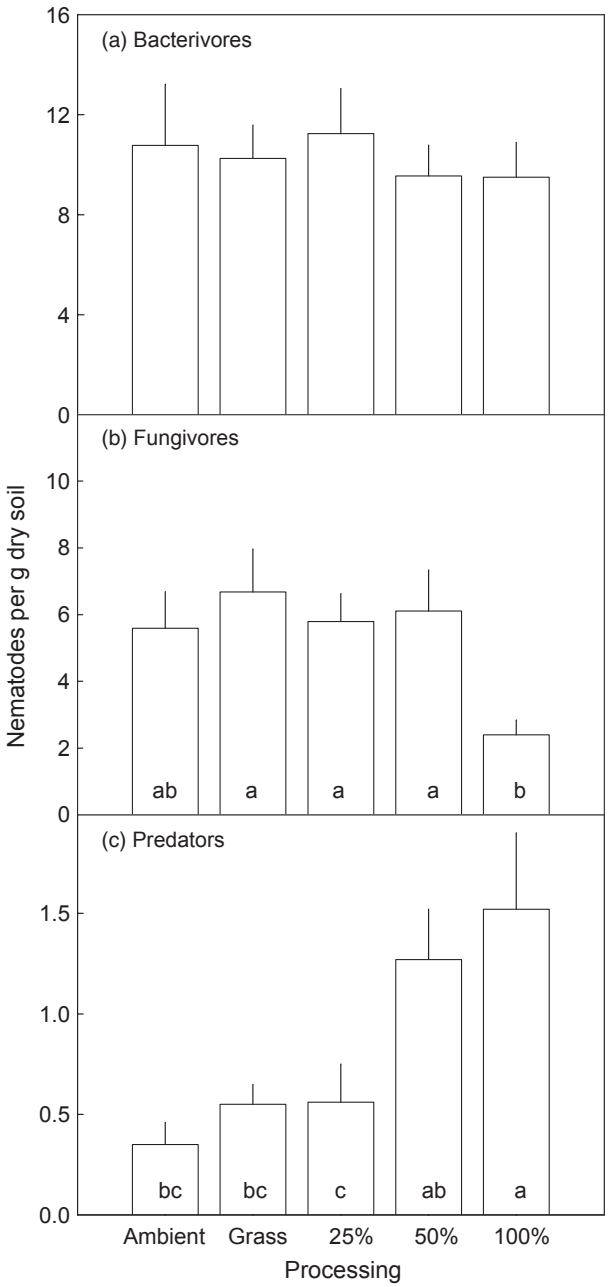

Fig. 3. The mean density (per g dry soil, ±SE) of bacterivorous (a), fungivorous (b), and predaceous (c) nematodes in the field experiment (averaging over all sampling dates). Different letters indicate treatments that are significantly different according to Tukey post-hoc test. Treatments are the same as in Fig. 2. High levels of simulated isopod processing of litter increased the densities of predaceous nematodes and suppressed fungivorous nematodes. Bacterivore densities did not differ among treatments.

atodes recovered after 24 days from 0·58 ± 0·15 to 3·58 ± 0·63 per microcosm in Predation Experiment 1 (Table 2). In the second predation experiment, recovered Mononchidae were significantly increased from 0·42 ± 0·19 per microcosm to 2·00 ± 0·37 after 23 days (Table 2).

Simulated isopod processing of litter significantly increased the abundance of bacterivores by 176% (from 51 ± 13 per g soil to 141 ± 13, averaging across predator treatments) in the first predation experiment, while predator addition significantly reduced their abundance by 39% (from 119 ± 19 per g soil to 73 ± 16 averaging across resource treatments, Fig. 4a, Table 2). In the second predation experiment, isopod processing significantly increased the abundance of bacterivores by 68%, while predator addition significantly reduced their abundance by 42% (Fig. 4b, Table 2). There was not a significant interaction between these two factors in either experiment. Neither predator addition nor simulated litter processing had significant effects on fungivorous nematode abundances in either of the predation experiments (Table 2).

