AN ABSTRACT OF THE THESIS OF

Samantha E. Colby for the degree of Master of Science in Botany and Plant Pathology presented on November 20, 2014.

Title: Seasonality as a driving factor of decomposition pathways in both meadows and forests: an exploration across a gradient of climate in Oregon.

Abstract approved:

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Andrew R. Moldenke

Soil food webs process the majority of terrestrial carbon, and influence overall ecosystem function. A primary distinction among soil food webs is based on fungal versus bacterial pathways of decomposition; these lead to fundamentally different soil function, and are expected to differ in dominance between meadows and forests. This assumption is the basis of ecological hypotheses, yet conclusive studies to test this assumption are lacking. To examine climatic factors which might relate to this property of soil food webs, I selected six sites along an Oregon (USA) transect of climate and productivity with paired forests and meadows. I compared biomass of active and total fungi and bacteria in meadows and forests throughout the year. Ratios of total fungal to total bacterial biomass are higher in forests than in meadows ($p = 0.01$), but also vary strongly by season ($p < 0.001$). Ratios of active fungal to bacterial biomass do not differ significantly between forests and meadows, but instead vary primarily by season ($p = 0.007$). This apparent seasonal difference is enhanced by the summer dry season, where fungi predominate in both forests and meadows along the transect. In conclusion, although total microbial biomass type differs between forests and meadows, there is a seasonal shift in active microbial biomass which dictates flow of nutrients via active decomposition in both forests and meadows. These systems are therefore dynamic, and decomposition pathways are determined by season as well as by ecosystem type.

Seasonality as a driving factor of decomposition pathways in both meadows and forests: an exploration across a gradient of climate in Oregon

by
Samantha E. Colby

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APPROVED:

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Samantha E. Colby, Author

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CONTRIBUTION OF AUTHORS

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Chapter 1: General Introduction

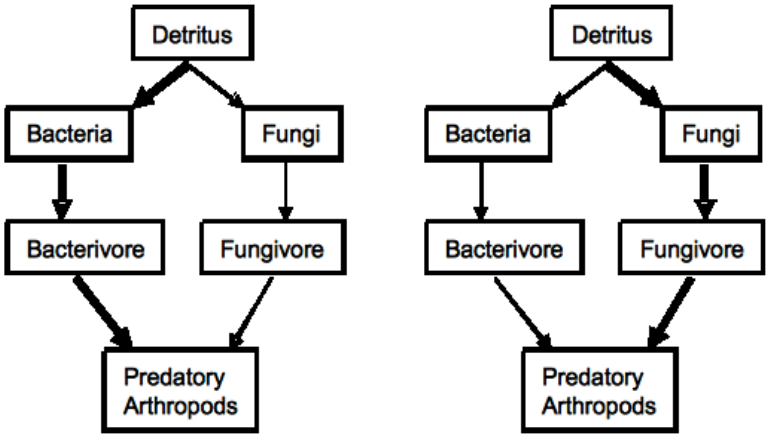
"The soil is the great connector of our lives, the source and destination of all."
(Wendell Berry, 1977).

Nearly all of the terrestrial carbon produced is ultimately processed in detrital-decomposer food webs in soil (Coleman et al., 1976). Trophic interactions in the soil are therefore critical to our understanding of ecosystems. These decomposition processes determine the stability of soil ecosystems to disturbance, and are responsible for the flow of nutrients (Moore et al. 2005). The forces driving food web structure are necessarily a critical focus in ecological studies, given the importance of food webs to ecosystem properties and processes. The base of soil food webs are microbial decomposers, and a focus on these is essential to understanding the functioning of ecosystems.

Coleman et al. (1983) observed two fundamentally different pathways of decomposition present in soil, and described them as 'fast' versus 'slow' pathways. These 'fast' pathways primarily incorporate carbon from root exudates, such as amino acids, and mono- and oligo- saccharides. The 'slow' pathways involve less labile sources of carbon, such as that found in plant cell walls. Later, Moore and Hunt (1998) identified another major distinction in soil decomposition pathways; fungal versus bacterial 'energy channels' or 'resource compartments'. The authors also reported that these energy channels are fairly discrete, and species within one energy channel interact with each other more than species in the other energy channel. Additionally, they reported that the two energy channels are mostly independent and do not affect each other.

In 2005 Moore et al. discovered that Coleman's 'fast' and 'slow' pathways of decomposition are in fact the same as the bacterial and fungal energy channels; bacterial pathways are 'fast', and fungal pathways are 'slow'. Again, these pathways are considered discrete and largely independent. The bacterial pathways have the following characteristics: rapid/short generation times (r-selected species), and rapid turnover rates, resulting in higher nitrogen mineralization and narrower C:N ratios.. The fungal pathways conversely have much longer generation times (K-selected species) by several orders of magnitude and much slower turnover rates, and result in lower nitrogen mineralization and wider C:N ratios. The bacterial

pathway and resultant food web is composed primarily of aquatic organisms who rely on water films, while the fungal-based organisms can occupy both water films and air-filled pores.



FAST	CHARACTERISTIC	SLOW
Agro-, grassland	Ecosystem	Forest
Increased	NPP	Decreased
Early	Succession	Late
Labile	Detritus	Recalcitrant
Narrow	C:N	Wide
Mineral soil	Habitat	Litter/humus
Winter	Seasonality	Summer
Months	Decomposition	Years

Bacterial (Fast) and Fungal (Slow) decomposition pathways and corresponding general ecosystem characteristics (after Moore et al. 2005).

A seminal study done by Ingham, Coleman, and Moore (1989) investigated the dominance of these microbial pathways in a prairie, meadow, and forest in Colorado. Their ratios of fungi to bacteria were 0.8. (prairie), 0.1 (meadow), and 8.0 (forest). They correspondingly found bactivorous nematodes and nitrogen in the nitrite and nitrate forms to be dominant in meadow and prairie, and microarthropods and ammonium dominant in the forest. They concluded that both in terms of biomass and resource compartmentalization/energy pathways, their prairie is slightly bacterially-dominated, their meadow strongly bacterially-dominated, and their forest strongly fungally-dominated. Since this finding, it has been the paradigm that the fungal pathway is dominant in forests and the bacterial pathway is dominant in meadows.

In Ingham et al. (1989), Moore and Hunt (1988), and Moore et al. (2005), the authors report findings that the bacterial pathway is more resistant to disturbance, while the fungal pathway is more responsive; the bacterial pathway recovers much more quickly from disturbance and returns to steady-state conditions, while the fungal pathway can take a long time to recover, due to the different life-history traits of species in these different pathways (Moore et al. 2005). Furthermore, they found that there is greater instability when energy shifts to primarily one pathway over the other. Several studies have shown that extreme forms of disturbance, such as agricultural management practices, can cause just such a shift to occur (Moore, 1986; Hendrix et al., 1986; Andre´n et al., 1990; Moore and de Ruiter, 1991). Results of this include a shift towards the bacterial pathway, more rapid loss of organic matter, and increased nitrogen mineralization prior to and after the growing season, leading to a likely loss of that nitrogen through leaching (Brussaard et al., 1988; Elliott and Coleman, 1988). Clearly, factors that influence the relative dominance of these pathways are important to understand, as shifts in these pathways have implications for nutrient availability as well as overall ecosystem function.

In chapter 2 of this thesis, I asked the following three major questions: 1) Whether meadows and forests consistently differ in bacterial- versus fungal-dominance across a gradient of climate in Oregon. 2) Whether bacterial and fungal biomass in forests and meadows vary significantly by season. 3) Whether sites with very different NPP vary significantly in terms of fungal- versus bacterial-dominance. These questions can provide a baseline of how these energy pathways are distributed in Oregon, as climate and season shift due to climate change. They may also prove important for management purposes, in order to inform decisions.

