DISSERTATION

SOIL MITE BIODIVERSITY: ITS RELATIONSHIP TO GRASS SPECIES AND INFLUENCE ON DECOMPOSITION IN THE KONZA TALLGRASS PRAIRIE

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 2005

COLORADO STATE UNIVERSITY

April 7, 2005

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY MARK GEORGE ST. JOHN ENTITLED "SOIL MITE BIODIVERSITY: ITS RELATIONSHIP TO GRASS SPECIES AND INFLUENCE ON DECOMPOSITION IN THE KONZA TALLGRASS PRAIRIE" BE ACCEPTED AS FULLFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

SOIL MITE BIODIVERSITY: ITS RELATIONSHIP TO GRASS SPECIES AND INFLUENCE ON DECOMPOSITION IN THE KONZA TALLGRASS PRAIRIE

Human activities are responsible for unprecedented extinction rates and global change. Species are disappearing faster than we can record their existence and before we determine their role in ecosystems. In no other system on Earth are we more uncertain about the true diversity of organisms and their roles than in soils. I have examined soil mite (Acari) species at the Konza Prairie Biological Station (KPBS), Kansas, USA, an uncutivated tallgrass prairie, to determine what mechanisms are responsible for their diversity, how alien invasive grasses may impact them, and what role their diversity plays in decomposition.

The hypotheses that soil mite species richness, abundance and taxonomic diversity is greater beneath grasses in dicultures (different species) compared to monocultures (same species), beneath grasses of higher resource quality (lower C:N) compared to lower resource quality, and beneath heterogeneous mixes of grasses (C_3 and C_4 grasses growing together) compared to homogeneous mixes (C_3 or C_4 grasses) were tested using natural occurrences of grass species as treatments. Increased grass diversity supported a more species and phylogenetically rich soil mite fauna. This relationship was significant at depth but not in the upper soil horizon. Soil mite richness increased non-linearly with grass species richness suggesting that simple extrapolations of soil faunal diversity based on plant species inventories may underestimate the richness of associated

soil mite communities. The proportion of mite size classes in dicultures was considerably different than those for monocultures. These data suggest that interspecific root competition results in increased mite habitat, abundance and diversity. There was no difference in soil mite richness between grass combinations of differing resource quality, or resource heterogeneity.

Soil mites sampled beneath six native and one alien-invasive species of grass were similarly abundant, species rich, diverse, and taxonomically distinct. There was no evidence that the community composition of soil mites was specific to grass species or that a significant number of mite species had affinities for different grass species. The soil mite community was weakly related to soil environmental conditions. Only oribatid mites were related to, marginally, the species of grass present. The alien invasive grass species did not support a successionally younger mite fauna and had no influence on mite community structure, possibly because it had not substantially altered the soil environment.

Rates of cotton strip decomposition (percent cotton strip tensile strength loss per day, *CTSL*), and soil mite abundance and species richness were measured at high and low fire frequency sites of the KPBS. Likelihood-based and information theoretic approaches were used to examine strength of evidence in data for models of *CTSL* representing the Null, Rivet and Redundant hypotheses of biodiversity and ecosystem function (BEF). The Null model including temperature, moisture and saturating effects in the total abundance of predatory mites (Mesostigmata) had more support in the data than any other models. Models representing Rivet and Redundant patterns of BEF settled on

parameter values distinct from the Null models but had less support in the data regardless of which mite group was being considered.

A significant trend was observed in the models' residuals from low fire frequency sites; trends not observed in high fire frequency sites. I speculate that annually burned sites more closely emulate the agricultural system the models were originally designed for than low fire frequency sites, accounting for differences in model performance. Biophysical properties on low fire frequency sites such as increased litter cover, different soil carbon constituents or a different microbial community may regulate decomposition in a manner not accounted for by only soil temperature and moisture driving variables.

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ACKNOWLEDGEMENTS

The work contained herein was truly collaborative from its conception to completion and would not have been possible without the assistance of my colleagues, committee, friends and family. Many people fulfilled two or more of these roles; to them I am especially grateful.

I thank my committee for offering great advice on drafts, life and mostly for being incredibly supportive. Their kind, encouraging words went a long way to helping me along. I am especially grateful for the incredible experience Diana Wall, my adviser, provided me throughout my graduate study. I was also fortunate to have Val Behan-Pelletier act as a second adviser on this project. It was with Val's generous and selfless help that I was able to complete this study.