Discussion

PROCESSING CHAIN FACILITATION AND PREDATION IN THE SOIL FOOD WEB

The abundance of bacterivorous nematodes in the coastal prairie of the Bodega Marine Reserve is affected by both the facilitative effect of litter processing by *P. scaber* and the top-down effects of predaceous nematodes. Although processing chain interactions are thought to be widespread in detrital food webs (Heard 1994a; Moore *et al.* 2004), their effects have rarely been studied in combination with other species interactions and in the context of the larger food web. Simulated processing of grass litter by *P. scaber* increased the abundances of bacterivorous nematodes in the laboratory experiments, suggesting that isopods facilitate the bacterial channel of the soil food web in the coastal prairie through their alteration of the quality and condition of detrital inputs. The 25% processing treatment in this study approximates the average contribution of *P. scaber* to litter decomposition at the Bodega Marine Reserve (based on a field litterbag study, Bastow, Preisser & Strong 2008). Pitfall trap data suggest that *P. scaber* has a very clumped distribution, however, so conditions more similar to the grass addition and 50% processing treatment are likely common in patches throughout this system.

Bacterivore abundances were unaffected by isopod processing of litter in the field experiment, however, despite soil moisture and temperature similar to the laboratory experiments for the first 60 days (i.e. the duration of the processing experiments). The highest level of isopod processing did significantly increase the abundance of predaceous nematodes in the field experiment by one predator/g soil. The addition of a comparable density of predaceous nematodes in the predation experiments suppressed bacterivore abundances. One possible explanation for these results is that isopod processing of litter facilitated bacterivores in the field experiment, but that predatory nematodes suppressed their response. Microbivorous nematodes are known to experience strong top-down control by predatory nematodes (Allen-Morley & Coleman 1989; Mikola & Setälä 1998), and predatory nematodes in other systems have responded to the stimulation of soil microbes even while microbivore abundances were