I hypothesized that overall my findings would be consistent with the 1989 study by Ingham et al., and forests and meadows would differ in their primary decomposition pathways. I expected forests to show consistently higher ratios of fungi to bacteria than meadows across my research sites. However, I hypothesized that there would be an increase in the importance of bacterial decomposition pathways in both forests and meadows during spring, due to warm and wet conditions and bacterial reliance on water films. I expected that this effect would be more pronounced in meadows than in forests, because meadow soils are

more immediately exposed to the warming effects of solar radiation, as forest soils are insulated by tree cover. Similarly, I expected to see an increase in fungal pathways during summer, when soils are dry and bacteria less able to function. I hypothesized that I would find higher overall microbial biomass where precipitation and NPP were higher, due to increased organic matter availability, and that these sites would also show less seasonal variation in bacterial versus fungal dominance.

In order to test these hypotheses, I selected sites along an established research transect: the Oregon Transect (Waring and Peterson 1994, Runyon et al. 1994, Turner et al. 2007). This transect has been heavily researched, and represents a steep gradient of climate and net primary productivity (NPP), making it an ideal set up for this study. I selected six locations along this transect, with an adjacent meadow and forest site at each location, yielding a total of twelve research sites. At each site I collected soil samples once per season over the course of two years, and measured biomass of total and active fungi and bacteria in each sample. The details of sampling technique and site selection are detailed in chapter 2; I also measured nematode abundance and biomass, which are presented in the Appendix.

Chapter two is the exploration of these questions of fungal versus bacterial dominance along this transect and with season. Chapter three is the discussion of the findings of this study and their implications.

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Chapter 2: Seasonality as a driving factor of decomposition pathways in both meadows and forests: an exploration across a gradient of climate and productivity in Oregon.

Introduction

Food webs represent and their linkage patterns may control the flow of energy and nutrients through an ecosystem, and soil food webs process the majority of terrestrial carbon produced by plants (Cyr and Pace 1993, Hairston and Hairston 1993, Polis and Strong 1996). The complexity and diversity of soil

food webs affect the rates of nutrient release, the capacity of soils to store water, and the very stability of systems (de Ruiter et al. 1995). Two primary functional distinctions among soil food webs have been identified. Coleman et al. (1983) recognized the presence of 'slow' and 'fast' decomposition pathways in soil systems. Later, Moore and Hunt (1988) identified separate bacterial and fungal decomposition pathways in soil. These ideas were consolidated by Moore et al. (2005): 'fast' pathways are bacteria-based, and 'slow' pathways are fungi-based. Bacterial decomposition pathways are the base of bacterial food webs, and possess the following characteristics: rapid decomposition rate, 'boom-bust' cycles of bacterial biomass/activity, inefficient recapture of released nutrients, r-selected fauna, abundant predators (Moore et al. 2005). Fungal decomposer pathways are the base of fungal food webs, and are characterized by the following attributes: slow decomposition rate, retention of nutrients, stable presence of fungal biomass, high biomass and diversity of fungivores, K-selected fauna (Moore et al. 2005).

Because of the fundamental functional differences between these two decomposition pathways, I sought to investigate the factors that determine whether soil food webs will be based on bacterial or fungal decomposition pathways. In a previous comparison of three semiarid ecosystems, Ingham et al. (1989) found that that bacterial biomass was higher overall in a meadow and shortgrass prairie than in semiarid forest. Since this finding, the paradigm has been that forests are fungi- dominated and meadows are bacteria- dominated. Relatively few studies have sought to further clarify the distinction between these soil food webs. Looking just at fungal biomass, studies have found higher fungal biomass in forests than in meadows (Imberger and Chiu 2001, Kageyama et. al 2008). Others have shown no difference in bacterial biomass between forests and meadows, but instead differences in bacterial community structure and function between meadows and forests (Rich et al. 2003, Kageyama et al. 2008). Further, meadow and forest soil properties have been shown to be fundamentally different, which corresponds to different microbial communities in meadows and forests (Heichen, 2002, Griffiths et al 2005). In this study, I investigated not only whether food webs differ between forest and meadow soils, but how they may change with climate and season.

I address these relationships using a natural laboratory in the Pacific Northwest, the Oregon Transect (Waring and Peterson 1994, Runyon et al. 1994, Turner et al. 2007). This transect encompasses a steep gradient of climate and net primary productivity (NPP), which has been shown to determine soil microbial biomass and structure (Wu et al. 2012). Sites are located along a transect representing a 5-fold range in NPP (Table 1), along a steep climatic gradient across a 200 km swath at ~ 44^{o} N Latitude where NPP and meteorological measurements are available. I measured soil food web attributes along this transect in paired meadows and forests once per season over two years.

I specifically sought to answer the following questions:

1) Do meadows and forests (community type) consistently differ in bacterial- versus fungal-dominance across a gradient of climate and NPP?

2) Do bacterial and fungal biomass vary significantly by season?

3) Do sites with very different NPP vary significantly in terms of fungal- versus bacterial-dominance?

Methods

Site Description

Sampling sites are located along an east-west transect in Oregon. Each of the following locations contains paired meadow and forest sites (see Franklin & Dyrness 1988).

Coast (1-C)

Cummins Creek Wilderness Area (forest) is located in Lane County, Oregon at 64m elevation (44.27°N, 124.10°W). This site is referred to in this paper as 1-C. The plant community is old-growth Sitka Spruce (*Picea sitchensis* [Bong.] Carr.) forest, with Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and Western Hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and a very dense ericaceous understory. Soils of both the forest and meadow site are Medial Ferrihydritic Isomeric Typic Fulvudands.

Cape Perpetua (meadow) is located on a sea-facing bluff in Lincoln County, Oregon at 174m (44.29°N, 124.11°W). The meadow is in constant early succession caused by landslides consequent of heavy rains and extremely thin soils. The plant community consists largely of European grasses and annual forbs together with *Lupinus littoralis* Dougl. ex Lindl. and shrubby *Baccharis pilularis* DC.

Coast ranges (subalpine) (2-CR)

Mary's Peak is located in Benton County, Oregon. This site is referred to in this paper as 2-CR. The forest site (44.50°N, 123.56°W) is near the summit, at 1000m, and is dominated by *Abies amabilis* [Dougl.] Forbes*, Acer circinatum* Pursh and a ground cover of diverse sclerophyllous perennials. Soils of both the forest and meadow site are gravelly loam Haplumbrept Inceptisols.

The meadow site (44.51°N, 123.57°W) is at 1050m, and is dominated by *Carex rossii* Boott *and Pteridium aquilinum* [L.] Kuhn, with diverse native grasses and forbs.

Cascades: low elevation (year 1) (3-CL)

This forest is in the H.J. Andrews Experimental Forest, located in Lane County, OR at 450m (44.22°N, 122.25°W). This site is referred to in this paper as 3-CL. It is dominated by *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Acer circinatum*, *Polystichum munitum* [Kaulf.] Presl and diverse perennial shrubs and herbs. No soil survey available, probably Medial or Medial-skeletal ferrihydritic or amorphic, mesic Alic Hapludrands.

Box Canyon Springs meadow is located in Lane County, OR at 1132m (44.91°N, 122.08°W). The site is characterized by a mixture of native and European grasses and diverse native forbs. This site was grazed by pioneers but never plowed. No soil survey available, probably Medial or Medial-skeletal, over loamy skeletal, amorphic, frigid Typical Hapludands.

Cascades: low elevation (year 2) (3-CL)

In year two we sampled from this site rather than the HJA and Box Springs in order to have winter access. Longbow forest is located in Linn County, OR at 365m (44.40°N, 122.36°W). This site is referred to in this paper as 3-CL. It is dominated by *Tsuga heterophylla*, *Acer circinatum*, *Polystichum munitum*, and diverse sclerophyllous perennials. No soil survey available, probably Medial or Medial-skeletal, ferrihydritic or amorphic, mesic Alic Hapludands.

Longbow meadow is located in Linn County, OR at 365m (44.40°N, 122.36°W). It is dominated by a mixture of European and native grasses and few native forbs. This meadow has lower overall diversity than Box Canyon Springs as it has been plowed for agriculture in the past. No soil survey available, probably Fine-loamy or Loamy-skeletal, isotic, mesic Andic Humudepts.

