Soil Macrofaunal Community Structure and Decomposition Processes Are Closely

Linked in a Northeastern Deciduous Forest

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Ellen Trimarco

ABSTRACT

Soil Macrofaunal Community Structure Influences Decomposition Processes in a

Northeastern Deciduous Forest

Ellen A Trimarco

Several factors are thought to influence litter decomposition including

temperature, litter quality and composition, edaphic factors, and the structure and

composition of decomposer assemblages. Numerous studies have documented a variety

of influences of invertebrates in litter decomposer microfaunal assemblages on rates of

decomposition, with most species enhancing decomposition rates and nutrient cycling,

though the importance of trophic structure is less well studied and the relative importance

of biotic over environmental control also appears to vary among studies. We conducted a

coarse scale ($25m^2$) observational study of macroinvertebrate and salamander

communities and their surrounding leaf litter environment at Black Rock Forest,

Cornwall, New York to assess the role of these organisms on litter decomposition. We

examined whether trophic structure was important in determining ecosystem function in

leaf litter decomposer communities by examining how increased carbon storage in the top

layer of soil (O and A horizons) responded to variation in community structure and

composition and trophic structure or whether control was primarily environmental.

Although salamander biomass had no effect on macroinvertebrate diversity, the percent

mass loss of woody substrates placed in all plots was significantly related to

macroinvertebrate diversity. Moreover, macroinvertebrate diversity was significantly

associated with total soil carbon and total soil nitrogen. The only invertebrate Order,

however, that was correlated with any factor by itself (outside of a functional group) was

the Araneae which was related to the percent mass loss of leaf litter. These results

confirm that trophic structure of the macroinvertebrate community may influence

decomposition processes within this and possibly other Northeastern deciduous forests.

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Acknowledgements

<u>Dedication</u>

To my grandfather, Giacomino Orlando who was a fine fisherman and naturalist as well

as a scholar of linguistics and science, and to my grandmother, Josephine Orlando, a wise

and loving woman with *joie de vie*.

INTRODUCTION

Several factors are thought to influence decomposition including differences of air and

soil temperature, composition of decaying organic mater, and structure of decomposer

assemblages (Swift et al. 1979; De A. Ribas et al. 2006). This last factor, the structure of

the decomposer assemblage, coupled with a specific ecosystem- Northeastern Deciduous

Forests, forms the focus of this study.

Northeastern Forests face such anthropogenic threats as over-harvesting (Petranka

et al. 2003), climate change (including unpredictable storms, more frequent storms and

changes in average air temperature) (Barron 2004), and invasive species (Lavelle et al.

1997). In light of the many threats posed to Northeastern Forests in the near future,

studies investigating the nature of vital biogeochemical processes, such as carbon storage,

within ecosystems may aid in predicting the fate of these processes and be applicable to

conservation and management efforts. The biogeochemical activities of carbon storage,

as facilitated by the decomposition of organic matter, is vital to the health and

maintainance of Northeastern Deciduous Forests. These biological systems have served

as a carbon sink since the glaciers receded during the Holocene some 10,000 years ago.

Black Rock Forest, located in Cornwall, New York, is an ideal location to study

decomposition processes and what factors drive or maintain them.   In order to decipher

what factors, whether biological or environmental, are driving decomposition at Black

Rock Forest, I tested the hypothesis of biotic dominance of forest litter decomposition

using the leaf-litter dwelling macrofaunal communities   Factors that I compared included

environmental factors such as, elevation and moisture, with biological factors, such as salamanders) and macroinvertebrates, in order to understand their relative influences over decomposition .

Numerous studies have documented that various invertebrates can enhance decomposition and nutrient cycling (Vossbrink et al. 1979; Douce and Crossley 1982; Seastedt and Crossley 1983; Whitford and Parker 1989; Reddy 1992; Hasegawa and Takeda 1996; Irmler 2000; Hunter et al. 2003). However, considerable debate surrounds which functional groups of macroinvertebrates affect biogeochemical processes such as decomposition. For instance, a rough division of leaf litter invertebrates and their functional groups could be based on trophic guild and consist of microbivores (i.e. mites and collembolans that graze on bacteria and fungi), fragmenters (i.e. earthworms and millipedes that consume leaf litter, thereby, increasing its surface area) and predators (i.e. spiders and ants that exert top-down trophic control) (Coleman et al. 2004). Most soil scientists seem to agree that higher taxonomic resolution provides better understandings of the roles of species or groups of species in influencing rates of decomposition (Coleman, 2004; Doblas-Miranda et al. 2007).

Weisser and Siemann categorize the ways in which insects influence nutrient cycling into six groups (2004) (1) Detritivores affect nutrient cycling through direct changes in carbon storage, resulting in a reduction of recalcitrant materials and an increase in decomposition rates (Weisser and Siemann 2004). (2) Ecosystem engineers, on the other hand, change the direction of carbon storage and modify habitat conditions for other organisms by substrate mixing, reduction and abrasion of particles, modification

of abiotic conditions, and a creation of fungal gardens (Weisser and Siemann 2004). (3) Predators and parasitoids alter food web interactions which affects trophic structure (Weisser and Siemann 2004). (4) Microbial feeders direct change of carbon storage and alter food web interactions through changing in decomposition rates and grazing on fungal hyphae (Weisser and Siemann 2004). Finally, (6) dispersal agents disperse other organisms through distribution of arbuscular mycorrhizal spores (Weisser and Siemann 2004). Intratrophic interactions can be as important as interactions among different trophic groups in terms of effects on biogeochemical processes such as decomposition (Lavelle et al. 1997; Lavelle 2002; Lawrence et al. 2004).

Detritivore communities also include vertebrates as well which are often much larger in body size and therefore of potentially greater influence on ecosystem processes and community structure. Salamanders are among the more common and well-studied vertebrates co-habiting decomposer communities and some studies have suggested that they can have significant impacts on rates of decomposition as predators of macrofaunal invertebrates (Wyman 1998).

North America is an ideal location in which to study the effects of salamander diversity on ecological functions because it harbors the greatest salamander diversity in the world (Larson 1996). Both families of northeastern salamanders, Plethodontidae and Ambystomatidae, face numerous threats to extinction which may in turn, lead to increased carbon efflux due to a decline in salamander populations. This may have broader ramifications for the northeastern deciduous forest systems carbon storage functions, and ultimately, forest functions as carbon sinks.