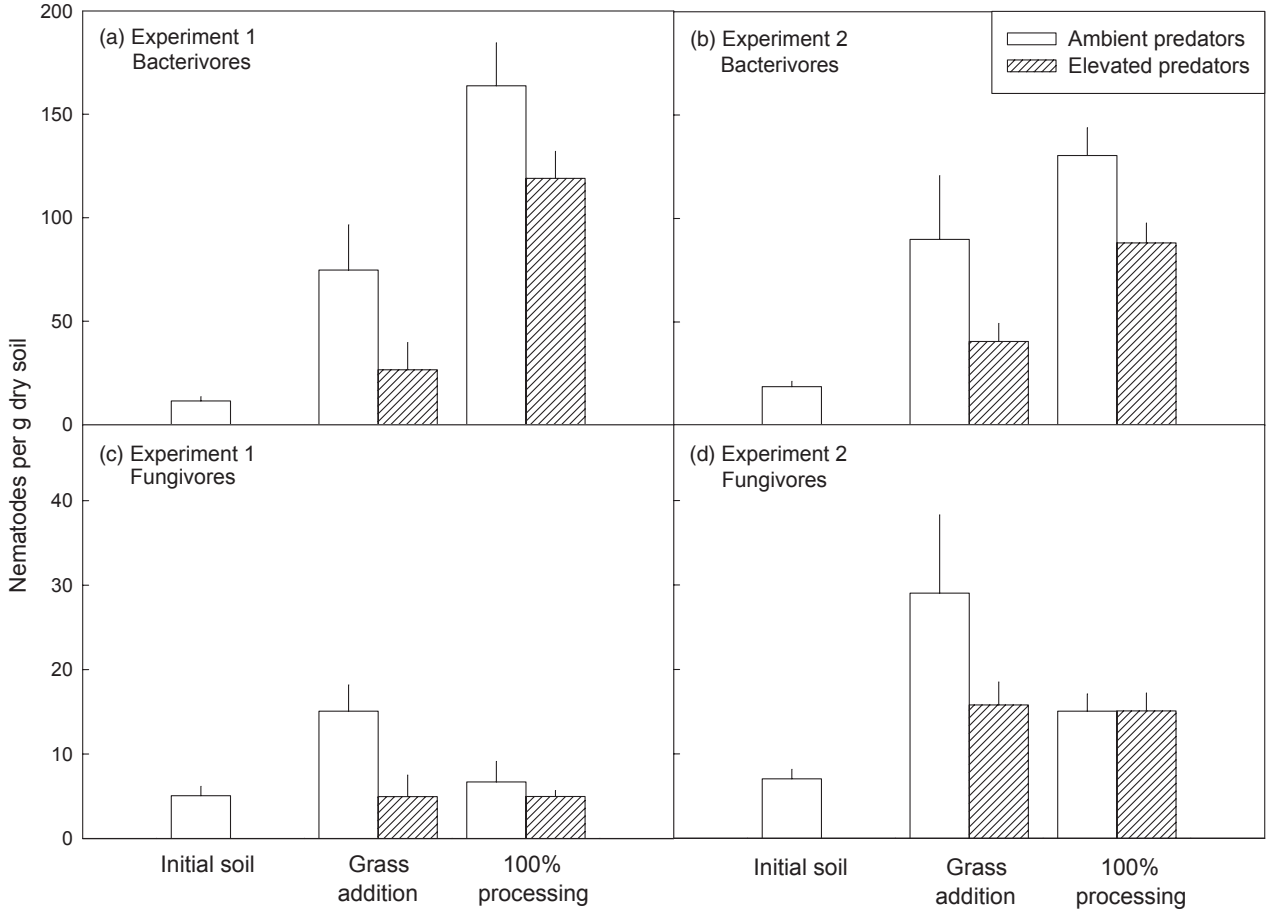

Fig. 4. The response of bacterivorous (a, b) and fungivorous (c, d) nematode density (per g dry soil, mean ± SE) to isopod processing of litter and predation by predaceous nematodes in Predation Experiments 1 (a, c) and 2 (b, d). While simulated litter processing increased bacterivore densities, the addition of predaceous nematodes suppressed them. Neither factor had significant effects on fungivore densities.

unaffected or responded only briefly (Yeates, Wardle & Watson 1999; Wardle *et al*. 2005). This is similar to the finding in bromeliad tanks that chironomid midge larvae are facilitated by detritivorous tipulid and scirtid larvae in the absence of predatory odonates, but strongly suppressed when odonates are present (Starzomski, Suen & Srivastava 2010).

There are two reasons why predatory nematodes may not have been able to respond to simulated isopod processing of litter in the laboratory experiments, despite an increase in the availability of their prey. The initial densities of predators in the Processing experiments (1·6 ± 1·0 per microcosm) would generally not have been sufficient for a reproductive response in gonochoristic species, because predaceous nematodes would have been unlikely to find conspecific mates within their microcosm. However, it is unclear whether their response in the field experiment was reproductive. Although the generation times of Monochida are not well studied, smaller microbivorous and herbivorous nematodes have generation times between 4 and 14 days under laboratory conditions at 18 °C (Vanc-oppenolle, Borgonie & Coomans 1999). Larger Mononchida at cooler temperatures in the field likely have longer generation times, so the rapid response of predatory nematodes in the field experiment (by day 16) suggests that predators were aggregating into soil cores in the high processing treatment rather than responding through increased reproduction. Although the dispersal of predaceous nematodes has not been studied, smaller plant parasitic and entomopathogenic nematodes can disperse up to 6–8 cm day^{-1} (Pinkerton *et al*. 1987; Strong *et al*. 1996). An aggregative response by predators would not have been possible in the laboratory microcosm experiments, however, where the soil cores were isolated.

Although Mononchid predators reduced bacterivore abundances in the predation experiments, they did not eliminate the difference in bacterivore abundances between grass addition and 100% processing treatments, as appears to have occurred in the field experiment. The movement of predators into and out of microcosms in the field may have reduced the differences in bacterivore abundances between treatments, because predators may have fed preferentially in microcosms with greater bacterial productivity, in which bacterivores had larger population growth rates. Conversely, the confinement of predators in laboratory microcosms may have exaggerated differences in abundance between treatments by preventing predators from leaving prey-depleted microcosms.

POSSIBLE MECHANISMS FOR THE FACILITATION OF BACTERIVOROUS NEMATODES BY *PORCELLIO SCABER*

Bacterivorous nematode populations are known to increase in response to elevated bacterial abundance or productivity (Mikola & Setälä 1998; Venette & Ferris 1998) and appear to have done so in the laboratory microcosm experiments. Isopod processing of litter may increase bacterivore abundances through two mechanisms; the direct addition of bacteria in isopod faeces or the stimulation of resident bacteria in the soil. The density of bacteria in isopod faeces, however, is generally similar to that of the litter consumed (Zimmer & Topp 1998; Kautz, Zimmer & Topp 2002; although see Gunnarsson & Tunlid 1986 for an exception). It is therefore unlikely that the addition of bacteria in faeces alone could account for increased bacterivore abundances over periods of 40–60 days. Bacterivorous nematodes are most likely responding to increases in the abundance of resident soil bacteria.