Cascades: high elevation (4-CH)

This forest is in the H.J. Andrews Experimental Forest, located in Linn County, OR at 1415m (44.25°N, 122.13°W). This site is referred to in this paper as 4-CH. It is characterized by *Abies amabilis, Tsuga mertensiana* (Bong.) Carr*., Abies procera* Rehd*.,* and is nearly free of shrub and herb cover. No soil survey

available, probably both meadow and forest are Medial or Medial-skeletal, ferrihydritic or amorphic Lithic Haplocryands.

The adjacent meadow is also in the H.J. Andrews experimental Forest, located in Linn County, OR at 1475m (44.25°N, 122.13°W). It is characterized by a diverse mixture of native forbs and few native grasses. It was probably never commercially grazed nor plowed.

Interior Conifer Forest (5-I)

Metolius Research Natural Area forest is located in Jefferson County, OR at 920m (44.49°N, 121.63°W). This site is referred to in this paper as 5-I. It is characterized by *Pinus ponderosa* Dougl. ex Loud., a shrubby understory of *Purshia tridentata* (Pursh) DC., and native grasses. Soils of both forest and meadow sites are ashy over loamy-skeletal, glassy over isotic, Frigid Alfic Vitrixerands.

Allingham Meadow is located in Jefferson County, OR at 891m (44.47°N, 121.64°W). It is characterized by *Festuca idahoensis and Poa sandbergii* Vasey with a diverse forb complement. It was plowed by early pioneers, but not since.

Basin:Steppe (6-BS)

A basin/steppe forest site is located in Jefferson County, OR at 860m (44.53°N, 121.38°W). This site is referred to in this paper as 6-BS. It is characterized by *Juniperus occidentalis* Hook., *Purshia tridentata, Artemisia tridentata* Nutt., and very sparse native grasses and forbs. Soils of both forest and grassland sites are fine loamy mixed superactive Mesic Aridic Haploxerolls.

The neighboring meadow is also located in Jefferson County, OR at 860m (44.53°N, 121.38°W). It is dominated by *Festuca idahoensis*, *Agropyron spicatum*, and *Poa sandbergii*. This site was unsuccessfully homesteaded in the 1930s.

Sampling Protocol

Samples were taken at each site once per season over two years, from October 2008 through September 2010. "Fall" samples were taken at least two weeks after the onset of regular rain at each site. "Winter" samples were taken at least a month after snow began to accumulate at sites under winter snowpack; the coast receives no snow, but we sampled there at approximately the same time as the other winter samples. Sites at high elevation (2-CR and 4-CH) were not sampled during the winter due to lack of road access. "Spring" samples were collected after roughly 250 Degree Days had accumulated at each site; the coast was sampled much later, during mid-July, as the cool maritime climate leads to slower Degree-Day accumulation. "Summer" samples were collected during the maximum drought period for each site.

At each site, five randomly located soil cores, roughly 50g each, were taken from the top 15cm. In forest sites, samples were taken at least one meter from a tree, except at 6-BS, in which samples were taken one meter from juniper trees. These were composited into one 250g sample per site. This was placed on ice and transported to Microbial Matrix in Tangent, OR for analysis.

Biomass Measurements

A 10-fold serial dilution of each sample is made upon arrival into the laboratory. Active bacteria and active fungi are assessed using a 1:10 dilution (Lodge and Ingham 1991) under epifluorescence microscopy with a 40x and 20x objective, respectively. To quantify total fungal biomass, a 1:10 dilution (the same dilution and slide used to evaluate active fungi) is used under DIC microscopy using a 20x objective. Biomass of total fungi, active fungi, and active bacteria is assessed using a known biofilm, and is calculated based on the known biovolume, dilution, optics, and gram dry weight. To assess total bacteria a 1:100 dilution of liquid samples is used under epifluorescence oil immersion with a 100x objective. The stain used to assess active bacteria and fungi is fluorescein diacetate (Ingham and Klein 1984). The stain used for total bacteria assessment is fluorescein isothiocyanate both from Sigma Aldrich. Total bacteria

biomass was assessed using a polycarbonate membrane filter. Ten readings were taken, and biomass was calculated using an average of these. Microscope: Leica DMLB (10x eyepiece) with fluorescense and DIC.

Nematodes were extracted using a Baermann funnel. 50-100 g of soil were used to fill the funnel, which was then filled with water. This was left to sit for 3-7 days. 50ml of the solution was filtered through a fine mesh. From this, a subset of 50-100 nematodes were identified to genus at 40x DIC, counted, and assigned to feeding groups. Biomass of each genus was calculated using the total number and grams dry weight of nematodes, and the number of individuals of each genus.

Weather Data

Thirty-year averages (1971-2001) for degree-days were downloaded from www.uspest.org. PRISM (PRISM Climate Group, 2010) was consulted to extrapolate precipitation data for all sites based on thirty-year averages (1971-2001). Measurements of forest NPP are from analogous sites located along the same transect, and are taken from Turner et al. (2007). Meadow NPP was not directly measured but meadows were assumed to have the same relative order as the forests; in Oregon, meadow communities average about 25% lower NPP values than adjacent forests (Runyon et al. 1994).

Data analysis

I analyzed all data using R version 2.9.2 (R Core Team, 2013). Fungal and bacterial biomass data were logarithmically transformed. Additive models were used to explain the ratios of total and active fungi to bacteria, using the variables 'site,' 'type' (forest vs. meadow), and 'season.' Additive models were also used to explain nematode biomass. The model for fungivorous nematode biomass used the variables 'site,' 'type,' 'season,' total fungal biomass,' and 'active fungal biomass.' The model for bactivorous nematode biomass used the variables 'site,' 'type,' 'season,' total bacterial biomass,' and 'active bacterial biomass.' One-way analysis of variance (ANOVA) was used to identify which variables best explain variability between means. Because we were not able to sample at all sites during each collection period, the data set

is unbalanced. In order to examine the effect of this imbalance, we first analyzed balanced subsets of the data. We then fit the entire unbalanced data set. These balanced subsets were sites 1, 2, and 6 for all seasons except for Fall (subset 1), and sites 3, 4, and 6 for all seasons except Winter (subset 2). We used the analysis of these balanced subsets to inform our interpretation of analysis of the entire unbalanced data set. We also separated years one and two for both balanced subsets as well as the entire data set, to test for effect of year.

The following ratios were compared between forests and meadows by site and by season using paired t-tests: total fungi to total bacteria, active fungi to active bacteria, active fungi to total fungi, and active bacteria to total bacteria Tables 2 and 3). Correlation between NPP and total biomass, and between NPP and total bacterial biomass were plotted, and a regression was run using Microsoft Excel 2007.

All data will reside permanently in the HJ Andrews Long Term Ecological Research Site database, with open access through www.andrewsforest.oregonstate.edu.

Results

Total fungi to total bacteria

When analyzing the full data set, mean ratios of total fungi to bacteria are best explained by ecosystem type; these ratios are significantly higher in forests than in meadows ($p = 0.01$, Fig. 2.1). However, the analysis of balanced subsets indicates that for total fungi to total bacteria, years one and two are different and were therefore analyzed separately. When analyzing years one and two separately, we find that in year one, the ratio of total fungi to total bacteria is still strongly influenced by ecosystem type ($p = 0.03$), as well as site/location ($p = 0.02$, Fig. 2.2). In year two, ecosystem type and site are again significant explanatory variables for ratios of total fungi to total bacteria ($p = 0.0007$ and $p = 0.002$), and we also see a significant interaction between site and ecosystem type ($p = 0.02$, not shown). However, the effect of season overrides this in significance ($p<0.001$) and most strongly explains the ratios of total fungi to bacteria.