Steve Blecker, Nicole DeCrappeo, Rebecca Lavier, Grace Li, Andy Parsons, Dorota Porazinska, Pilar Prentiss, Stella Salvo and Todd Wojtowicz assisted with grass and soil physico-chemical analyses, cotton strip analyses, mite identification/curation and project co-ordination. Heather Reed, Tim Seastedt and Hu Zhengjun graciously provided soil temperature and moisture data as well as assisted with statistical analyses. John Blair, Melinda Smith and Tom Van Slyke provided much assistance at the Konza Prairie Biological Station (KPBS). Val Behan-Pelletier, Evert Lindquist and David Walter graciously provided additional mite taxonomic expertise.

I am grateful for the support I received from my friends, and especially my family, through the years it took me to complete my dissertation. I know they felt my

pain and struggled along with me! Nobody had to endure more than my wife, Siphone. Her love and support allowed me to get through the some of the most difficult times.

Financial support for this study was provided by a grant from the National Science Foundation (DEB 9806437) and the Francis and Evelyn Clark Soil Biology Scholarship.

This dissertation is dedicated to Dr. Francis Clark and his late wife, Evelyn; philanthropists, champions of soil biology and all around great people.

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1. INTRODUCTION

Most of the species known to science are macroscopic organisms and relatively easy to census (May 1988). While the total number of species on Earth is debated (Erwin 1982, Ødegaard 2000, Novotny et al. 2002), there is no question that the majority are microscopic, undocumented and of immense importance to the functioning of Earth's ecosystems (Wilson 1987). Soil systems are particularly poorly studied (Fitter 2005) yet contain the highest diversity and abundance of all terrestrial organisms (Giller 1996).

It is urgent that we tackle the problems of predicting the diversity of soil organisms and what role this diversity plays in the functioning of ecosystems. Human activities continue to alter Earth's ecosystems and drive extinction rates to unprecedented levels in geological history (Ehrlich and Ehrlich 1981). Not knowing the diversity of soil organisms and the role soil species play in terrestrial ecosystems before they are lost forever is negligent and potentially disastrous (Wall et al. 2001, Wall 2004). This dissertation aims to be one step towards remedying this situation by determining patterns and mechanisms responsible for soil faunal diversity and the role of this diversity in decomposition processes.

I took advantage of a manipulative field experiment at the Konza Prairie Biological Station (KPBS), a Long-Term Ecological Research (LTER) site and collaborated with taxonomic experts for my research. This allowed me to test hypotheses on the relationships between grasses and the diversity of soil mites (a hyper-diverse group of soil organisms), and between soil mites and rates of decomposition (a measure of ecosystem functioning) in a natural setting without many of the simplifying assumptions of a laboratory study.

1.1. The "enigma" of soil biodiversity

Soil biota are probably the least tractable of terrestrial organisms to current survey methods and to discrimination by taxonomic experts. The identification of individual soil organisms to species remains a constraint on understanding soil ecology because soil is an opaque medium where *in situ* identification of the mostly microscopic organisms is impractical. Additionally, taxonomic expertise for soil organisms is in decline (Ananthakrishnan 2000, Coomans 2002).

We have only rudimentary knowledge of soil biodiversity in a few ecosystem types (Hawksworth and Ritchie 1993, O'Donnell et al. 1994, Brussaard et al. 1997), and it is difficult to even make sensible guesses about the true diversity of soil taxa (Lawton et al. 1998). Molecular techniques show soil biotic diversity is rich, but, for example, the functional roles of the 5000 bacterial types inhabiting 100 g of Norwegian soil remain unknown (Torsvik et al. 1990).

The richness of the soil fauna seems to defy traditional ecological theory, most of which is based on studies of aboveground, terrestrial ecosystems. In soils, there appears to be an overabundance of omnivores, little niche separation, high redundancy and no

consistent relationships with productivity, disturbance or competitive exclusion (Bardgett 2002, Setälä 2002). However, new evidence indicates that there may be more niche separation in the soil fauna than previously believed (Schneider et al. 2004). The spatially complex soil environment is believed to be an important mechanism driving soil biodiversity to a level greater than that for aboveground (Anderson 1978, Hansen 2000, Bardgett 2002).