Salamanders can be found in nearly all northern temperate regions of the world overlapping with moist and cool habitat types (Larson 1996) including North, Central, and South America, Europe, and Eastern Asia (Duellman 1999). Salamanders have a particularly large impact on ecosystem functions due to their relatively high abundance among vertebrate predators (Davic and Welsh 2004). Some of these ecosystem functions include providing direct control of salamander prey, altering prey species diversity, translocating resources between terrestrial and aquatic migration habitats, altering soil dynamics via underground burrows, storing and providing a high energy food source to tertiary consumers throughout ecological succession (Davic and Welsh 2004) and decreasing the rate of carbon decay due to predation of various decomposer species (Wyman 1998). Especially important is the latter ecological function of salamanders, or the slowing of the rate of decomposition, since this function leads to increased carbon storage in forests with the presence of highly abundant salamander species (Wyman 1998).

Salamanders inhabit a diverse array of ecosystems including moist forest leaf litter, grasslands, subterranean dwellings , tree canopies, talus slopes, headwater streams, riparian ecotones, swamps, caves, ponds, and seasonally inundated pools (Petranka 1998). In their review, Davic and Welsh (2004) identified: controlling decomposer diversity and its impacts on detrital pathways that connect energy and matter between aquatic and terrestrial habitats through migration routes, contributing to soil dynamics through the construction of underground burrows, and supplying high energy food stores

for tertiary consumers throughout ecological succession as important roles, among others, that salamanders can play in the decomposer community.

Studies generally agree that a single salamander species tends to dominate local terrestrial salamander guilds (Davic and Welsh 2004). In Northeastern deciduous forests, the Northern redback salamander (*Plethodon cinereus*) is the most abundant salamander species (Shelford 1913). It is unknown whether salamanders are functionally redundant as reducers of decomposition rates, but it seems very likely that they are due to the mechanism of this function. In a calculation by Hairston in 1987, a southern Appalachian salamander guild consumed 5.80 kcal/m^2 annually (Davic and Welsh 2006). As functional controllers of prey species diversity, changes in salamander species richness may have an affect on the composition of prey species diversity (Davic and Welsh 2004).

Salamanders, as generalist predators, are known to decrease the rate of decay due to predation of species that consume and break down leaf-litter and essentially prevent efflux of this carbon from the forest to the atmosphere, furthering the overall function of northeastern deciduous forests as carbon sinks (Wyman 1998). For this reason, Wyman designed the only study of amphibian interactions with leaf-litter invertebrate communities and decomposition processes of the Northeastern United States. Experimental systems containing salamander abundances of 2/m^2 were compared with systems of 0/m^2 salamander abundance in a study by Wyman (1998). According to Wyman, the system containing salamanders prevented the loss of 261-476 kg/ha of carbon to the atmosphere due to decreasing the rates of decomposition by consuming both leaf matter and the organisms that break down leaf littler (1998). Wyman calculated

that the amount of carbon salamanders prevented from leaching the system was significant and resulted from a reduced rate of decomposition by between 11 and 17% due to salamander predation (1998).

Here, I test the possibility that salamander control over macrofaunal invertebrate community composition and structure alters rates of decomposition and soil carbon and nitrogen storage at Black Rock Forest. Given the considerable extent of Northeastern temperate forests in North America, climate change, and the potential importance of salamanders in controlling macroinvertebrate community structure, and hence, rates of decomposition, I pose that where salamander abundance is highest, soil carbon will be greatest and rates of decomposition will be least. Moreover, I seek to answer how exactly sites with greater rates of decomposition differ from sites with lower rates of decomposition in macroinvertebrate community structure organized by Order.

MATERIALS AND METHODS

Study Site: Black Rock Forest, New York

Located in the Hudson Highlands of Cornwall (Orange County), New York, Black Rock

Forest spans 1530 hectares (lat. 41^024^0N, lon. 74^001^0W) (Barringer and Clemants, 2003;

Schuster et al. 2005). Mean annual precipitation is about 1190 mm with an air

temperature range of $–2.7^0$C in January to 23.4^0C in July (Schuster et al. 2005). Soils in

the forest are generally acidic (pH 3.65-4.55) and include medium-textured loams that are

usually no deeper than 0.25-1.0m (Schuster et al. 2005).

The forest is composed of mostly upland mixed hardwood (Barringer 2002) and

oak-dominated forests where red oak (*Quercus rubra*) can be found as the most common

oak species (Barringer and Clemants, 2003). Other terrestrial habitats include: Cliffs and

rock outcrops, limestone erratics, grassy balds, hilltop scrub, hilltop woods, chestnut oak

woods, oak slope woods, sugar maple woods, hemlock coves, meadows and roadsides,

barberry/blueberry scrub, successional woods, conifer plantations, lawns, roads and paths

and rock quarries (Barringer 2002).

Survey Design

All observations and data collection for this study occurred within an oak dominated

northern facing slope of Black Rock Mountain (termed the "north slope" for this reason).

There is a single stream cutting through the study site, creating a brief discontinuity in the

plot delineations. The 50 hectare mature oak forest of the north slope is roughly 120

years of age and is representative of the surrounding area (Schuster et al. 2005). The

north slope was designed, experimentally, after the Harvard Forest in Petersham,

Massachusetts, so that results could be compared across sites (Schuster et al. 2005) and

consists of a three scale nested design. At the coarsest scale there are twenty $75m^2$ plots

that are aligned in three rows, with each row reaching a degree of higher elevation,

marked by stakes at each corner (termed "master plots") (Appendix B). Within each of

these plots lies a $25m^2$ center within which long-term studies are conducted (termed the

"center plots"). Within each of the center plots there are ten subplots arranged in two

parallel rows that measure $1m^2$ (termed "study plots").