Isopod digestion alters the quality and condition of detritus in a variety of ways which may affect soil bacteria. Comminution of litter has long been considered the primary role of detrivores in decomposition (Swift, Heal & Anderson 1979) and is believed to facilitate bacteria by increasing the surface area to volume ratio of detritus. *Porcellio scaber* in the coastal prairie reduces grass litter with length generally > 10 cm and widths 1–8 mm to faeces with an average length of 1·0 mm and width of 0·5 mm (J.L. Bastow unpublished data; Nguyen *et al*. 2007). Although mechanically ground litter increases bacterivore abundances 85%, relative to intact litter, it supports lower densities of bacterivores than isopod faeces (Bastow 2007). This suggests that comminution contributes to the facilitative effect of isopods on bacterivorous nematodes, but that other changes to detrital resource quality are important as well.

In addition to reducing the particle size of detritus, isopod digestion reduces the carbon-to-nitrogen ratio (C : N) (Gunnarsson & Tunlid 1986; Kautz, Zimmer & Topp 2002) of detritus. In experiments in which I independently varied the carbon lability and nitrogen content of artificial substrates, high nitrogen substrates increased the abundance of bacterivorous nematodes in the Bodega Marine Reserve soil by between 20% and 236% (Bastow 2007). This suggests that the effect of isopods on detrital C : N may be important in understanding the interaction between *P. scaber* and soil nematodes.

ISOPOD LITTER PROCESSING MAY NEGATIVELY AFFECT FUNGIVOROUS NEMATODES

Fungivorous nematodes were not affected by simulated litter processing by isopods in the laboratory microcosm experiments, although their abundance was reduced by the highest level of isopod processing in the field experiment. Although isopod faeces contain high densities of fungal propagules (Gunnarsson & Tunlid 1986; Hassall, Turner & Rands 1987), isopods are known to suppress fungal standing crops in microcosms (Hanlon & Anderson 1980; Kayang, Sharma & Mishra 1996). Fungi are better able to use litter on the soil surface than are bacteria (Beare *et al*. 1992) and are therefore less likely to benefit when detritivores accelerate the incorporation of surface detritus into soil. Surface feeding detritivores, like *P. scaber*, may directly compete with fungi for surface litter and may reduce fungal biomass through direct consumption. Additionally, because fungal hyphae can penetrate detritus, comminution by detritivores will likely have less of a stimulatory effect on fungi than bacteria. It is therefore surprising that fungivores were not suppressed by simulated isopod processing of litter in laboratory experiments.

The highest level of isopod processing did suppress fungivores in the field experiment, and this effect was apparent on the time-scale that the laboratory experiments had been conducted (i.e. the first 60 days). This suggests that the difference between laboratory and field experiments in fungivore response is not a temporal artefact, but instead arose from differences in experimental conditions or interactions with the larger food web. Predaceous nematodes were also more abundant in the 100% processing treatment, so the reduced abundance of fungivores may have resulted from increased top-down control.

THE TEMPORAL AND SPATIAL CONTEXT OF ISOPOD–NEMATODE INTERACTIONS IN THE COASTAL PRAIRIE

Heard's (1995) processing chain model predicts that upstream consumers will have a short-term facilitative effect on downstream consumers if they increase the rate of resource processing. It is perhaps not surprising then that terrestrial isopods, which can increase decomposition rates (Kautz & Topp 2000; Hättenschwiler & Bretscher 2001; Zimmer, Kautz & Topp 2005), soil organic matter (J.L. Bastow unpublished data) and soil microbes (Hanlon & Anderson 1980; Hassall, Turner & Rands 1987; Kayang, Sharma & Mishra 1996) facilitate bacterivorous nematodes in the short term. At equilibrium, however, Heard's (1994a) model predicts that whether upstream consumers positively or negatively affect downstream consumers depends only on whether they increase or decrease the efficiency of resource processing, and not on whether they increase the rate of resource processing. In the absence of isopods or other detritivores, litter would become available to soil microbivores through surface litter feeding by microbes and abiotic degradation of litter. Although it is unclear how efficiently grass litter is converted into soil organic matter or soil bacteria in the coastal prairie through these processes, it is likely that *P. scaber* reduces the efficiency of this conversion by assimilating 50% of the grass litter it consumes. If *P. scaber* reduces the efficiency of resource processing, the facilitative interaction between isopods and the bacterial channel of the food web observed in these experiments would be predicted to shift to a negative interaction at some longer time-scale, although this was not seen in these experiments.