1.2. Soil mites

There are estimated to be over a million species of mites worldwide, with most of these species being soil dwellers (Walter and Proctor 1999). Mites are typically the most abundant and diverse arthropods in soil systems (Behan et al. 1978) fulfilling the roles of fungivores, saprivores, herbivores, omnivores and predators. Their overwhelming diversity and abundance can be an impediment to soil investigations at the species level. Additionally, our poor knowledge of each species functional role can be an impediment to investigations at the functional level. Yet we know through exclusion and microcosm experiments that they have significant influences on decomposition and nutrient cycling (Seastedt 1984c).

Given the potential importance of soil mites, and other soil fauna, to ecosystem processes it is imperative that we determine the mechanisms for their diversity in natural systems. Understanding mechanisms will lead to a more predictive science.

1.3. Above and below ground relationships

Biotic inventories are presently heavily plant biased. Often when the diversity of a region is being assessed, plant richness is measured with the assumption that it is a surrogate for other groups of organisms. This assumption has been tested for some

animals, such as birds and insects (Currie 1991, Ødegaard 2000, Simonson et al. 2001, Novotny et al. 2002); however, it has not been adequately tested for soil organisms. It is often presumed that plant species diversity influences the diversity of soil communities, but, "there has been no systematic documentation of the effects of reducing resource variety on the diversity of soil biota" (Swift and Anderson 1994). My research will provide the first evidence for how plants in natural systems, via their richness, quality of litter and roots, and heterogeneity of litter and roots, as well as invasiveness, influence the diversity of soil mites associated with those plants.

In Chapter 2 I test the hypotheses that soil mite diversity and abundance is positively related to increasing grass richness, resource quality and resource heterogeneity. In Chapter 3, I test the hypotheses that soil mite communities are unique to grass identity and that an alien invasive grass alters this relationship. These chapters address two ways in which aboveground diversity may be a predictor of belowground diversity.

1.4. Soil biodiversity and ecosystem functioning

An important issue in contemporary ecology is the role of biodiversity in ecosystem processes (Loreau et al. 2001, Tilman et al. 2001, Naeem 2002, Naeem et al. 2002, Naeem and Wright 2003, Symstad et al. 2003, Wall et al. 2004, Fitter 2005). We urgently need to understand the ways that species contribute to ecosystem functioning because of species extinctions and the frequently deleterious global changes resulting from management decisions, habitat fragmentation, and altered climate. In soil, biogeochemical cycling is a fundamental ecosystem process, where many of the critical

steps (e.g., decomposition, C and N transformation, trace gas generation) are mediated by soil organisms (Swift et al. 1979, Swift and Anderson 1994, van der Putten et al. 2004).

In establishing the relationships between ecosystem processes and contributions of soil taxa, the complexities of natural ecosystems make it seemingly prohibitive to move beyond patterns of correlation to knowledge of causality. In order to isolate cause and effect, the control of ecosystem and soil biotic variables sometimes reduces the research design to simplistic laboratory experiments involving few species (Setälä 2002), or to a highly imprecise simultaneous elimination of targeted biotic groups (Moore et al. 1996). I address this in Chapter 4 by testing several hypothetical relationships between biodiversity and ecosystem functioning (BEF) against data collected for soil mite diversity and rates of decomposition at the KPBS.

Without accurate information on the roles and determinants of soil biodiversity, one cannot manage soil ecosystems, rigorously understand the structure and interactions of soil communities, the relationships of soil biology to rates of ecological processes, or model ecosystem function in order to predict regional and global environmental change scenarios.

My research goals were to inventory and quantify the taxonomic diversity of soil mites at the KBPS, test hypotheses to determine what factors controls their diversity and then, determine what relationship, if any, exists between soil mite biodiversity and ecosystem processes.

2. DOES GRASS SPECIES CO-OCCURRENCE INFLUENCE SOIL MITE DIVERSITY?

2.1. ABSTRACT

Few studies have considered whether plant taxa can be used as predictors of belowground faunal diversity in natural ecosystems. Soil mite diversity was examined beneath six grass species at the Konza Prairie Biological Station, Kansas, USA. The hypotheses that soil mite (Acari) species richness, abundance and taxonomic diversity are greater (1) beneath grasses in dicultures (different species) compared to monocultures (same species), (2) beneath grasses of higher resource quality (lower C:N) compared to lower resource quality, and (3) beneath heterogeneous mixes of grasses (C_3 and C_4 grasses growing together) compared to homogeneous mixes (C_3 or C_4 grasses) were tested using natural occurrences of grass species as treatments. This study is the first to examine the interaction between above- and belowground diversity in a natural setting with species-level resolution of a hyper diverse taxon.

