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Trophic structure of a macroarthropod litter food web in managed coniferous forest stands: a stable isotope analysis with δ^{15}N and δ^{13}C

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Summary

We studied the composition of a litter detrital community in a temperate coniferous forest using stable isotopes of nitrogen and carbon. Samples of mineral soil, bulk litter material, macroarthropods and understory plants were collected from ten experimental forest stands. Half of the stands were previously thinned 17–42 years ago, the other half served as controls. Values of δ^{15}N and δ^{13}C were based on the analysis of almost 500 individuals of at least 22 species in 11 arthropod families. The isotopic analysis showed a significant increase in δ^{15}N and δ^{13}C values with soil depth. Isotopic signatures of macroarthropods ranged from −26.51‰ to −20.52‰ for δ^{13}C and −2.85‰ to 5.10‰ for δ^{15}N. All consumers showed levels of ^{13}C enrichment substantially higher than those of primary producers and litter. Predators were generally significantly more ^{15}N enriched than detritivores and herbivores, but their δ^{13}C levels were similar to those of primary consumers. Our data indicate that this community consists of at least 2–3 trophic levels with a considerable amount of variation in the ^{15}N enrichment among detritivores and predators. We suggest that the spread of δ^{15}N values of predators likely reflects the diversity of potential prey among detritivores and a varying degree of intraguild predation among different species. Our findings generally agree closely with the results of similar studies from other forest litter communities. Thinning did not appear to influence the overall isotopic composition of the detrital food web. Extensive omnivory and intraguild predation among litter consumers may buffer long-term effects of thinning on the trophic structure of these species-rich communities.
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Introduction

Analysis of trophic relations with natural abundance measurements of stable isotopes has gained popularity in contemporary ecological research. The ratio of concentrations of heavy to light isotopes of an element in consumer tissue largely reflects that of its food resource and can provide integrated information on the feeding history of the organism over time (Peterson and Fry, 1987). Isotopic signatures of carbon ($^{13}C/^{12}C = \delta^{13}C$) and nitrogen ($^{15}N/^{14}N = \delta^{15}N$) are the most commonly used ratios, and in combination can help construct the food chain of a system under investigation (Peterson and Fry, 1987; Rundel et al., 1989). Since the increase in $^{13}C/^{12}C$ at each trophic transfer averages less than $<1‰$ (Fry et al., 1978; Fry and Sherr, 1984; McCutchan et al., 2003), the carbon ratio can help identify the consumer's diet and ultimately trace the basal carbon source in food webs (Araujo-Lima et al., 1986; Peterson and Fry, 1987; Anderson and Polis, 1998). Conversely, the value of $\delta^{15}N$ increases more rapidly as nitrogen passes from one consumer to another, with average estimates of $\Delta\delta^{15}N$ of $2.3 \pm 0.2‰$ (McCutchan et al., 2003), $2.5 \pm 0.1‰$ (Vanderklift and Ponsard, 2003) or as much as $3.4 \pm 1.1‰$ (Minagawa and Wada, 1984). Historically, the trophic enrichment of nitrogen was assumed to be relatively constant among a wide range of animals (Minagawa and Wada, 1984; DeNiro and Epstein, 1981), and consequently nitrogen ratios have been used as indicators of trophic position, or the degree of intraguild predation and cannibalism among consumers (Peterson and Fry, 1987; Hobson and Welch, 1995; McNabb et al., 2001). Recent reviews, however, caution that rates of nitrogen enrichment are more variable among different organisms and may reflect their position in the food web (McCutchan et al., 2003; Vanderklift and Ponsard, 2003).

Despite the potential of stable isotopes in soil food web research, their application in this field has been limited to a few studies (Neilson et al., 1998, 2002; Tayasu, 1998; Ponsard and Arditi, 2000; Scheu and Falca, 2000; McNabb et al., 2001; Setala and Aarnio, 2002). More recently, two large food web analyses of forest soil and litter were conducted by Scheu and Falca (2000) in beech forests in Germany and by Ponsard and Arditi (2000) in mixed deciduous forest stands in France. Both studies showed close similarities in the trophic structure between the two communities, with the majority of consumers belonging to 2–3 trophic levels largely comprising two broad categories of detritivores and predators.