Environmental Data

Decomposition

Decomposition was measured within center plots using two methods: litter bags (percent

mass loss) and popsicle sticks (rate of decomposition). Litter bags consisted of wire

screening with fine gaps large enough for microinvertebrates (fungi, bacteria, nematodes)

to pass through freely. Screening was cut to create a 10 x 10 x 1cm pocket and then filled

with red oak (*Quercus rubra*) leaves taken just outside the study site and dried at 60°C for

36 hours. Prior to stuffing the screening, red oak leaves were carefully cut into roughly

equal pieces the size of the pocket so that leaves would not be folded or broken when

making the litter bags. Litter bags were individually weighed and their weight adjusted

to roughly of 1.3g litter per bag. Litter bags were placed one per subplot per center plot

on 20 July 2006. Litter bags were collected on 10 September 2006 and oven dried in the

same manner as before. The difference between the initial and final oven dry mass was used to calculate percent mass loss of leaf litter.

In order to calculate percent mass through time, six popsicle sticks were arranged together in a bundle, stacked flush together and bound with gardening wire. For all bundles, all six sticks were labeled with a random subplot assignment and a stick number and then dried at 60°C for 36 hours and affixed to a systematic location within the chosen subplots on July 20, 2006. Sticks were then retrieved on the dates of August 17, 2006 (31 days elapsed), November 11, 2006 (102 days elapsed) and April 26, 2007 (283 days elapsed). Once retrieved, sticks were oven dried in the original manner mentioned previously and dry weight was recorded as percent mass lost of popsicle sticks.

Soil Carbon, Nitrogen, and Moisture

Soil cores were taken for each center plot in 2005 and percent soil carbon and nitrogen was determined using a COSTECH Analytical ECS 4010. Soil moisture was taken on July 17, 2006 (one week post-rainfall) with a Reotemp moisture meter. Moisture was read using the moisture meter on a conductance scale of 1-10 through a brass alloy probe. Three values were taken and averaged for four subplots within each center plot (subplots 1, 5, 6 and 10), and these four values were averaged again to produce the value of center plot average moisture.

Canopy Transmittance

Canopy photos were taken at a 1 meter height from ground level during August, 2006 and used to calculated canopy transmittance, or uMol light entering through the forest canopy.

Biological Data

Salamanders

Each center plot was surveyed during two time periods for salamanders by turning over all visible rocks and logs and recording for all individuals found, weight (g), SVL (mm), species and habitat substrate. All salamanders' ventral sides were photographed so that salamanders caught during the first sampling period were not counted twice during the second sampling period. For each center plot, time spent searching (per person hour) was also recorded so that the same effort would be spent on the second sampling period as in the first. Sampling periods were conducted from 24-27 July 2006 and again on 31 July - 2 August 2006.

Macroinvertebrates

Marcoinvertebrates were sampled from July 7, 2006 through August 22, 2006. Four subplots were systematically chosen for macroinvertebrate surveying. These subplots were the corner plots which provided coverage across the widest possible area. Macroinvertebrates were sampled over a constant surface area of 346cm^2 (in the form of a circle) placed 10cm outside each of the four 1m^2 subplots within each center plot. All leaf litter flush to the soil within this surface area was collected in a plastic bag. Once at

the laboratory, the wet weight of leaf litter was recoded for each sample.

Macroinvertebrates were extracted using the Berlese funnel method and sorted into

morphospecies.

Species were sorted to Order and then divided into functional groups for

preparation of statistical analysis according to a recent article by Doblas-Miranda et al.

(2007). Trophic functional groups were also confirmed with alternate literature (Wardle

2002; Coleman, 2004). A reference collection of digital images and preserved specimens

was maintained and contained all morphospecies types (available upon request of author).

Statistics

Diversity Measures

The Shannon diversity index was used to calculate the diversity of macroinvertebrate

morphospecies. From this value, morphospecies evenness was calculated. Species

richness was reported as the number of macroinvertebrate morphospecies types observed.

Linear Regression

Data were analyzed using SYSTAT 10.2 (SYSTAT 1994). Variables were tested for

normality and were log transformed where necessary. Bonferroni corrections were used

to account for multiple tests and significance was reported in terms of these transformed

P values (Tables 1 and 3).

Test for Sampling Date Bias

Julian dates for biological data collected (salamanders and macroinvertebrates) were

checked for correlation with all biological data so that sampling date bias could be ruled

out. It has been shown that macroinvertebrates (Doblas-Miranda et al. 2007) and

salamander communities (Davic & Welsh 2004) are vulnerable to seasonal population

flux, however, all collection dates were uncorrelated with population data, suggesting that

collection date did not influence data.

RESULTS

Salamanders

Salamander biomass was not a significant predictor for either macroinvertebrate

community structure or decomposition processes (Table 1). No significant association

between salamander biomass and macroinvertebrate diversity was detected. The density

of salamanders was generally lower than expected for this area (e.g., expected average

abundance of redback salamanders (*Plethodon cinerus*), is 1 per 1.5m^2 for the

Northeastern United States (Wyman 1998; David & Welsch 2004)), but diversity was

good. Four salamander species, including the redback (*Plethodon cinereus*, including the

"leadback" color phase), the northern slimy (*Plethodon glutinosus*) the northern two-

lined (*Eurycea bislineata*), and the red eft (*Notophthalmus viridescens*), were found in

modest densities (Figure 2). The redback salamander was the most abundant, but shared

near co-dominance with the northern slimy salamander (Figure 2).

Macroinvertebrates

Macroinvertebrate diversity, richness and evenness were regressed against environmental

and biological variables to test for significant relationships (Table 1). No regression

analysis resulted in significant results, however, four regression analyses were nearly

significant and these results are reported here as non-significant but are worth further

investigation. Both Shannon diversity and richness were related, although not according

to a Bonferroni corrected P-value, to the average percent wood mass loss (P = 0.053 (R^2

= 0.0439); P = 0.004 (R^2 = 0.609)) and evenness was related to both percent soil carbon

$(P = 0.002 \ (R^2 = 0.650))$ and percent soil nitrogen $(P = 0.001 \ (R^2 = 0.690))$ (Table 1; Figures 2 and 3).

An identical outlier was found for both regressions involving percent wood mass loss (Figure 3). It is possible that this outlier was due to higher average transmittance of light through the canopy than other plots coupled with a decrease in soil moisture. This higher average transmittance may mean a higher local temperature, which, when combined with lower moisture, predicts a higher local rate of decomposition for these plots. For this reason, a slightly elevated PML and decomposition rate of wood mass is not unreasonable.