Active fungi to active bacteria

Within the full data set, ratios of active fungi to bacteria are best explained by season, and are significantly higher in summer than the remaining three seasons ($p = 0.001$, Fig. 2.3), which is supported by analysis of balanced subsets. Ratios of active fungi to bacteria show no significant difference either between sites or ecosystem type. Though my subset analysis of ratios of active fungi to bacteria did not indicate separation by years, I also analyzed years one and two separately. When analyzed by year, season is still the strongest determinant of active fungi to active bacteria in both years one and two ($p = 0.007$, $p < 0.001$), which agrees with analysis of the full data set. We also see a significant interaction between ecosystem type and season in year one ($p = 0.02$), and an interaction between site and season in year two ($p = 0.03$, not shown).

Transect

Overall there is correlation ($p = 0.04$, $r^2 = 0.67$) between mean biomass of total fungi and annual NPP (Fig. 2.4); there is no such correlation between mean biomass of total bacteria and NPP. However, there is correlation between mean biomass of total bacteria and annual precipitation ($p = 0.05$, $r^2 = 0.56$, Fig. 2.5). The correlation between fungal biomass and NPP breaks down when the ratio is compared to either the estimates of above-ground NPP or below-ground NPP alone (Runyon et al. 1994).

Discussion

Total fungal biomass (both active and dormant/dead) predominates in forests and total bacterial biomass predominates in meadows; this is true at nearly all sites and in all seasons ($p = 0.01$, Fig. 2.1, Table 2.2), which provides support for the paradigm that forests are dominated by the fungal pathway and meadows are dominated by the bacterial pathway (Ingham et al. 1989, Imberger and Chiu 2001, Kageyama et. al 2008). However, while overall the ratio of total fungi to bacteria is explained by ecosystem type (forest versus meadow) and location along the transect, in year two it is best explained by season; in year

two both forests and meadows were fungally-dominated during the summer. This indicates that season may play a more important role than has been previously recognized, and can lead to shifts in primary decomposition pathway. This finding is particularly significant because shifts to just one pathway can lead to instability (Moore et al. 2005).

In both years of this study, we see that *metabolically active* microbes vary significantly by season ($p = 0.001$, Table 2.3), which overwhelms any differentiation by community type or site. In the summer, metabolically active fungi greatly outweigh active bacteria in both forests and meadows and at all individual transect sites (Table 2.3). This is presumably largely due to the strong effect of summer drought; during the summer critically low soil moisture and high vapor pressure deficit are estimated to reduce NPP by 38% east of the mountains and by 13-20% in the lower and higher Cascade Mountains (Runyon et al. 1994). In this Mediterranean-type climate, most bacteria are probably unable to function in such dry conditions (Moore-Kucera and Dick, 2008). Again, this means that during summers in Oregon, ecosystems experience a dramatic shift to the fungal decomposition pathway.

Mean ratios of active fungi to active bacteria are also higher in forests than meadows in winter (table 2.2) (though 2-CR and 4-CH were not sampled in winter due to snowpack), which may be the result of greater insulation provided by forest cover. Mean ratios of active fungi to active bacteria are higher in forests than meadows overall at the coast, high-elevation cascades, and the interior (1-C, 4-CH, 5-I). Mean ratios of active fungi to bacteria are higher in meadows than forests at the Coast range and low-elevation Cascades (2-CR and 3-CL). Previous studies by Imberger and Chiu (2001) and Kageyama et. al (2008) had found overall higher fungal biomass in forests than in meadows, and in this study we do not find that relationship to be consistent. Instead, the relative proportions of fungal and bacterial biomass in forests and meadows appear to vary by season and by position along the transect.

Ratios of total fungi to total bacteria vary along the transect; we see very low total fungi to total bacteria ratios in both forests and meadows at the Basin/Steppe (6-BS), and very high ratios of total fungi to total bacteria at the coast forest (1-C). Additionally, there is a weak trend for the ratios of total fungi to total bacteria to increase from east to west along our transect, which corresponds roughly with NPP

(R^2=0.67, Fig. 2.2). This indicates that fungi accumulate more standing biomass where more plant biomass is produced and where annual precipitation is higher. This may be due to mycorrhizal relationships, or to higher amounts of organic matter for fungi to colonize (Schnurer et al. 1985, Wu et al. 2012). Additionally, soil fungal biomass has been shown to increase with plant diversity (Wu et al. 2012), though I did not measure plant diversity at my sites. This may also be due to higher soil moisture in sites with higher NPP; Cregger et al. (2012) found increasing fungi to bacteria ratios with higher volumetric water. However, we see no direct relationship between total fungal biomass and annual precipitation at these sites. This is perhaps in contrast with studies that have shown an increase in microbial activity in response to pulses of precipitation (Jacobson and Jacobson 1998, Sponseller 2007), and certainly in contrast with studies that have found increases in fungal biomass in response to water additions (Williams and Rice 2007).

In this study neither total nor active bacterial biomass show any relationship to NPP; instead, it correlates with annual precipitation (R^2=0.56, Fig. 2.5). This difference between bacteria and fungi may reflect their life strategies. Overall, fungi tend to be K-selected, and their life cycles take days to weeks to complete, while bacteria are r-selected and complete their life cycle within hours (DeAngelis et al 2013). Fungi may therefore have time to accumulate biomass at sites with higher productivity and organic matter, whereas bacteria do not. Bacteria instead may be responding to the favorability of conditions for them to be active, rather than availability of organic matter.

The low ratio of total fungi to bacteria (and high bacterial biomass) in the Basin/Steppe (6-BS) site is particularly surprising, as conditions there are very dry for nearly the entire year (PRISM Climate Group, 2010). Pasternak et al found the opposite trend, with lower bacterial biomass in dry/arid soils (2013), whereas we see high bacterial biomass at the driest site. Perhaps here we have an abundance of bacteria that specialize in dry conditions, such as GM bacteria (Moore-Kucera and Dick, 2008).

Conclusion

I return now to my original questions. 1) Do meadows and forests (community type) consistently differ in bacterial- versus fungal-dominance across a gradient of climate and NPP? There is some evidence that forests and meadows differ in bacterial- versus fungal- dominance, as analyzing the full data set as well as the data from the first year of this study alone reveals a distinction between forests and meadows along the transect and throughout the year. When looking at total bacterial and fungal biomass, meadows are consistently bacterially-dominant and forests are consistently fungally dominant across the transect. However, year two of the data reveal that season can play an important role, as the strong effect of summer overrides this relationship.

2) Do bacterial and fungal biomass vary significantly by season? Ratios of metabolically active fungi to active bacteria vary most strongly by season in both years of this study, and are highest in summer at all sites. Therefore, the primary distinction between bacterial and fungal pathways cannot be made simply between forests and meadows. Instead, these different decomposition pathways are dynamic and respond within a year between seasons.

3) Do sites with very different NPP vary significantly in terms of fungal- versus bacterial-dominance? Total fungal biomass as well as ratios of total fungi to total bacteria increase with NPP, while total bacterial biomass does not. Instead, total bacterial biomass increases with annual precipitation. These findings indicate that, in general, higher NPP favors the fungal pathway.

While many previous studies have addressed components of this study in various systems, literature treating soil ecosystems over large spatial scales and encompassing multiple seasons are lacking. This study provides insight into how forest and meadow soil systems function at a basic level across climate regions and throughout the year, and shows that they are more dynamic and responsive than has been suspected.