Results indicate that grasses in diculture supported a more species and phylogenetically rich soil mite fauna than for monocultures and that this relationship was significant at depth but not in the upper soil horizon. Mite species richness was not

linearly related to grass species richness, which suggests that simple extrapolations of soil faunal diversity based on plant species inventories may underestimate the richness of associated soil mite communities. The distribution of mite size classes in dicultures was considerably different than those for monocultures. There was no difference in soil mite richness between grass combinations of differing resource quality, or resource heterogeneity.

2.2. INTRODUCTION

Knowledge of how, or even if, aboveground and belowground diversity are related is important to our understanding of biodiversity, conservation, ecology and the services ecosystems provide to society (Hooper et al. 2000, Wall et al. 2004, Wardle et al. 2004). We are experiencing unprecedented global change be it climate, land use or species extinctions; yet there is a critical lack of information as to what the implications of these changes are to soil organisms and the ecological processes they impact (Wall et al. 2004, Fitter 2005). Part of the problem is that the overwhelming diversity and abundance of soil organisms requires many experts and intense labor for study in all but the most simplified laboratory experiments (Giller 1996, Lawton et al. 1998). Plant richness can be a useful indicator of aboveground animal diversity at local scales (Currie 1991, Simonson et al. 2001); however, whether plant species richness is a determinant of belowground species richness has not been tested in a natural ecosystem. The few studies addressing this question this were laboratory experiments (De Deyn et al. 2003), field-plot manipulations (Wardle et al. 1999, De Deyn et al. 2004, Wardle et al. 2004), studies of human-created disturbance (Korthals et al. 2001, St. John et al. 2002, Huhta and Niemi 2003), and/or used higher taxonomic or functional groupings (Wardle et al. 1999,

Porazinska et al. 2003). Soil mites were examined rarely, at high taxonomic levels, and generally showed no consistent patterns relating to aboveground diversity (Hooper et al. 2000, Wardle et al. 2004). In response, I investigated the relationship between above- and belowground diversity using grass species and soil mites, a hyper diverse taxon in uncultivated tall grass prairie.

Soils communities are primarily detrital-based (Hunt et al. 1987, Coleman and Crossley 1996). Their function and composition are implicitly linked to the quantity and quality of resources from plant matter aboveground and to the roots of these plants (Bardgett and Cook 1998, Jones et al. 1998). Laboratory and field manipulations demonstrate that plant richness may be positively related to the diversity of soil litter quality or litter types that enter the detrital food web (Anderson 1978, Sulkava and Huhta 1998). This resource heterogeneity may support a greater diversity of soil fauna through both the provision of food substrate and additional microhabitats (Anderson 1978, Berg et al. 1998, Hansen 2000, Clapperton et al. 2002). Aboveground plant richness and diversity may be considered a surrogate for, or determinant of, belowground faunal richness and diversity through mechanisms of altering aspects of resource quantity, quality and heterogeneity.

This hypothesis was tested using grass species' characteristics and the communities of soil mites (Acari) associated with them, at the Konza Prairie Biological Research Station (KPBS; 39.1˚ N, 94.6˚ E). The KBPS is part of the last remaining tracts of unplowed tallgrass prairie in the U.S. and among the National Science Foundation's network of Long Term Ecological Research (LTER) sites.

Mites are the most abundant members of soil arthropod communities, accounting for as much as 95% of all individuals (Behan et al. 1978, Seastedt 1984b, Walter and Proctor 1999). Mites affect decomposition by feeding on microbes, detritus, as predators, omnivores and as plant parasites (Walter 1987, Kethley 1990, Siepel and De Ruiter-Dijkman 1993, Walter and Proctor 1999). Their global taxonomic richness is estimated to exceed 1 million species, with the majority of species thought to be soil dwellers (Walter and Proctor 1999). As with many soil mesofauna, feeding habits and functional roles for most species are often inferred from studies of closely related species (Marshall et al. 1987, Wall et al. 2001).