The regression of soil carbon and nitrogen against macroinvertebrate evenness identified one point that that had large leverage. This point of leverage requires a cautious interpretation of the relationships between these variables. Therefore, this relationship could only truly be confirmed upon further data collection in the future if possible.

Order Level Analysis Results

All macroinvertebrate Orders were tested one at a time for relationships with decomposition variables (PML popsicle sticks, PML litter, % Soil Carbon and % Soil Nitrogen). Again, a Bonfferoni correction was applied to the significance value, α, of all regression analysis. This produced a highly conservative α of 0.0007 when all Orders identified from the study (Appendix C) were tested for relationships for the aforementioned environmental factors. Considering this stringent P-value the Bonferroni

correction produced, none of the Orders studied were significantly related to PML

popsicle sticks, PML litter, % Soil Carbon or % Soil Nitrogen. One Order shared a slight

relationship with a decomposition process variable, the spiders (Araneae). The Araneae

produced a regression coefficient with PML of popsicle stick (P = 0.042; R^2 = 0.459),

however, plot C2 served as an outlier in the regression (Figure 5).

Functional Group Analysis

Macroinvertebrate Orders fell into a functional group distribution, summed across all

plots, within some unevenness (Table 2). This uneven distribution of macroinvertebrate

Order abundance across the study site was due mostly to a single plot that contained a

large amount of ants which were classified functionally as omnivores which set plot B6

apart from other plots in terms of mean omnivores. This may explain why plot B6 held

so much leverage in previous regressions (Figure 4).

Next, functional groups were tested for relationships with decomposition. The

relationships between predators and PML wood and PML litter were significant (Table

1). The omnivore and herbivore functional groups produced significant results with

percent soil nitrogen and percent soil carbon in regards to p-values (Table 3), however,

these results were deem insignificant when large leverage occurred once again from plots

C2.

DISCUSSION

Overall, there is no support for salamanders exhibiting top-down control of macroinvertebrate community structures. The hypothesis that macroinvertebrate communities may affect decomposition, however, was supported for the northern slope of Black Rock Forest. These results are in agreement with a study by Huang et al. (2007) which experimentally enclosed toads (*Bufo bankorensis*) with invertebrates and measured the effects on invertebrate community structure or decomposition. Their findings show that the presence of the toads affected litter chemistry but not densities of litter invertebrates or rates of litter decomposition. Beard et al. (2003), however, found that experimental enclosures at two spatial scales containing the frog *Eleutherodactylus coqui* and various invertebrates revealed no influence of frog presence on invertebrate densities. In the same way these two studies differ in their test of vertebrate control over macroinvertebrate communities, this study differs from Wyman (1998). Wyman's (1998) study, however, was at a different temporal scale (long-term as opposed to this sing-season study), thus direct comparisons are difficult to make.

The relationship between spider densities and the wood percent mass loss does, however, suggest that top predators may control decomposer communities. The linear relationship identified in this study suggests that where spider densities are high, there is a slower rate of decomposition occurring. This result confirms a previous study by Lawrence and Wise (2004), which showed that spiders do, indeed, slow down the rate of decomposition by 20%, although the results were marginally significant (P = 0.057). Hence, spiders seem to be filling the functional niche salamanders were predicted to- that

of grazing on fungivores such as collembola in order to keep densities of decomposer

organisms lower, thereby lessening the rate of decomposition (Lawrence and Wise 2004).

Another result, although insignificant according to a Bonferroni correction, was

that of macroinvertebrate species richness (P = 0.004) and diversity (P = 0.053) as

important factors in the percent wood mass loss. This result suggests that as richness and

diversity of leaf-litter invertebrates increases, the rate of decomposition decreases.

When paired with the result that high spider and predator densities correlate with

lower rates of decomposition, it seems logical that invertebrate species richness and

diversity would also be correlated with lower rates of decomposition because the greater

the number of spiders or predators are present, the more trophic niches are created due to

predation by spiders on lower trophic levels. This availability of trophic niches creates a

space for a greater number of trophic levels- more trophic levels that solely detritivores

(i.e. earthworms) the functional group which is associated with the fastest rate of

decomposition (Lavelle et al. 1997)

Limits to inference

There are several limitations of this study that constrain inference. The fine mesh

of the litter bags may have underestimated decomposition of leaf litter (Coleman 2004).

Moreover, the microclimate within leaf litter bags is usually moister than that of outside

the bag, which can cause more favorable environments for microbial activity, and hence,

faster rates of decomposition (Vossbrinck et al., 1979). In either case, what this study

attempted to do was keep all error consistent across the twenty master plots so that data could be fairly compared across sites when site comparisons were appropriate.

Moreover, although spatial scale was roughly accounted for within the means of available labor and time, the temporal scale of variables may have been less than ideal. For instance, the wood percent mass loss was collected for over 200 days, whereas the macroinvertebrate data were only collected once, at one single time point. Considering that macroinvertebrate communities are temporally variable (Doblas-Miranda et al. 2007), this discrepancy could be important when interpreting results.

In addition, salamander sampling was conducted at a time when salamander subterranean densities are known to be highest (Davic and Welsh 2004) meaning that detection of individual salamanders is most likely grossly underestimated. However, the relatively high species richness of four salamander species is a good indicator that the sampling method was not species biased towards the most common species of this area, redback salamanders.

CONCLUSIONS

This study did not support a significant role for salamanders in regulating macroinvertebrate community composition and structure and the decomposition processes they regulate, but did identify the possibility that spiders do. It is possible that invertebrate richness is reduced which results in a slower rate of decomposition which leads to greater carbon storage in Northeastern Deciduous Forests. Spiders exhibited an inverse linear relationship with wood percent mass loss which suggests that where spiders are present in higher densities, grazing by lower trophic groups on litter or microorganisms may be lead to lower leaf fragmentation and lower decomposition. This, in turn, provides less surface area for microinvertebrates to colonize and digest, meaning a slower rate of decomposition. Factors that could be controlling spider densities remain unknown.

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FIGURES AND CAPTIONS

Figure 1. The proposed relationships between biological and environmental factors that influence the rates of decomposition in the leaf litter ecosystems of Black Rock Forest. Arrows indicate the direction of influence and plus and minus signs indicate whether the influence increases another factor (+) or diminishes it (-).