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Figures

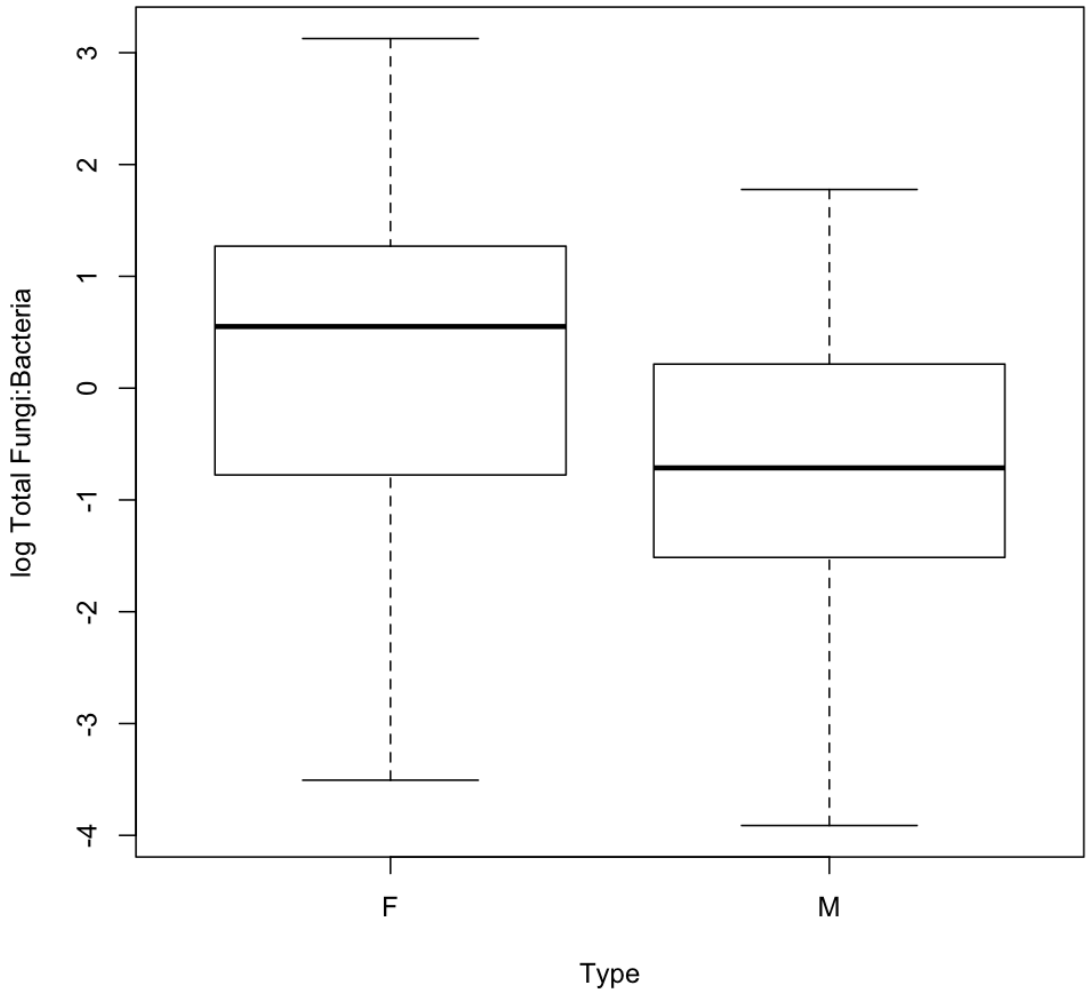

Figure 2.1. Total fungi:bacteria in forests and meadows. The x-axis distinguishes between forests (F) and meadows (M). This figure supports the view that forests tend to be dominated by fungal biomass, while meadows are bacterially dominated. (ANOVA, F=19.9 on 1 df, $p<0.01$).

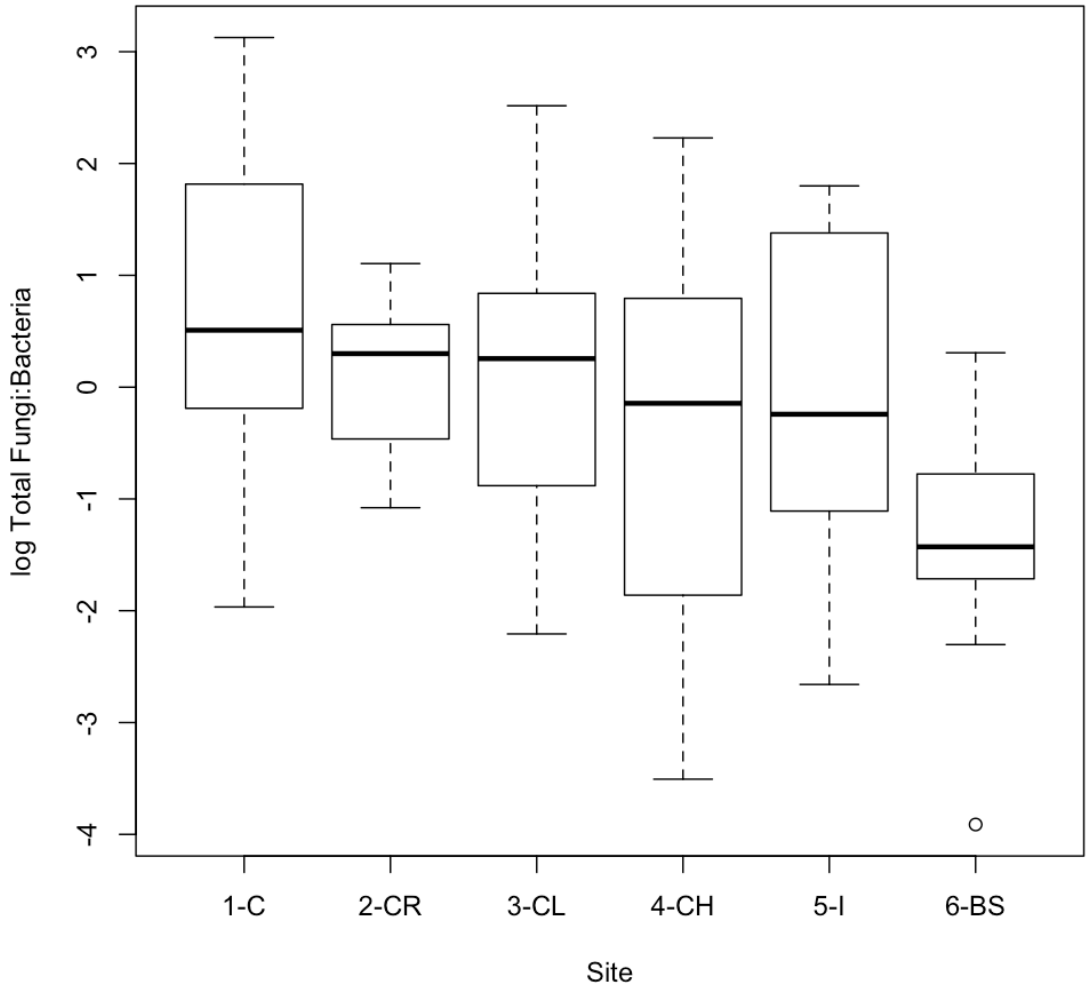

Figure 2.2. Total fungi:bacteria by location along the transect. This figure combines data from both forests and meadows at each of the 6 sites along the transect, from both years. The y-axis represents log-transformed ratios of total fungi to bacteria. The x-axis shows sites going from west to east along the transect, as follows: 1-C = Coast, 2-CR = Coast Ranges, 3-CL = Cascades low elevation, 4-CH = Cascades high elevation, 5-I = Interior conifer forest, and 6-BS = Basin/steppe. The Basin/Steppe site (6-BS) is

significantly different from all other sites, and is overall bacterially-dominated. (ANOVA, F= 5.1 on 5 df, *p= 0.002*.)