Selective stand thinning has become an essential tool of forest management in the western United States. Despite its increasing use in the region, consequences of this management technique to soil and litter food webs are poorly understood. Evidence from a few studies shows that thinning can trigger significant shifts in the population dynamics of forest litter invertebrates, presumably in response to alterations of the temperature and moisture regimes of soil and litter following tree removal. Huhta (1971) found short-term negative effects of thinning on spider abundance and an increasing dominance of species characteristic of open habitats in pine stands in Finland. Hoekstra et al. (1995) reported an increased abundance of litter detritivores and reduced densities of predaceous arthropods in selectively harvested stands in coastal redwood forests of central California. In contrast, intensive thinning appears to increase the carrying capacity of litter for earthworm populations, likely as a result of improved microclimatic conditions and litter palatability (Castin-Buchet and André, 1998). In the current study system, Peck and Niwa (unpubl. data) found significantly higher densities of several species of spiders and carabid beetles (Carabidae) in thinned stands compared to unthinned stands 16–46 years after thinning. The implication of these findings is that community changes among litter invertebrates following thinning may alter feeding interactions among key functional groups in the food web, which can have consequences for litter decomposition and nutrient cycling processes.

Stable isotopes may prove a useful tool to evaluate effects of habitat alteration on food web dynamics. Blüthgen et al. (2003) found that ant colonies of the same species had significantly lower levels of ^{15}N enrichment in early successional forest habitats compared to mature stands. The work by Neilson et al. (2002) showed that sheep grazing can alter the community of primary producers, which can then modify isotopic values of soil detritivores and predators.

In the current study, we used a stable isotope technique to gain a better understanding of trophic links among soil arthropods in a temperate coniferous forest. Our objectives were to: (1) test general patterns of the soil food web structure suggested by previous stable isotope studies and (2) to evaluate the extent of food web change due to thinning suggested by our ongoing work in this system. Although we examined a wider range of organisms, we focused on spiders and carabid beetles since these taxa figure prominently in the dynamics of litter food webs (Wise et al., 1999; McNabb et al., 2001; Halaj and Wise, 2002; Moore

et al., 2002) and appear particularly sensitive to changes in forest structure (Huhta, 1971; Hoekstra et al., 1995; Peck and Niwa, unpubl. data).

Materials and methods

This study was conducted in the Cascade Mountains of southern Oregon, USA, near 42°07′, 122°26′, in a forested area spanning an elevation from 1092 to 1556 m. The habitat was a late-successional coniferous forest dominated by white fir (*Abies concolor* Lindl. Ex Hildebr.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with minor components of sugar pine (*Pinus lambertiana* Dougl.), ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws), and incense-cedar (*Libocedrus decurrens* Torr.). This region is characterized by moist winters and hot, dry summers, with mean monthly temperatures ranging from 2.0 (January) to 16.4 °C (July) and annual precipitation averaging 870 mm.

Samples of mineral soil (0–5 cm), litter, arthropods and plant material were collected at five sites (locations) within the study area July 15–17, 2001. Each site included a thinned and unthinned (control) stand situated less than 0.5 km apart. Paired experimental stands were similar in terms of tree age and composition, elevation, aspect and slope and ranged in size from 12 to 82 ha. The thinned stands were the result of selective harvesting implemented 16–46 years ago for the purpose of overstory reduction, mortality salvage or commercial thinning. This study area has been the focus of ongoing research investigating long-term effects of forest thinning on micro- and macroarthropods and rates of litter decomposition (Peck and Niwa, unpubl. data).

All stands were systematically searched for litter arthropods; specimens were hand-collected from litter, fallen woody debris and short (<1 m) understory vegetation (limited to linyphiid spiders; Linyphiidae) and placed singly in glass vials with moist cotton. In the laboratory, arthropods were sorted, identified and stored in a freezer at −34 °C until processing. Representative samples of understory plants (stems and leaves, excluding roots), litter and mineral soil were collected at 5–10 sampling points within each stand. Samples within the same category were pooled into a single composite sample for each stand. Litter samples comprised mostly conifer needles and twigs. Within each stand, we sampled 4–6 plant species with the greatest canopy coverage. Plant samples were stored in paper bags and air dried before processing. Samples of soil and litter were kept chilled in

3.8 l ziplock plastic bags during transport to the laboratory and were stored in paper bags at room temperature until further processing. Litter extraction failed to provide adequate amounts of microarthropod biomass for analysis therefore our isotopic assessment of detritivores is limited to macroarthropods. Due to budgetary limitations, only samples of arthropod and plant taxa with the greatest abundance and widest distribution across all study sites were analyzed for stable isotopes.