Table 1. Linear regression analysis for relationships between environmental factors and the log of macroinvertebrate morphospecies Shannon diversity index, richness and evenness. Asterisks represent statistical significance, adjusted according to Bonferroni corrections, (*$\leq$ 0.0017) and NS represents not significant.

Figure 2. Total number of individual salamanders of each species found for the study site summed for both catch days with counts of individuals found at abundance value and total proportion of individuals found at each abundance value (Pcin = *Plethodon cinereus*; Pglut = *Plethodon glutinosus*; Ebisl = *Eurycea bislineata*; and Nviri = *Notophthalmus viridescens*)..

Figure 3. Inverse relationships between average percent mass loss for average percent mass lost popsicle stick and a) log macroinvertebrate morphospecies Shannon diversity index (P = 0.05 (R^2 = 0.044)) b) log macroinvertebrate morphospecies richness (P = 0.004 (R^2 = 0.609)).

Figure 4. Effect of log macroinvertebrate evenness on a) percent soil carbon (P = 0.002)

b) percent soil nitrogen (P = 0.001).

Figure 5. Inverse linear relationships between Araneae and average percent mass lost

(PML) popsicle stick (P = 0.042).

Table 2. Total number of individuals summed across all plots within each

macroinvertebrate functional group.

Table 3. Linear regression analysis for relationships between environmental factors and

the log of macroinvertebrate morphospecies Shannon diversity index, richness and

evenness. Asterisks represent statistical significance, adjusted according to Bonferroni

corrections, (*≤.002) and NS represents not significant.

Figure 1.

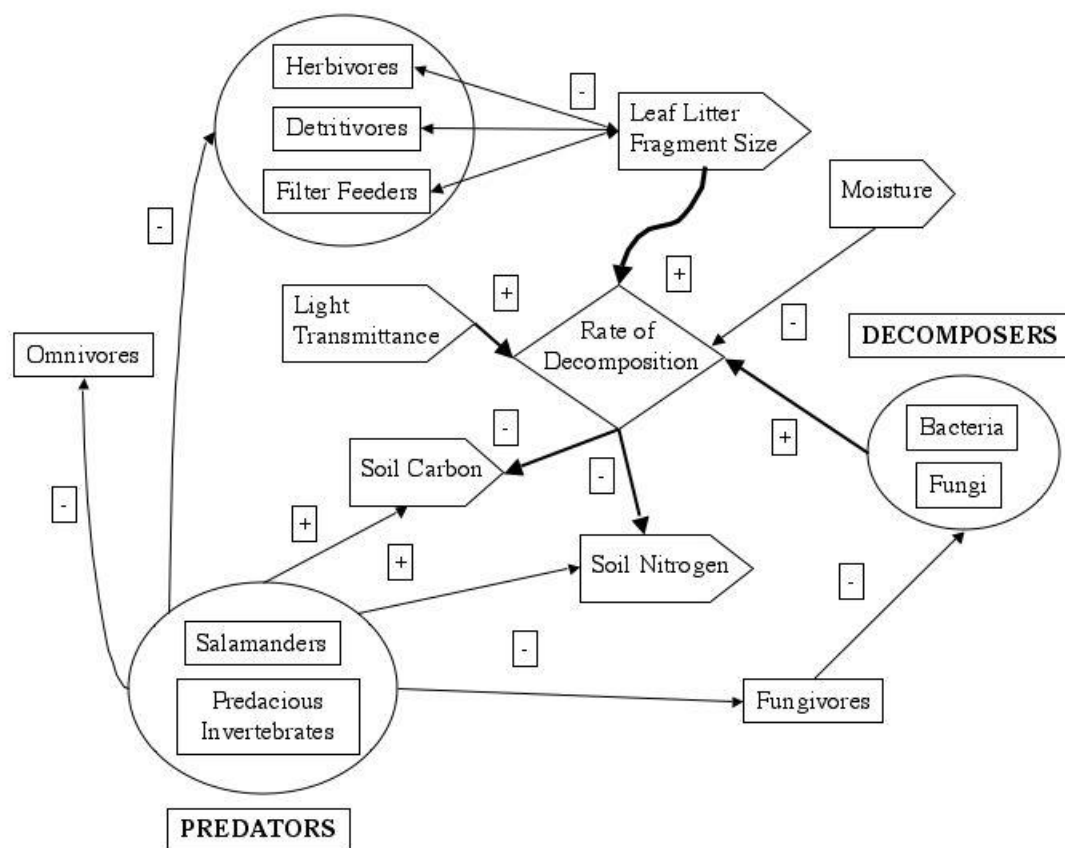Table 1.

|	Shannon Diversity	Richness	Evenness
Soil Moisture	NS	NS	NS
Slope Elevation	NS	NS	NS
Canopy Light Transmission	NS	NS	NS
Average Percent Mass Loss Popsicle Sticks	NS	NS	NS
Average Percent Mass Loss Leaf Litter	NS	NS	NS
Average Percent Moisture Leaf Litter	NS	NS	NS
Average Dry Mass Leaf Litter	NS	NS	NS
Percent Soil Carbon	NS	NS	NS
Percent Soil Nitrogen	NS	NS	NS
Log Salamander Biomass	NS	NS	NS