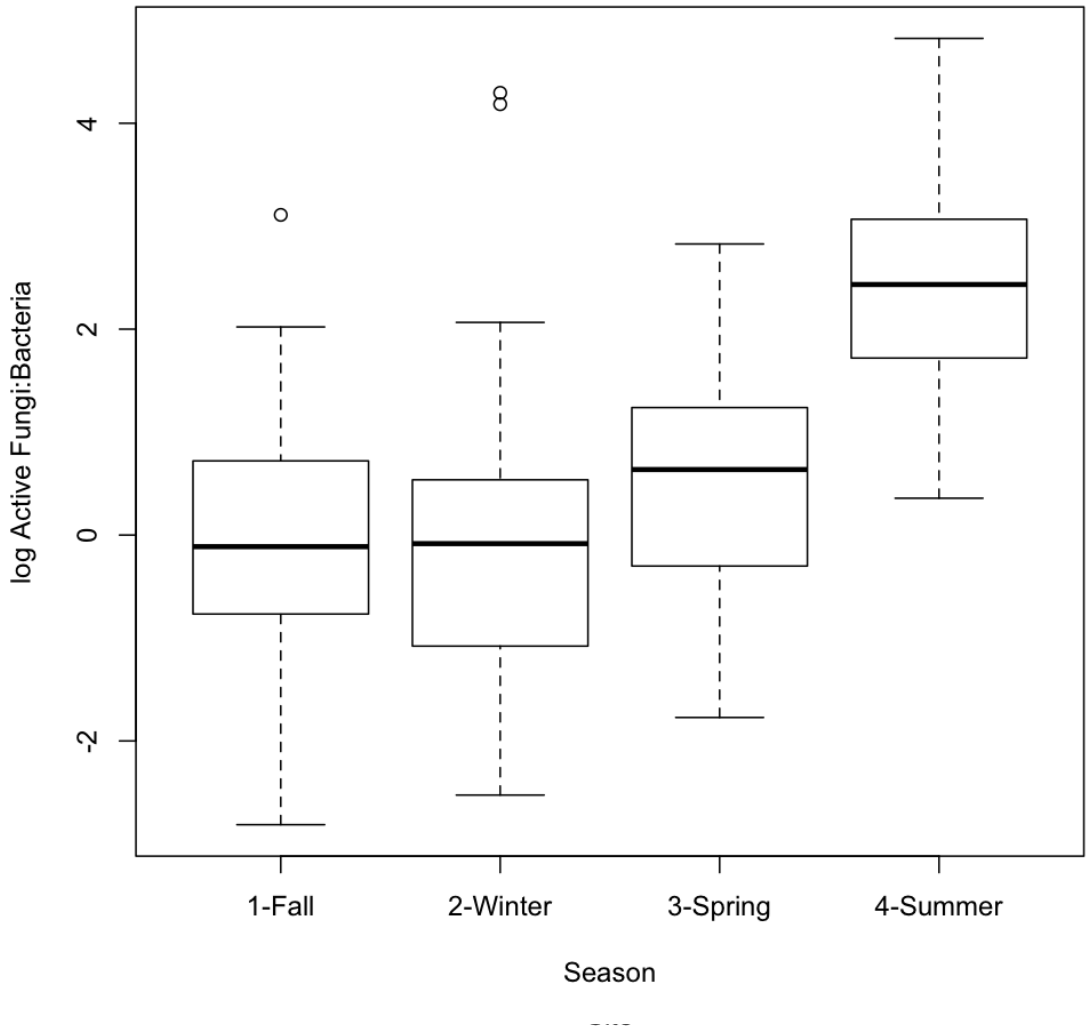

Figure 2.3. Active fungi:bacteria by season. This figure combines data from both forest and meadow at all 6 sites along the transect.The y-axis represents log-transformed ratios of metabolically active fungi to bacteria. Active microbial biomass varies strongly by season. Both forests and meadows at all sites are dominated by fungal biomass during the summer. (ANOVA, F= 14.4 on 3 df, *p=0.001*.)

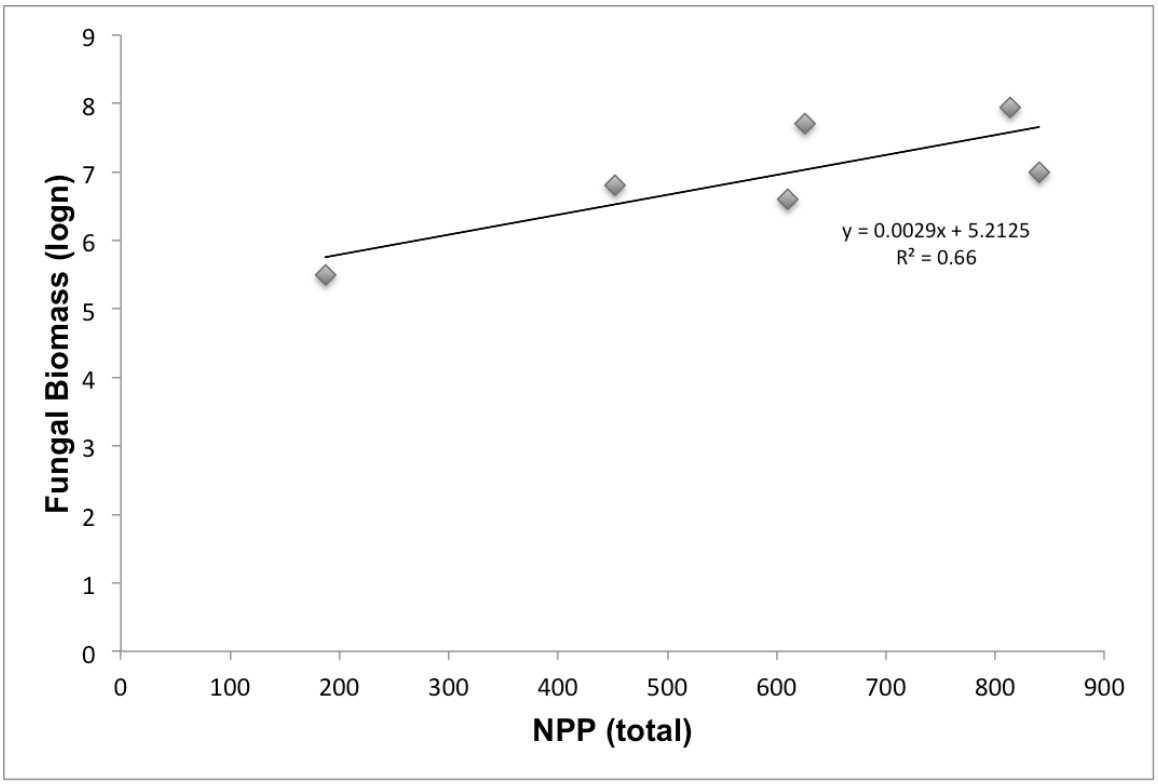

Figure 2.4. Correlation between total fungi and NPP. The y-axis represents mean NPP (gC m2 yr-1, see Table 1). The x-axis represents log-transformed mean fungal biomass from both forests and meadows, at all seasons. ($p = 0.04$, $r^2 = 0.66$).