Isotopic analysis of carbon and nitrogen was performed by the Stable Isotope Research Unit of the Department of Crop and Soil Sciences, Oregon State University, using continuous flow-isotope ration mass spectrometry (CF-IRMS). Isotopic values of both elements were determined in separate runs of subsamples to achieve optimum results. All samples were oven dried at 60 °C for 24 h and ground in a ball mill or with a mortar and pestle until powdered. Arthropod, plant and litter samples comprised 1–1.5 mg dry weight for carbon analysis and 3–3.5 mg for nitrogen analysis. For soil analysis, 3–10 and 30 mg of dry material was analyzed for carbon and nitrogen, respectively. To ensure adequate amounts of dry animal tissue for the analysis, samples of the majority of taxa included bodies of more than one individual ($n = 1-10$). The prepared samples were combusted in an Europa Scientific Roboprep C/N analyzer (Dumas combustion/reduction apparatus) and combustion gases were analyzed on a PDZ Europa Hydra 20/20 isotope ratio mass spectrometer (PDZ Europa, Northwich, Cheshire, UK). Laboratory working standards were analyzed after every ten samples. Values of stable isotope ratios are reported as parts per thousand (‰) deviation (δ) from the international standard of the PeeDee limestone (carbon) and air (nitrogen): $\delta^{15}N$, $\delta^{13}C = [(R_{sample}/R_{standard})-1] \times 10^3$, where R corresponds to $^{15}N/^{14}N$ or $^{13}C/^{12}C$ (Peterson and Fry, 1987). The instrument precision for the mass spectrometer was <0.2‰.

Data were analyzed using ANOVA models for a randomized complete block design with five blocks (sites) and two stand treatments (thinned vs. unthinned). Stand-level averages were used for all response variables to avoid pseudoreplication (Hurlbert, 1984). Testing of thinning effects was restricted to the level of arthropod families or higher taxonomic groupings to ensure a meaningful sample size in the analysis. Differences in stable isotope values among different components of the food web were compared with two-tailed *t*-tests using combined data from thinned and control stands. To control the Type-I (i.e. false-change) error rate in our analysis, we applied a sequential

Bonferroni correction to tables of the ANOVA tests (Holm, 1979; Rice, 1989). All results are reported here as the original means and standard errors. JMP Statistical Software (SAS Institute, 1997) was used for all analyses.

Results

Our analysis found that thinning had relatively few effects on isotope signatures of litter consumers. Most of the predator families showed elevated nitrogen ratios and depleted carbon ratios in thinned stands but this pattern was not statistically significant (Table 1). The only group that showed a statistical difference was wolf spiders (Lycosidae) whose δ^{15}N values were significantly higher in thinned stands compared to unthinned stands ($P = 0.043$; Table 1). However, a posteriori significance assessment by a sequential Bonferroni test declared all ANOVA tests for δ^{15}N and δ^{13}C nonsignificant ($P > 0.004$) at a table-wide α level of 0.05, which suggests that the result for lycosids could have been spurious, caused by Type-I error due to a high number of comparisons ($k = 14$). Since thinning did not appear to be a major determinant of isotopic values in this study, we pooled data from thinned and control stands for subsequent analysis of food web structure.

Isotopic signatures of the soil profile showed a wide range of values for both carbon and nitrogen (Fig. 1). Compared to the litter layer, the sample material from the mineral soil horizon was significantly enriched in ^{15}N and ^{13}C by as much as 3.76‰ and 3.00‰ (t-test, P's < 0.001), respectively. With a mean δ^{15}N of -0.86, forest understory plants showed a significantly higher ^{15}N ratio than litter ($t_{18} = 3.02$, $P = 0.007$) but their ^{13}C values were depleted by 1.2‰ compared to the dead organic matter ($t_{18} = 5.46$, $P < 0.001$). Individual species of primary producers, however, spanned a wide range of nitrogen and carbon ratios (Table 2). For example, samples of *Symphoricarpos mollis* (trailing snowberry) were more depleted in ^{15}N than those of the litter (Table 2, Fig. 1).