Figure 2.
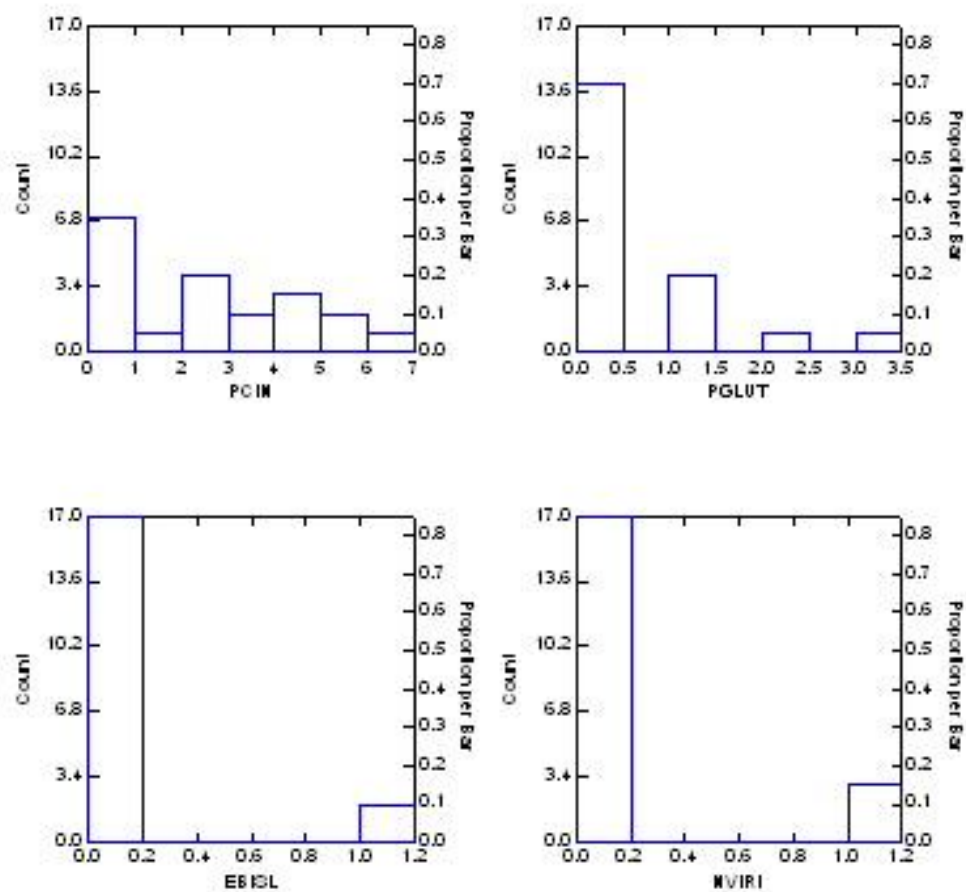
Figure 3.

a)
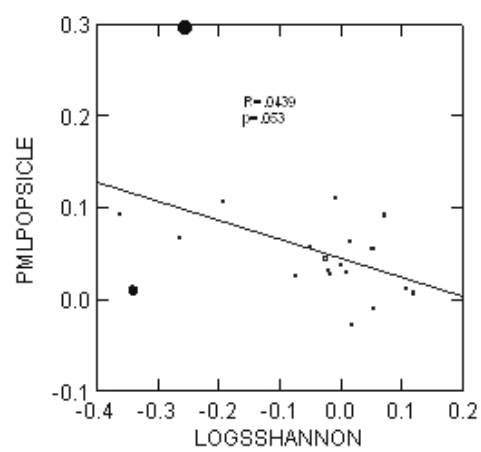
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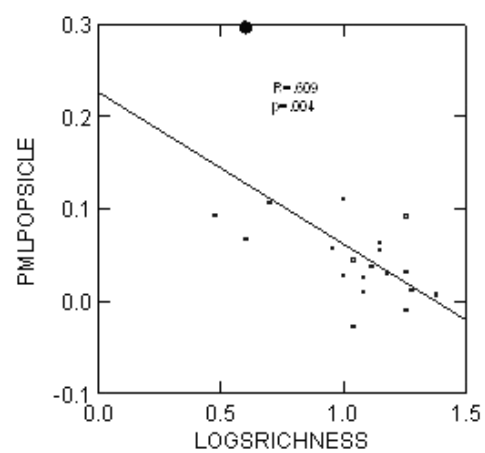
Figure 4.

a)
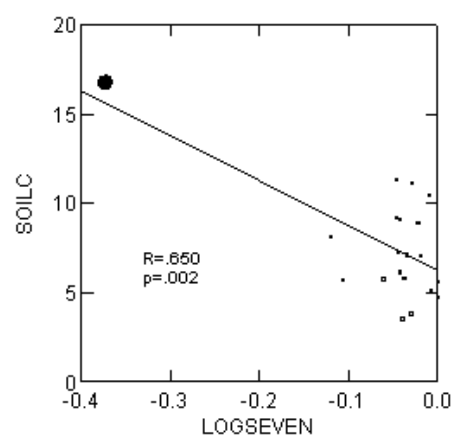
b)
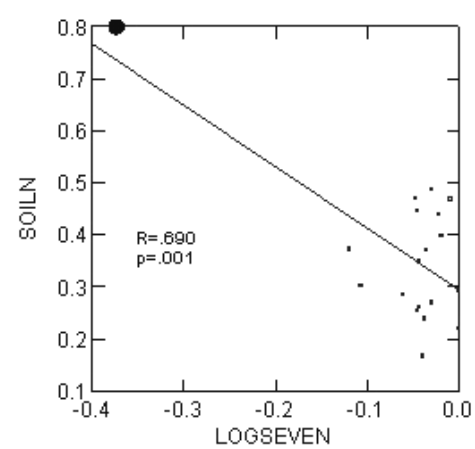
Figure 5.
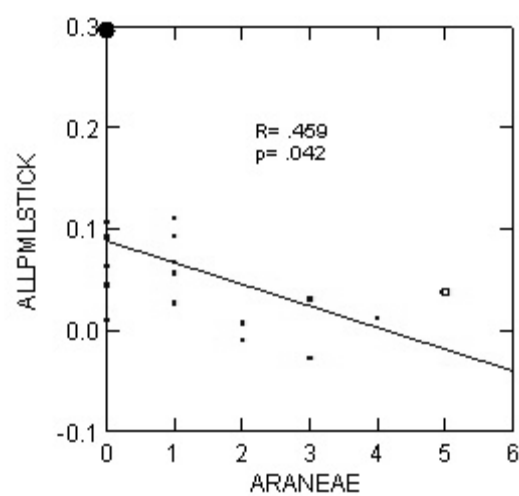
Table 2.

Site Plot	Predators	Omnivores	Herbivores	Filter Feeders	Fungivores	Detritivores
A0	1	0	0	1	13	14
A1	2	3	0	0	2	2
A2	6	12	0	0	0	2
A3	0	7	0	0	3	0
A4	2	0	0	0	2	0
A5	4	6	0	0	1	1
A6	2	24	0	0	6	6
B1	3	9	0	0	1	1
B2	7	19	0	0	5	2
B3	2	7	0	2	2	1
B4	0	32	0	0	8	4
B5	5	12	0	0	9	3
B6	1	190	3	0	3	0
B7	5	20	0	0	8	12
C1	1	37	0	0	12	0
C2	0	7	0	0	3	0
C3	1	9	2	0	4	0

C4	2	14	1	0	5	1
D0	2	8	0	0	4	2
Z5	3	20	0	0	5	7

Table 3.