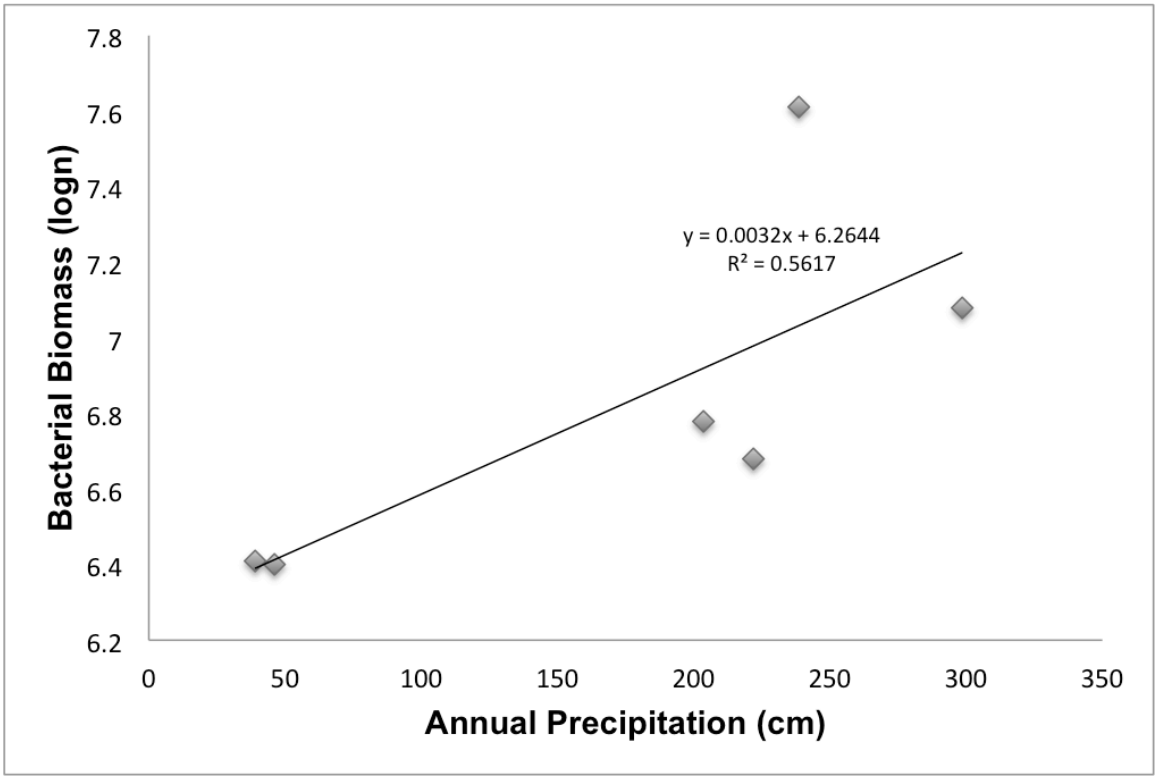

Figure 2.5. Correlation between total bacteria and precipitation. The y-axis represents annual precipitation (cm). The x-axis represents log-transformed mean bacterial biomass from both forests and meadows, at all seasons. ($p = 0.05$, $r^2 = 0.56$).

Tables

Table 2.1. Climate and NPP data. These are based on 30-year historical averages (1971-2000). Mean NPP measurements taken from Turner et al. (2007); 2-CR estimated from Runyon et al. (1994) with 25% reduction from 1-C due to winter freezing, but without decrease in drought and vapor pressure due to windward fog exposure throughout the year. Cumulative degree days (all at base 41^{o}C) at 2-CR estimated from nearby Laurel Mt data.

Site	Annual Cumulative Degree-Days	Annual Precipitation (cm)	Mean NPP (gC m2 yr-1)
1-C	4492	203.4	814
2-CR	2000	298.4	610
3-CL	3596.8	221.9	840
4-CH	2552.7	238.7	626
5-I	3074.8	46.3	452
6-BS	382.8	39.2	187

Table 2.2. Paired t-tests comparing ratios of total fungi: total bacteria (biomass) between forests and meadows, broken down by season and transect site. Paired t-tests are based on $\log_e$ transformed data. Transect sites as described and abbreviated in Methods.

Season	Forest	Meadow	p	t	df
Fall	2.22	0.98	0.07 *	2.05	9
Winter	2.97	0.69	0.01 *	3.91	7
Spring	2.23	0.53	0.04 *	2.30	10
Summer	4.63	1.28	0.02 *	2.62	11
mean	3.01	0.87	0.02 *	5.10	3
Transect Site					
1-C	6.87	1.10	0.01 *	3.58	7
2-CR	1.33	1.35	0.63	-0.50	5
3-CL	2.83	1.02	0.04 *	2.57	6
4-CH	3.14	0.46	0.06	2.45	5
5-I	2.84	1.19	0.11	1.89	6
6-BS	0.68	0.19	0.01 *	3.62	6
mean	2.95	0.89	0.01 *	3.83	5

Table 2.3. Paired t-tests comparing ratios of active fungi: active bacteria (biomass) between forests and meadows, broken down by season and transect site. Paired t-tests are based on $\log_e$ transformed data. Transect sites as described and abbreviated in Methods.

Season	Forest	Meadow	p	t	df
Fall	3.27	2.20	0.91	0.11	9
Winter	16.76	1.49	0.08	2.05	7
Spring	3.78	1.74	0.13	1.64	10
Summer	18.54	26.88	0.32	-1.04	11
mean	10.59	8.08	0.41	-0.95	3
Transect Site					
1-C	12.83	7.84	0.31	-1.10	7
2-CR	3.43	8.59	0.85	0.20	5
3-CL	3.39	20.72	0.52	-0.68	6
4-CH	25.86	11.04	0.36	-1.00	5
5-I	14.46	3.94	0.11	1.86	6
6-BS	5.86	3.21	0.98	0.03	6
mean	10.97	9.22	0.36	-1.01	5

Chapter 3. General Conclusions

In chapter 2 of this thesis, forests and meadows show an overall difference in relative biomass of total fungi and bacteria, which indicates that in general, forest soil systems primarily utilize the fungal decomposition pathway and meadows the bacterial pathway. However, at times seasonal effects can overwhelm this distinction, and lead to a shift in meadows from the bacterial to the fungal pathway during extreme summer drought.

Furthermore, factoring in the metabolically active components of these systems adds complexity to the story. The biomass of active fungi and bacteria reveal that relative dominance of these pathways is determined primarily by season, and both forests and meadows can shift back and forth between them. Total fungi to bacteria ratios are generally less than 1 in meadows, meaning bacterial biomass is dominant. Active fungi to bacteria ratios in meadows are typically just above 1. This indicates that both pathways are utilized in meadows most of the year. However, in summer, ratios of both active and total fungi to bacteria are above 1, and the active ratio is especially high (26.88, table 3), showing what is perhaps a dramatic shift to the fungal pathway. Moore et al.warn that shifting to just one or the other pathway can result in instability (2005), which may be the case here.

In addition to microbial data, I also collected and analyzed nematode data for this study. Though they are not a part of chapter 2 of this thesis, they provide an interesting extra piece to the story. Fungivorous nematode biomass is best explained by season, and is significantly higher in fall than any other season ($p < 0.001$, Fig. 3.1). Fungivorous nematode biomass does not vary significantly by ecosystem type, site, active fungal biomass, or total fungal biomass. Bactivorous nematode biomass shows a parallel significant increase during fall ($p = 0.02$, Fig. 3.2), again with no overall ecosystem type or site difference. Both fungivorous and bactivorous nematodes experience peak biomass during the fall. The high biomass of both fungivorous and bactivorous grazers during the fall indicates that this is a particularly important season for many food web dynamics. In terms of climate, in Oregon fall is the most unpredictable season. Onset of the rainy season (measured as soils becoming significantly moistened) and subsequent first frost

define a season of variable duration. For instance, during the second year of sampling no precipitation occurred at the sites east of the Cascades (5-I and 6-BS), completely negating the critical pre-winter growing season.

Fall is apparently a critical period for microbial grazing by nematodes. A six-month study in a grassland in Greece (with a similar Mediterranean climate) also found the highest density of soil bactivorous nematodes in September-October, which is within our typical range of Fall (Papatheodoru et al. 2004). Fungivorous nematodes may become abundant in the fall due to a combination of food source availability (active fungal biomass has been high during summer) and favorable climatic conditions (precipitation has moistened the soil for nematode activity). Following this logic, I would predict to see greatest bactivorous nematode biomass in spring, when soil is moist and bacterial biomass is high. Instead, their biomass is also highest in fall. This apparent disconnect between their peak biomass and that of their food source may indicate top-down control by predators during the spring (Lenoir et al 2007).

Study limitations

This study would be strengthened by additional replication. Soil cores from each sampling event were consolidated, yielding one sample per site per season. Further information about potential heterogeneity in sites might be useful in understanding the structure and function of these ecosystems. In addition, one sample per season is not enough to truly capture the conditions of a season. Instead, multiple samples in each season would improve statistical certainty of these temporal relationships.

Broader Impacts

Primary decomposition pathways have been previously shown to differ between forests and meadows (Ingham et al. 1989, Imberger and Chiu 2001, Kageyama et al. 2008). This fundamental and crucial aspect of ecosystems was previously thought to be a characteristic of ecosystem types. This thesis provides strong evidence that decomposition pathways are not a fixed attribute of ecosystems, and instead they are subject to the influence of other outside factors. In particular, I have shown that seasonality strongly influences these decomposer pathways. Due to the important role of microbes in nitrogen

mineralization and immobilization, this has significant implications for the larger question of what time of year nutrients are made available and where across this transect. In terms of active biomass, the fungal pathway appears strongly dominant in both forests and meadows in summer, and in forests in winter (Table 2.3). Therefore, if climate change does result in extended summers and shorter, wetter winters in Oregon as predicted (IPCC 2011), we would expect to see longer periods of fungal dominance in the summer in these ecosystems, and perhaps more bacterial dominance in the winter. How this would interact with the rest of the soil food web is currently unknown.