Isotopic signatures of litter macroarthropods ranged from -2.85‰ to 5.10‰ for δ^{15}N and from -26.51‰ to -20.52‰ for δ^{13}C (Table 2, Fig. 1). All consumers showed a significant enrichment shift along the carbon axis and their δ^{13}C values were on average 3.96‰ and 1.05‰ higher than those of primary producers and litter, respectively. Thysanura and millipedes (Diplopoda) showed the lowest ^{15}N enrichment and could be classified as primary consumers in this food web. Surprisingly, both groups of detritivores exhibited δ^{15}N values similar to that of bulk litter, though millipedes were marginally more enriched in ^{15}N ($t_{12} = 2.18$, $P = 0.05$) (Fig. 1). Diplopoda showed a great deal of variation in δ^{13}C among study sites, spanning

Table 1. Results of a randomized block design ANOVA for the effect of thinning on stable isotopic values of carbon (δ^{13}C) and nitrogen (δ^{15}N) for different components of the forest litter food web

Taxon	δ^{13}C				δ^{15}N				N^{b}
	Block F_{df}	Treatment F_{df}	Thinned Mean ($\pm$SE)	Control Mean ($\pm$SE)	Block F_{df}	Treatment F_{df}	Thinned Mean ($\pm$SE)	Control Mean ($\pm$SE)	
Araneae (total)	$5.14_{4,4}$	$3.54_{1,4}$	-23.95 (0.39)	-23.04 (0.75)	$2.54_{4,4}$	$0.45_{1,4}$	3.20 (0.14)	3.08 (0.19)	5
Agelenidae	$2.19_{2,2}$	$0.22_{1,2}$	-25.38 (0.20)	-25.19 (0.46)	$0.25_{2,2}$	$0.30_{1,2}$	2.36 (0.21)	2.62 (0.31)	3
Amaurobiidae	$3.60_{3,3}$	$2.61_{1,3}$	-24.40 (0.46)	-23.28 (0.95)	$2.55_{3,3}$	$0.38_{1,3}$	3.70 (0.55)	3.34 (0.52)	4
Cybaeidae	$3.33_{2,2}$	$0.002_{1,2}$	-23.47 (0.80)	-23.44 (0.51)	$2.22_{2,2}$	$0.71_{1,2}$	3.73 (0.27)	3.45 (0.32)	3
Linyphiidae	$1.54_{4,4}$	$0.004_{1,4}$	-23.03 (0.97)	-22.96 (0.94)	$0.49_{4,4}$	$0.78_{1,4}$	2.04 (0.10)	2.29 (0.22)	5
Lycosidae	$0.93_{3,3}$	$1.76_{1,3}$	-23.34 (0.64)	-22.06 (0.70)	$3.36_{3,3}$	$11.38_{1,3}{}^{c}$	3.97 (0.17)	3.51 (0.10)	4
Carabidae[a]	$2.14_{4,4}$	$3.30_{1,4}$	-23.98 (0.89)	-25.33 (0.28)	$3.34_{4,4}$	$0.03_{1,4}$	3.38 (0.31)	3.32 (0.34)	5
Chilopoda	$2.30_{4,4}$	$2.08_{1,4}$	-23.94 (0.38)	-23.43 (0.25)	$0.80_{4,4}$	$0.76_{1,4}$	3.73 (0.54)	3.20 (0.21)	5
Formicidae	$2.24_{4,4}$	$0.42_{1,4}$	-23.57 (0.73)	-23.98 (0.34)	$0.88_{4,4}$	$3.59_{1,4}$	0.03 (0.21)	0.75 (0.31)	5
Orthoptera	$1.98_{2,2}$	$0.06_{1,2}$	-24.97 (0.60)	-24.82 (0.46)	$0.55_{2,2}$	$0.16_{1,2}$	-0.08 (0.48)	0.15 (0.18)	3
Tenebrionidae	$0.49_{2,2}$	$0.10_{1,2}$	-23.41 (0.65)	-22.97 (1.04)	$0.19_{2,2}$	$0.59_{1,2}$	0.67 (0.28)	0.15 (0.44)	3
Plants	$1.25_{4,4}$	$0.29_{1,4}$	-28.78 (0.82)	-29.28 (0.56)	$1.35_{4,4}$	$0.09_{1,4}$	-0.76 (0.70)	-0.96 (0.22)	5
Litter	$7.13_{4,4}{}^{c}$	$3.11_{1,4}$	-25.90 (0.31)	-26.33 (0.39)	$2.40_{4,4}$	$0.23_{1,4}$	-2.14 (0.35)	-1.99 (0.22)	5
Soil	$0.44_{4,4}$	$0.63_{1,4}$	-23.50 (0.61)	-22.73 (0.54)	$0.70_{4,4}$	$1.31_{1,4}$	1.42 (0.33)	1.97 (0.30)	5

[a]Includes Cicindelidae.