We tested three hypotheses that soil mite richness and taxonomic distinctness (a measure of how unrelated species are to each other) (Warwick and Clarke 1995) are determined by 1) grass species richness, 2) grass resource quality, based on photosynthetic pathway, and 3) grass resource heterogeneity based on mixtures of photosynthetic pathways. Mite species were inventoried from soil sampled between two individuals of six pre-determined species of grasses, three C_3 and three C_4. The photosynthetic pathways C_3 and C_4 represent quality of grass resources, including roots, with C_3 grasses characterized by lower C:N and lignin content than C_4 grasses (Wedin and Tilman 1990, Tilman et al. 1997). Several soil quality covariates including C:N of soil, roots and shoots, and soil textures were measured from these grass combinations. It was determined if juxtaposed grass species in diculture results in a non-additive increase (overyielding) of soil mite richness compared with two grass species in monoculture.

2.3. MATERIALS AND METHODS

2.3.1. Study site description

The KPBS has over 300 documented species of plants in the area and is dominated by big bluestem (*Andropogon gerardii* Vitm.) and little bluestem (*Schizachyrium scoparium* (Michx.) Nash), both C_4, perennial grasses (Freeman 1998). We chose a watershed (KPBS designation "4B") that is experimentally burned every four years. The last burn occurred the year previous to this study (May of 1998). Its intermediate fire frequency is thought to mimic natural wildfire conditions and supports a diverse mixture of both C_3 and C_4 grasses (Collins and Steinauer 1998). For more descriptions of the soil characteristics and site see a parallel study, Porazinska et al. (2003).

2.3.2. Sampling design

On 18 May 1999 four replicate blocks (≈ 20 m × 20 m) were established approximately 100 m apart on the upper side of watershed 4B's slope. Grass species pairs in 12 different combinations (Table 2.1) were marked with a pin flag and replicated five times within each block. Selection of grass pairs was non-random in order to minimize the influence of non-target grass species' roots; the distance between pairs was never more than 10 cm and no shoots of non-target plant species were within a 20 cm diameter. The selected grass species were: (A) big bluestem (C_4), (B) little bluestem (C_4), (C) Scribner's panicum (*Dichanthelium oligosanthes* (Schult.) Gould) (C_3), (D) Kentucky bluegrass (*Poa pratensis* L.) (C_3), (E) prairie dropseed (*Sporobolus heterolepis* (A. Gray) A. Gray) (C_4), and (F) prairie junegrass (*Koeleria nitida* Nutt.) (C_3). Soils for every grass

species combination, from one of the randomly selected 5 replicate pin flag locations within each block, were sampled with a soil corer (4.8 cm in diameter).

Table 2.1. Sampling design for the collection of soil cores and their subsequent use in testing the hypotheses for grass richness (H1; monoculture (1) vs. diculture (2)), quality (H2; low (C_4C_4) vs. high (C_3C_3)) and heterogeneity (H3; low (C_3C_3 or C_4C_4) vs. high (C_3C_4)) effects on soil mite richness.

Grass Combination[1]	Grass Richness	Grass Quality	Grass Heterogeneity
AA	1	C_4	*1*
BB	1	C_4	*1*
CC	1	C_3	*1*
DD	1	C_3	*1*
EE	*1*	C_4	*1*
FF	*1*	C_3	*1*
AB	2	*C_4*	1
AC	2	*C_3C_4*	2
AD	2	*C_3C_4*	2
BC	2	*C_3C_4*	2
BD	2	*C_3C_4*	2
CD	2	*C_3*	1

Note: Text in italics indicates samples not used for given analyses. [1](A) big bluestem (*A. gerardii*) (C_4), (B) little bluestem (*S. scoparium*) (C_4), (C) Scribner's panicum (*D. oligosanthes*) (C_3), (D) Kentucky bluegrass (*P. pratensis*) (C_3), (E) prairie dropseed (*S. heterolepis*) (C_4), and (F) prairie junegrass (*K. nitida*) (C_3).to two depths (0–5 cm, 5–10 cm). Two more core samples were each taken from another of the replicate set of pin flag locations for grass and soil chemical and physical analyses. Additionally, soil samples from beneath the remaining replicate pin flag locations were collected to analyze other members of the soil community (Porazinska et al. 2003).

Table 2.1 shows how the twelve grass species combinations were used to test the three hypotheses of this experiment. Grass species richness was defined as the number of grass species (one or two; monoculture or diculture) within 10 cm of the soil core. Where both individuals of grass were the same species and had a C_4 photosynthetic pathway (C_4C_4) resource quality was considered to be low compared to grass pairs of the C_3 photosynthetic pathway (C_3C_3). Where two grasses of different species and had the same photosynthetic pathway (C_3C_3 or C_4C_4) resource heterogeneity was considered to be low or homogeneous compared with heterogeneous photosynthetic grass pairs (C_3C_4).