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Appendix

Figures

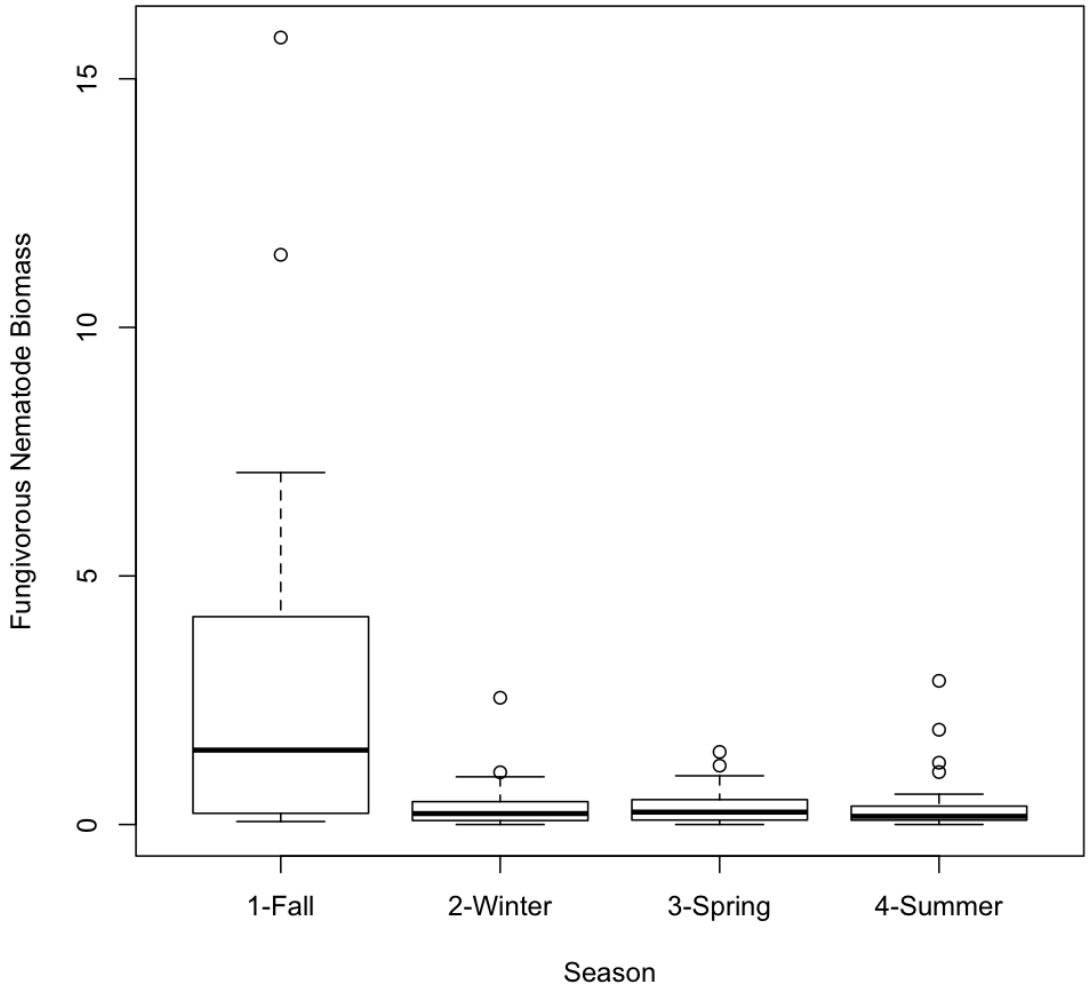

Figure 3.1. Fungivorous nematode biomass by season. This figure combines data from both forest and meadow at all 6 sites along the transect. Fungivorous nematode biomass is significantly higher in fall than any other season. Peak fungivorous nematode biomass does not occur simultaneously with peak fungal biomass (summer). (ANOVA, F= 7.5 on 3 df, *p= 0.001*).

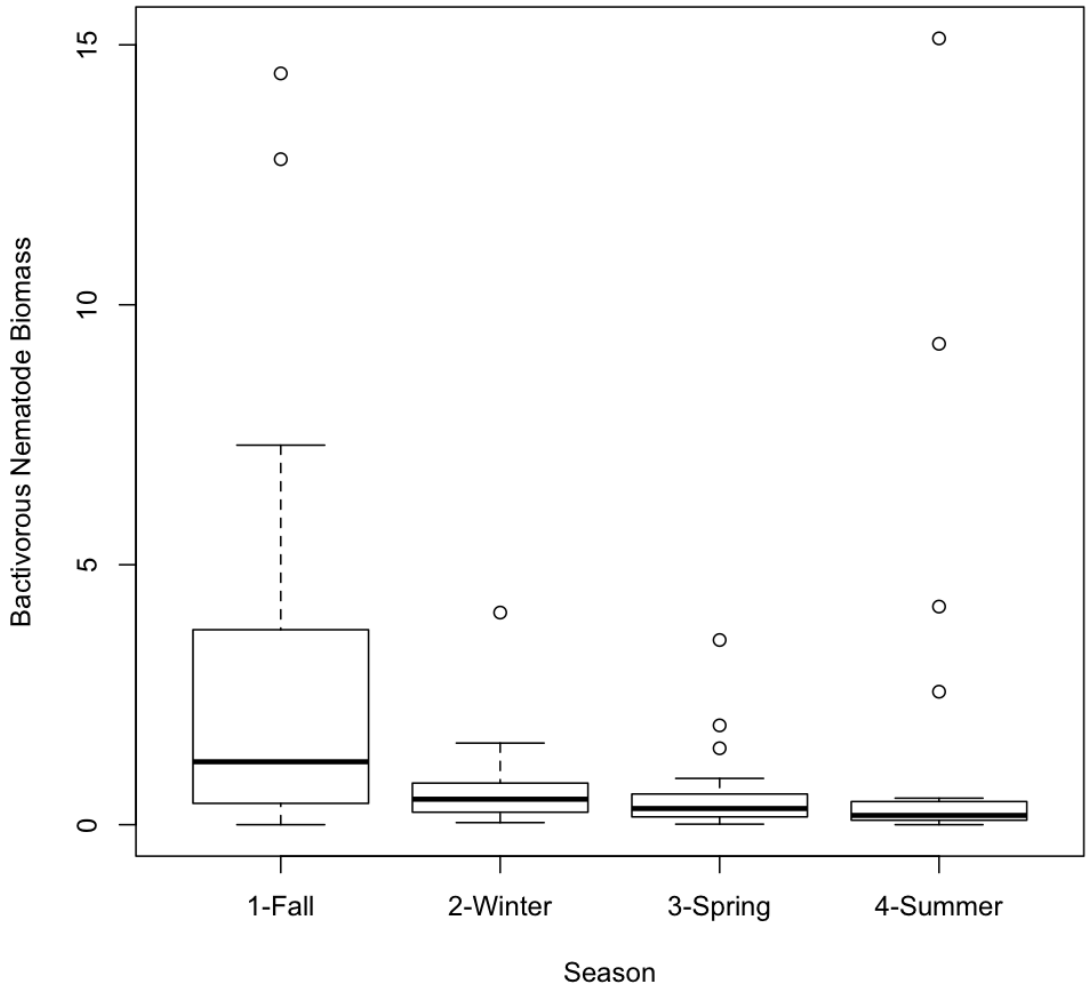

Figure 3.2. Bactivorous nematode biomass by season. This figure combines data from both forest and meadow at all 6 sites along the transect. Bactivorous nematode biomass is highest in fall, and does not coincide with peak bacterial biomass (spring). (ANOVA, F=3.6 on 3 df, *p=0.02*).