[b]Number of study sites (blocks) used in the analysis.

[c]$P < 0.05$ without a Bonferroni correction; P = n.s. if adjusted for multiple comparisons at a table-wide α level = 0.05 and $k = 14$ taxa categories; test results without notations were nonsignificant.
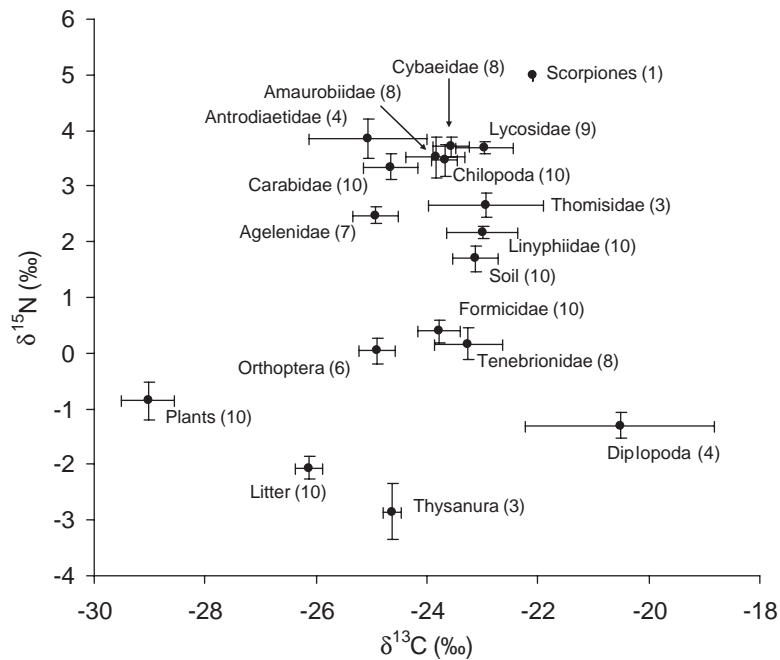
Figure 1. Mean values ($\pm$SE) of δ^{13}C and δ^{15}N for different components of the forest floor food web in combined data from thinned and unthinned stands. The number in parentheses indicates the number of stand-level values used in the calculation of the mean. See Table 2 for a detailed list of species included in the analysis.

more than 7‰. Grasshoppers (Orthoptera: Gryllacrididae and Acrididae), ants and tenebrionid beetles (Tenebrionidae) had overlapping values of δ^{15}N and clustered at an intermediate trophic position among the consumers (Fig. 1). Both ants (Formicidae) and tenebrionids, however, included taxa with distinctively higher δ^{15}N; *Formica* sp. and *Coelocnemis californicus* were more than 2‰ above the rest of the species in their respective families (Table 2). Orthoptera showed marginally lower levels of ^{13}C enrichment compared to ants ($t_{14} = 1.99$, $P = 0.066$) and tenebrionids ($t_{12} = 2.15$, $P = 0.05$). Mean isotopic values of the detritivore/herbivore assemblage (excluding ants) were -0.99‰ for δ^{15}N and -23.33‰ for δ^{13}C.

As expected for predatory arthropods, this group showed the highest δ^{15}N values among consumers. Predator δ^{15}N values ranged from 0.34‰ to 5.10‰ with a mean of 3.11‰. With the exception of ants, the levels of ^{15}N enrichment of predators were significantly higher that those of detritivores and herbivores. In contrast to nitrogen, however, ^{13}C enrichments of predators were generally within the range observed for detritivores, with the majority of top consumers clustering between the δ^{13}C values of Thysanura and millipedes (Fig. 1). Although a substantial amount of overlap was present in the degree of ^{15}N enrichment among predators, three trophic subgroups were apparent within this guild. The bottom of the predatory