2.3.3. Soil mites

Soil samples were carefully wrapped in aluminum foil, placed in coolers and transported to the KPBS soil laboratory within 2 hours of sampling. There, microarthropods were actively extracted from the soil cores using a high-gradient modified Tullgren method (Crossley and Blair 1991) into 95% ethanol and stored until identified. All sampled mites from the three suborders Mesostigmata, Oribatida and Prostigmata were enumerated and identified, in order of increasing taxonomic resolution, to superfamily, family, genus and species based on manuals from the Acarology Summer Program (The Ohio State University), numerous published descriptions and texts (Krantz 1978, Dindal 1990) and the assistance of mite systematists (Valerie M. Behan-Pelletier, Evert E. Lindquist and David E. Walter). Only adult mites were used in statistical analyses since many groups have polymorphic immature stages that cannot be reliably assigned to a species. Adult mites were assigned to the seven functional groups (fg): comminuting microbivores-detritivores (grazers and browsers), piercing-sucking

microbivores, plant parasites, nematophages, arthropod predators, generalist predators and omnivores (Anderson 1975, Walter and Proctor 1999).

The size of each mite species was determined from average length and widths obtained by measuring random subsets of up to 10 adult individuals per mite species for total body length and maximum width (exclusive of mouthparts and appendages).

2.3.4. Grass and soil covariates

See Porazinska et al. (2003) for procedures used to measure microbial carbon (C) and nitrogen (N), soil C and N mineralization rates, root C and N, total soil moisture, C, N and organic matter (SOM) and soil texture (percent sand, silt and clay).

2.3.5. Data analysis

Statistics were calculated with SAS version 8. Stepwise regressions (maximum R^2) of measured soil and grass covariates against treatment designations (e.g., C_3 vs. C_4) and mite richness were performed to determine which covariates should be used in ANCOVAs. Richness was calculated for each core, for each horizon, and compared using repeated measures ANOVA in PROC MIXED where horizon was repeated within core. Block (1 to 4) was entered as a random factor while grass richness (1 vs. 2), quality (C_3C_3 vs. C_4C_4) and heterogeneity (C_3C_3 or C_4C_4 vs. C_3C_4) were entered as fixed factors. The distribution of mite width classes between mono- and diculture samples was compared using a Chi-square test.

To test for overyielding of mite richness with grass richness, composite samples were created from the unions of monoculture samples and compared in a repeated measures ANOVA, to the union of two appropriate diculture samples:

$$\cup \quad < \quad \cup$$

where X and Y are two different species of grasses and XX, YY and XY represent the mite fauna recorded from soil cores taken from between two individuals of grass. This was repeated for every possible combination producing unique samples.

2.4. RESULTS

Mites were, as expected, numerous (6961 mites total from all cores; average density of 84000 mites · m^{-2} at 0–10 cm depth) and species rich (162 species within 3 soil mite taxonomic Suborders Mesostigmata, Oribatida and Prostigmata). All species of grass had similar associated mite richness ($F_{5, 33} = 1.59$, $P = 0.19$) and mite abundance ($F_{5, 33} = 0.89$, $P = 0.50$).

See Porazinska et al. (2003) for results of grass and soil chemical analyses. Stepwise regression showed significant and positive relationships between initial NO_3 and NH_4 and soil mite richness ($F_{2, 53} = 10.74$, $P < 0.0001$). These were not significant when entered as covariates in ANCOVAs and were not considered in further analyses.

2.4.1. H1: Grass species richness influences on soil mite richness

Grass and mite species richness were positively related at 5–10 cm depth and 0–10 cm depth at taxonomic levels higher than species (Figures 2.1 and 2.2). Functional group richness ($F_{1, 35} = 4.10$, $P = 0.05$) was positively related to grass richness only in the lower soil horizon (Figure 2.1). Mites beneath dicultures were more taxonomically distinct (Δ^*; less related) than in monocultures ($F_{1, 35} = 13.71$, $P < 0.001$; Figure 2.3).