Heard's (1994a) equilibrium predictions come from a model with a continuous input of unprocessed resource, however, while the soil food web in the California coastal prairie

experiences an annual pulse of litter. Because of this annual input of litter, short-term facilitative effects of isopod processing may overwhelm any equilibrium negative interaction, if that equilibrium is not reached within a year. Longer experiments, ideally including the episodic input of grass litter, would be necessary to determine whether isopod processing of litter negatively impacts the bacterial channel of the soil food web at any ecologically relevant time-scales.

Although bacterivorous nematodes increased in response to even the lowest level of processing in laboratory microcosm experiments, predaceous nematode abundance in the field experiment increased only in the 100% processing treatment. It is therefore unclear whether the predator response is important at the average level of isopod processing at the Bodega Marine Reserve. Because of the consistent response of bacterivorous nematodes in laboratory microcosms to 25% litter processing by isopods in multiple experiments (Bastow 2007), it seems likely that this level of processing is sufficient to stimulate the bacterial channel of the soil food web. The apparent lack of response to the 25% processing treatment by either bacterivorous or predaceous nematodes in this field experiment may reflect the fact that background heterogeneity is greater for the less abundant predaceous nematodes, or that there is some variation in the occurrence of the processing chain facilitation. Alternately, it may be related to the aggregative mechanism behind predator responses. If the surrounding matrix of coastal prairie experiences an average 29% litter processing by isopods (Bastow, Preisser & Strong 2008), predaceous nematodes may only respond to experimental increases in isopod processing above the background level (such as the 50% and 100% processing treatments).

These experiments deliberately isolated litter processing by *P. scaber* from other effects that the isopod may have on soil food webs. Macroscopic soil invertebrates, such as isopods, millipedes and earthworms, often have considerable effects on the physical structure of the soil ('bioturbation', Scheu & Setälä 2001), and isopods are also known to feed on live plants (Paris & Sikora 1965) and other invertebrates (Edney, Allen & McFarlane 1974). Bacterivorous and predaceous nematodes may, therefore, be negatively affected by *P. scaber* through other mechanisms excluded from these experiments by the absence of live isopods. Hoekman, Winston & Mitchell (2009), for example, found that detritivorous midge larvae directly predated rotifers, thus negatively impacting a member of the food web which might have benefited from its processing of detritus. The net effects of isopods on this soil food web are, therefore, not clear from this study, and future experiments that measure the response of soil nematodes to different densities of live isopods would be very informative. Litter processing by isopods appears to have widespread effects on soil nematodes, and hopefully having isolated these effects in this study will make it easier to understand the mechanisms underlying the results of such experiments.

Moore *et al.* (2004) refer to processing chains as 'a fundamental feature of detritus-based food webs.' Consumer succession is a well-known phenomenon in detrital food webs, and processing chain interactions are likely the mechanism behind many such successions. Since early successional consumers tend to reduce total resource quantity (through their assimilation of ingested detritus), facilitative interactions are more likely if resource quality or condition has larger effects on late successional consumers than resource quantity. Resource quality appears to be of particular importance for detrital food webs (Wardle & Lavelle 1997), and processing chain interactions are likely to be a common feature of such systems. Although further studies are necessary to determine the long-term dynamics of processing chain interactions at the Bodega Marine Reserve, this study demonstrates that a processing chain facilitation affects the assemblage of soil nematodes in the coastal prairie. Additionally, this study shows that top-down forces may determine how processing chain interactions are manifest in complex food webs.

Acknowledgements

This study would not have been possible without the generosity of Bruce Jaffee, who provided laboratory space and nematology expertise. I thank Donald Strong, Bruce Jaffee, Thomas Schoener, Camille McNeely and three anonymous reviewers who provided helpful comments on drafts of this manuscript, and Brian Bastow, who constructed Baermann funnels for this project. Jeanne Mai was an enormously helpful laboratory assistant. This study was made possible by funding from the National Science Foundation (Graduate Research Fellowship and Doctoral Dissertation Improvement Grant DEB #0508759) and the Center for Population Biology. I acknowledge the Bodega Marine Reserve, and its managers, Peter Connors and Claudia Luke.

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Received 19 January 2011; accepted 3 April 2011
Handling Editor: Daniel Stouffer

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Soil moisture content and rainfall during the field experiment.

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