spectrum was represented by three spider families, including sheet-web weavers (Linyphiidae), funnel-web builders (Agelenidae) and crab spiders (Thomisidae) with mean δ^{15}N values ranging from 2.17‰ to 2.65‰ (Table 2, Fig. 1). Carabid beetles, centipedes (Chilopoda: Lithobiidae), and spider taxa comprising Amaurobiidae, Lycosidae, Cybaeidae and Antrodiaetidae (trap-door spiders), showed intermediate levels of ^{15}N enrichment (3.35–3.85‰). Mean values of δ^{15}N and δ^{13}C in combined samples of spiders ($n = 10$) were 3.14‰ (± 0.11) and -23.49‰ (± 0.43), respectively. *Uroctonus* sp. (Scorpiones) appeared to be the apex consumer in this trophic chain, with δ^{15}N of 5.0‰, although some wolf spiders and carabid beetles appeared to share this ecological rank (δ^{15}N = 4.36–4.45‰) (Table 2). Surprisingly, spiderlings of *Allopecosa kochii* showed the highest level of ^{15}N enrichment among predators (δ^{15}N = 5.10‰). We speculate that this outlier value was perhaps the result of cannibalism among siblings.

Discussion

The bulk litter material was significantly more depleted in ^{15}N and ^{13}C than mineral soil in this study. Similar patterns have been reported from

Table 2. Mean values ($\pm$SE) of stable isotopic signatures of carbon (δ^{13}C) and nitrogen (δ^{15}N) for different species of the forest litter food web in combined samples from thinned and unthinned (control) stands

Taxon	δ^{13}C Mean ($\pm$SE)	δ^{15}N Mean ($\pm$SE)	N^a
Araneae			
Agelenidae			
Novalena intermedia	−24.14	3.10	1
Novalena sp. (juvenile)	−24.95 (0.40)	2.48 (0.16)	7
Amaurobiidae			
Callobius paynei	−23.62	3.75	1
Callobius severus	−24.10 (0.32)	3.51 (0.43)	4
Callobius sp. (juvenile)	−23.71 (0.85)	3.53 (0.52)	5
Antrodiaetidae			
Antrodiaetus pacificus	−24.01 (0.19)	3.99 (0.45)	3
Antrodiaetus sp. (juvenile)	−28.27	3.42	1
Cybaeidae			
Cybaeus sp. A	−24.07 (1.05)	3.00 (0.30)	2
Cybaeus sp. (juvenile)	−23.55 (0.34)	3.81 (0.17)	7
Linyphiidae			
Neriene litigiosa	−23.00 (0.64)	2.17 (0.12)	10
Lycosidae			
Alopecosa kochii	−22.82 (2.01)	3.94 (0.21)	2
Alopecosa sp. (juvenile)	−22.74 (0.88)	3.68 (0.15)	5
Alopecosa sp. (spiderlings)	−23.63	5.10	1[b]
Pardosa dorsalis	−21.87 (1.30)	4.45 (0.24)	4
Pardosa sp. (juvenile)	−23.42 (0.64)	3.57 (0.20)	9
Thomisidae			
Xysticus locuples	−22.81	2.79	1
Xysticus pretiosus	−23.95 (0.83)	2.67 (0.51)	2
Xysticus sp. (juvenile)	−21.22	2.45	1
Coleoptera			
Carabidae			
Pterostichus herculaneus	−24.46 (0.72)	3.26 (0.19)	10
Pterostichus inanis	−24.78 (0.96)	4.36 (0.95)	3
Pterostichus lama	−25.31 (0.03)	3.72 (1.62)	2
Pterostichus setosus	−26.51 (0.21)	2.50 (0.22)	2
Scaphinotus rugiceps	−26.23	2.53	1
Cicindelidae			
Omus cazieri	−26.37	2.97	1
Tenebrionidae			
Coelocnemis californicus	−20.84	2.66	1
Eleodes (*Blapylas*) sp.	−25.58 (0.36)	0.25 (0.57)	6
Iphthimus serratus	−20.99 (0.10)	0.25 (0.32)	2
Scotabaenus parallelus	−21.55 (0.23)	0.09 (0.32)	6
Hymenoptera			
Formicidae			
Camponotus sp.	−23.74 (0.38)	0.34 (0.18)	10
Formica sp.	−24.99	2.29	1
Plants			
Symphoricarpos mollis	−29.77 (0.48)	−2.56 (0.85)	4
Trientalis latifolia	−28.47 (0.89)	−0.23 (0.36)	10
Unidentified grass sp.	−27.48 (0.96)	−1.38 (0.78)	4

Mean δ^{13}C and δ^{15}N for arthropod families and higher taxonomic groupings are presented in Fig. 1.
[a]Number of stands used in calculations of mean values of isotopic signatures.
[b]Based on analysis of one clutch with 40 spiderlings.