Mite species richness was greater in the lower soil horizon of juxtaposed (XY∪XY) samples compared with similar paired (XX∪YY) samples ($F_{1, 101} = 11.96$, $P = 0.0008$) indicating that mite richness increased in a non-additive manner with grass

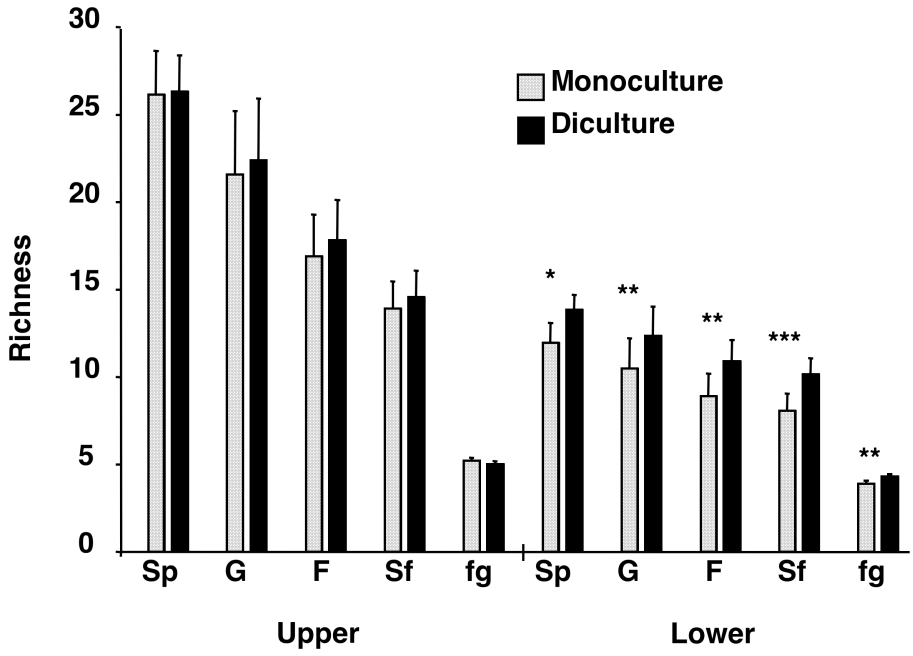

Figure 2.1. Taxonomic and functional richness of mites from grass mono- and dicultures, split by upper (0–5 cm) and lower (5–10 cm) sampled horizons, at the Konza Prairie Biological Station. Mites are grouped according to resolution of identification on the x-axis (Sp, species; G, genus; F, family; Sf, superfamily; fg, functional group). Significant differences between mono- and dicultures are indicated by the number of asterisks (0, $P \geq 0.1$; 1, $0.1 > P > 0.05$; 2, $0.05 > P > 0.01$; 3, $0.01 > P > 0.001$; 4, $P < 0.001$).