	Average Percent Mass Loss Popsicle Sticks	Average Percent Mass Loss Leaf Litter	Percent Soil Carbon	Percent Soil Nitrogen
Predators	NS	NS	NS	NS
Omnivores	NS	NS	0.000*	0.000*
Herbivores	NS	NS	NS	NS
Filters	NS	NS	NS	NS
Fungivores	NS	NS	NS	NS
Detrivores	NS	NS	NS	NS

Appendix A. Map of Black Rock Forest, Cornwall, New York

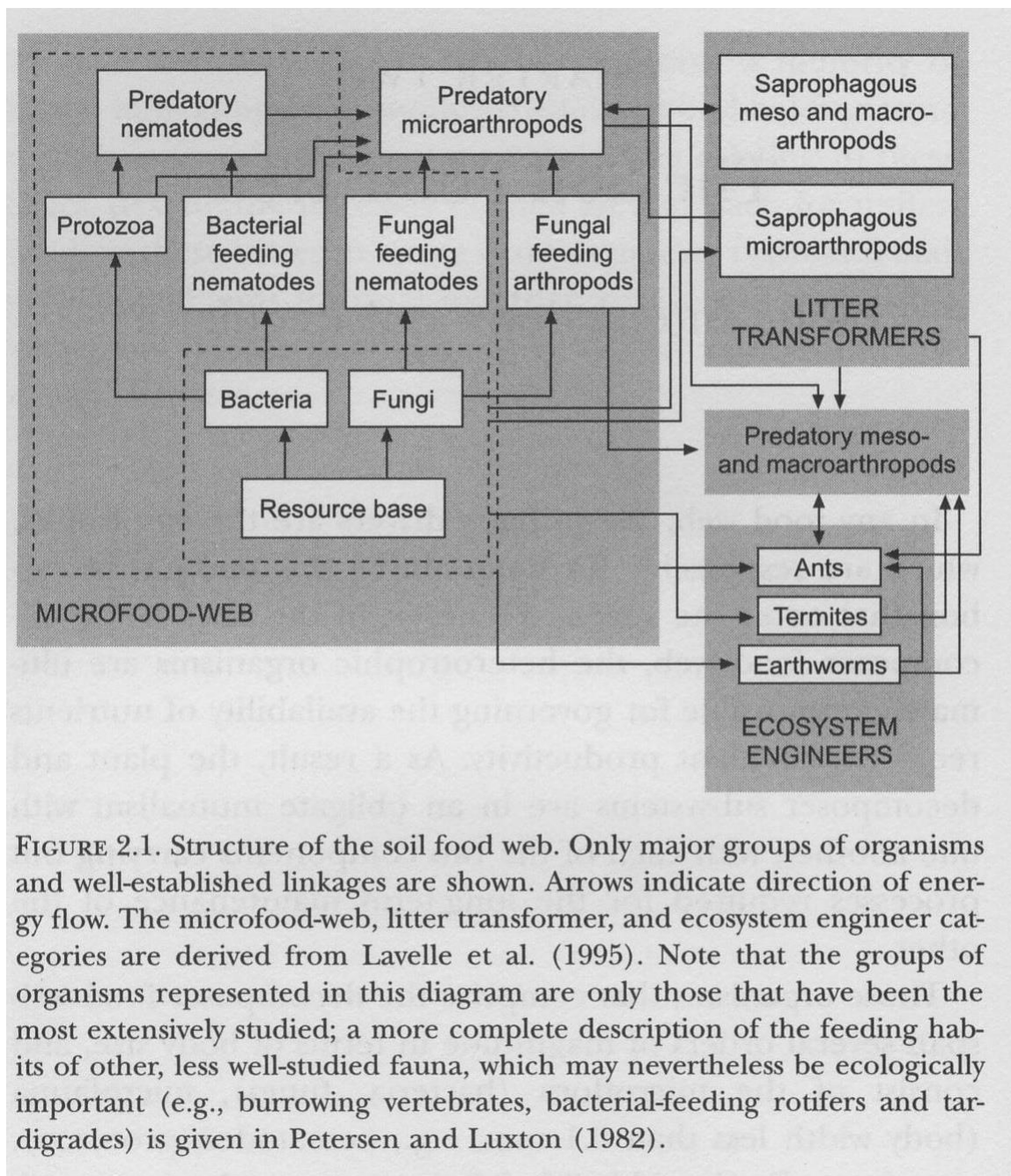(http://www.blackrockforest.org).
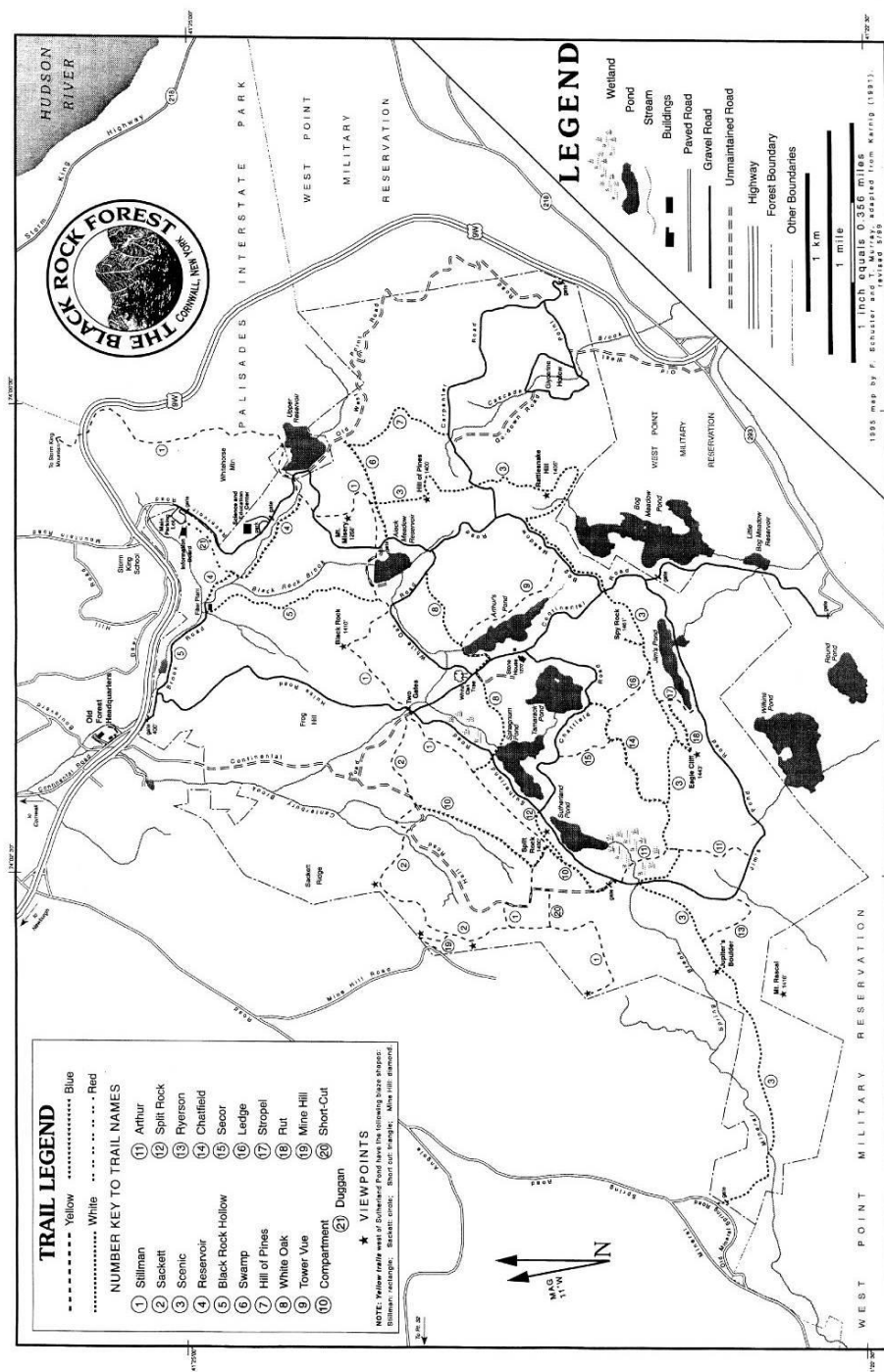
Appendix B. Map of Study Site Master Plots on Northern Slope, Black Rock Mountain