other forest soil systems for ^{15}N (e.g. Ponsard and Arditi, 2000; Scheu and Falca, 2000) and ^{13}C (e.g. Balesdent et al., 1993; Ponsard and Arditi, 2000). Instances of increasing isotope ratios δ^{15}N and δ^{13}C with soil depth appear widespread and are generally related to the decay and migration of organic matter into deeper soil horizons during litter mineralization and export of ^{15}N-depleted nitrogen from soil via plant uptake and leaching (Balesdent et al., 1993; Nadelhoffer and Fry, 1994; Ponsard and Arditi, 2000). This process can lead to a relative depletion of ^{15}N in plants and produce largely positive δ^{15}N values of soils (Nadelhoffer and Fry 1994), a prediction supported by our findings. The extent of ^{15}N depletion in plants was highly variable in this study, which may reflect interspecific differences in metabolism and rooting depth or gradients of nitrogen availability in the soil (Lajtha and Marshall, 1994).

The δ^{15}N values of our consumers spanned a gradient of 7.9‰. A similar range of values has been documented for invertebrates in other forest litter communities (Ponsard and Arditi, 2000; Scheu and Falca, 2000) and crops (McNabb et al., 2001). Assuming a mean value of δ^{15}N for one trophic transfer to approximate 2.3–3.4‰ (Minagawa and Wada, 1984; McCutchan et al., 2003; Vanderklift and Ponsard, 2003), the range of nitrogen ratios of consumers in this study exceeded two trophic levels (2.31) but could be as high as 3.4 trophic levels. These results, however, should be interpreted with caution since the true $\Delta\delta^{15}$N of our consumers is unknown and its value may change singificaly with the consumer's diet. For example, the results of a recent meta-analysis suggest that whereas the mean $\Delta\delta^{15}$N of carnivores and herbivores can reach 2.7–3.0‰, a comparative value for detritivores can be as low as 0.5‰ (Vanderklift and Ponsard, 2003). In contrast to the highly ^{13}C depleted values of plants, isotopic signatures of litter and soil corresponded more closely with those of arthropods, supporting the prediction that detritus is the predominant source of carbon for local consumers and forms the trophic base of this community. Nonetheless, all consumers showed ^{13}C levels of enrichment substantially higher than that expected for one trophic level (>0.3‰) above the litter. Martin et al. (1992) and Ponsard and Arditi (2000) report similar results and suggest that detritivores may show dietary preferences and physiological bias toward assimilating compounds rich in ^{13}C.

Thysanura and millipedes showed the least amount of ^{15}N enrichment among the consumers, suggesting that these groups feed close to the bottom of the food web. The mean δ^{15}N values of detritivores were only within 1‰ of that of the

litter, which supports the results of Vanderklift and Ponsard (2003) and is consistent with the findings of Ponsard and Arditi (2000) and Scheu and Falca (2000) who report strikingly similar levels of ^{15}N enrichment between detritivores and litter. Ponsard and Arditi (2000) speculate that detritivores may selectively consume decomposers colonizing the litter or some chemical fractions of the litter that are more depleted. Since considerable differences in the level of ^{15}N enrichment may exist among different litter components (Scheu and Falca, 2000), stable isotope analysis of the bulk litter material alone may not provide the best estimate of the true trophic base in detrital food webs.

Ants and tenebrionid beetles appear to represent transitional consumers in this food web, trophically positioned between more typical detritivores and predators. Extensive evidence suggests that ants are omnivorous feeders (Carroll and Janzen, 1973). In a more recent study, Blüthgen et al. (2003) analyzed isotopic signatures of 50 ant species in a tropical rainforest in Australia and showed a considerable range of values among individual ant species as well as overlap with isotopic values of other herbivorous and predators. The majority of ants in our samples were Camponotus sp. Interestingly this genus showed one of the lowest levels of ^{15}N enrichment among the species investigated by Blüthgen et al. (2003), suggesting that these ants feed lower in the food web. A high consumption of nectar, honeydew or even fungal mycelia by Camponotus spp. (Ayre, 1967; Blüthgen et al., 2003) could deplete ^{15}N levels in these ants.

Tenebrionid beetles are predominantly generalist plant feeders (Calkins and Kirk, 1973; Rogers et al., 1988) but some species occasionally consume dead or live animal material (Kramm and Kramm, 1972; Rogers et al., 1988). Feeding on more enriched litter compounds or opportunist consumption of animal tissue could elevate the δ^{15}N values of some tenebrionid species above those of more typical detritivores as suggested by high nitrogen values of C. californicus (2.66‰ δ^{15}N) and Eleodes sp. (1.61‰ δ^{15}N; one sample of five individuals) in our study.

Grasshoppers are not typical members of the detrital food web since they primarily consume living plants. Our observations, however, show that these grazers spend considerable time on the litter surface and could become functionally linked to this community through predation by litter predators, especially spiders. Tissue of several spider families in this study was enriched by more than 3.4‰ above that of Orthoptera (0.04$\pm$0.23‰ δ^{15}N) supporting this prediction. Compared to the

isotopic signatures of individual plant species, grasshoppers showed exceedingly high values of ^{13}C ($>2.58‰$). This contrasts with findings of Fry et al. (1978) who found a close correspondence between δ^{13}C values of grasshoppers and their host plants for a wide range of species. It is possible that grasshoppers in our study consume different plant species than those analyzed here. Some members of the family Gryllacrididae are also likely omnivorous (Lightfoot, 1986), which may further obscure the trophic position of this group. Overall, isotope results for "typical" plant feeders in our study support conclusions of Gunn and Cherrett (1993) who suggest that high levels of omnivory and feeding complexity among consumers can blur boundaries between the herbivore and decomposer compartments of some soil food webs.

Predaceous arthropods occupied the highest position in this food web, with a mean value of δ^{15}N more than 4‰ above that of detritivores, but they did not form a homogenous group of consumers. Individual species showed a considerable variation in the level of nitrogen enrichment spanning a gradient of 4.7‰ δ^{15}N. Similar findings showing predators positioned more than one trophic level (3.4‰ δ^{15}N) above their potential prey species and a wide range of δ^{15}N values of predators were also reported by Ponsard and Arditi (2000) and Scheu and Falca (2000). These results may not be surprising given the diversity of potential prey among detritivores, and the fact that a high percentage of litter predators are generalists that opportunistically engage in cannibalism and intraguild predation. Scheu and Falca (2000) suggest that some predators may selectively prey on more nitrogen-enriched groups of detritivores that consume a higher proportion of microorganisms (secondary decomposers), which would tend to increase the isotopic variation among these consumers. In contrast, Ponsard and Arditi (2000) view the above patterns primarily as being the result of intraguild predation. As pointed out by Scheu (2002), however, these explanations should not be viewed as a dichotomy since both of these trophic pathways will to some extent be present in all soil food webs. It is difficult to establish the relative contribution of IGP to ^{15}N enrichment among generalist predators in this food web. This issue is complicated by the fact that the true range of δ^{15}N values of detritivores is unknown unless a more comprehensive sampling of the detritivore community is performed. In addition, more precise determination of trophic position for predators will require laboratory experiments to ascertain levels of nitrogen enrichment for individual taxa.

In conclusion, we found no clear evidence of long-term effects of thinning on the isotopic content of the litter community. Our results indicate that the effect of thinning is either non-significant or mostly confined to some top consumers, as suggested by the tentative results for lycosids. Neilson et al. (2002) showed that effects of grazing can propagate through a food chain and affect the isotopic signatures of consumers within at least two trophic levels. In contrast to our study, Neilson et al. (2002) focused on relatively short-term effects of disturbance (4 years) in a simpler, grassland community. We suggest that extensive omnivory and IGP among generalist feeders in a species-rich litter system may buffer long-term effects of thinning for most consumers. This study provides more evidence that stable isotopes can be a useful technique to investigate trophic links in detrital food webs. With the exception of Diplopoda and several spider taxa, which showed an increased variation in their δ^{13}C values, isotopic signatures of most consumers were remarkably similar among individual study sites, which supports the robustness of our findings. Our data show a high degree of omnivory among arthropods and suggest that most taxa in this food web fall within two broad categories of consumers, comprising arthropods predominantly consuming detritus and plant material and predatory species, which is in close agreement with the findings from other forest litter communities (Ponsard and Arditi, 2000; Scheu and Falca, 2000). Future studies will be needed to further clarify food resources of predators in this food web and to evaluate their role in structuring litter communities in general. Experimentation will be an indispensable and likely the most promising approach to advance our understanding of these systems (Scheu, 2002).

Acknowledgments

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