(Schuster et al. 2005).
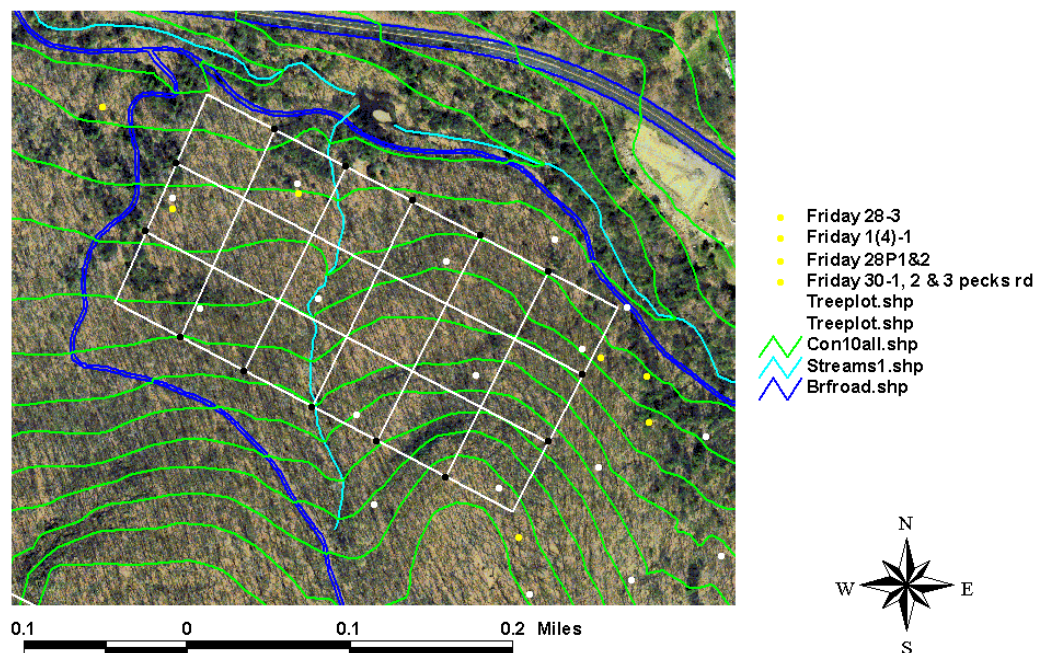
Appendix C. Interpretation of soil food web in Wardle (2002).

FIGURE 2.1. Structure of the soil food web. Only major groups of organisms and well-established linkages are shown. Arrows indicate direction of energy flow. The microfood-web, litter transformer, and ecosystem engineer categories are derived from Lavelle et al. (1995). Note that the groups of organisms represented in this diagram are only those that have been the most extensively studied; a more complete description of the feeding habits of other, less well-studied fauna, which may nevertheless be ecologically important (e.g., burrowing vertebrates, bacterial-feeding rotifers and tardigrades) is given in Petersen and Luxton (1982).

Appendix D. Functional Grouping of Invertebrates and Summed Number of Individuals

for All Center Plots.

Class	Order	Total No. Indiv.	Trophic Group
Arachnida	Araneae	29	Predator
Chilopoda	Scolopendromorpha	19	Predator
Diplopoda	Julida	25	Detritivore
Gastropoda	Pulmonata	11	Omnivore
Hexapoda	Hymenoptera (Formicidae)	268	Omnivore
	Collembola	91	Fungivore
	Coleoptera	80	Omnivore
	Diptera	10	Omnivore
	Pscoptera	5	Detritivore
	Orthoptera	4	Herbivore
	Hemiptera	2	Herbivore
	Trichoptera	1	Detritivore
	Mantodea	1	Predator
Oligochaeta	Haplotaxida	22	Detritivore
	Euchatreida	5	Fungivore
Malacostraca	Isopoda	5	Detritivore
	Decapoda	3	Filter Feeder