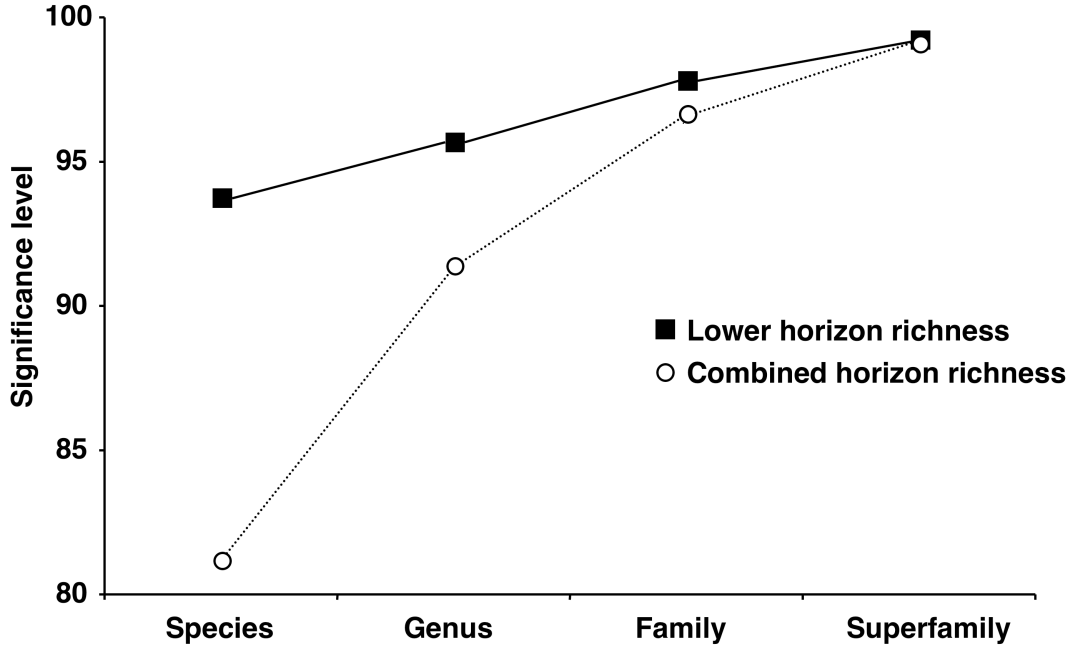

Figure 2.2. Significance of grass richness effect (mono- vs. diculture) on mite taxonomic richness. Significance level = $100 \cdot (1 - P)$.

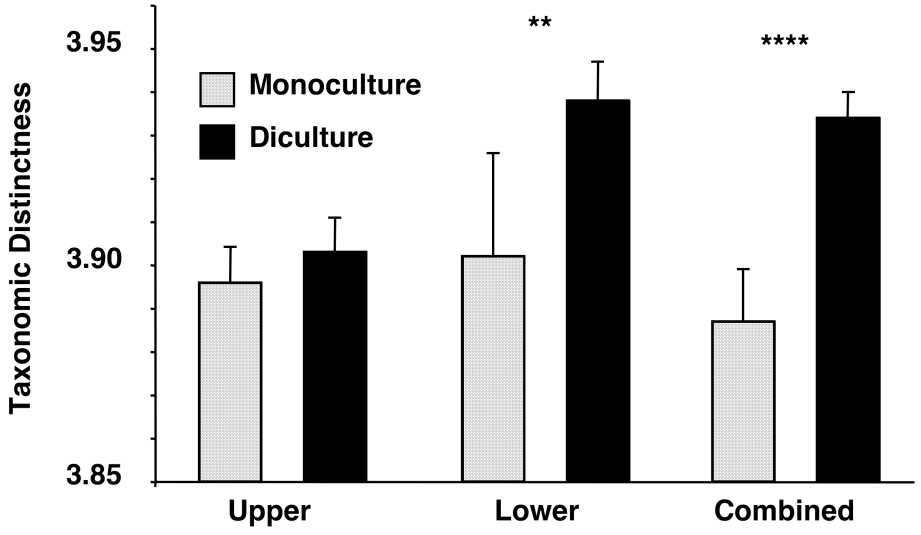

Figure 2.3. Taxonomic distinctness (*Δ**) of mites from grass mono- and dicultures, split by horizon, and in combination (i.e., recomposed upper and lower horizon samples).

richness at lower soil horizons but not in the upper soil horizons ($F_{1, 101} = 0.08$, $P = 0.7746$; Figure 2.4).

There was an interaction between grass species richness and soil horizon ($F_{1, 72} = 4.96$, $P = 0.0291$) indicating that total numbers of mites were more equitably distributed in the soil profile of dicultures than monocultures (Figure 2.5).

Mite body length (l) and widths (w) were highly correlated ($w = 0.713l - 27.218$, $R^2 = 0.88$) thus only widths were used for the discussion of mite sizes. The size class distribution of mites was distinctly different between mono- and dicultures ($X^2_{19} = 132$, $P < 0.001$; Figure 2.6). Dicultures supported the highest proportion of smaller mites in the 50–75 μm width class while the greatest proportion of larger mites in monocultures was in the 100–125 μm width class.

2.4.2. H2: Grass resource quality influences on soil mite richness

There was no effect of grass resource quality (C_3 vs. C_4) on mite richness at any taxonomic level or functional grouping considered (Figure 2.7).

2.4.3. H3: Grass resource heterogeneity influences on soil mite richness

Grass resource heterogeneity (C_3C_4 vs. C_3C_3 or C_4C_4) had no relationship to mite richness at any taxonomic level or functional grouping considered (Figure 2.8).

2.5. DISCUSSION

The diversity (species richness) of soil mites in tallgrass prairie was positively related to the diversity of grass species at the scale of individual grasses. This relationship also held for mite taxonomic levels above species, their taxonomic distinctness and functional group richness. Additionally, the co-occurrence of grass species overyielded mite species richness compared to what would be expected from those grasses in

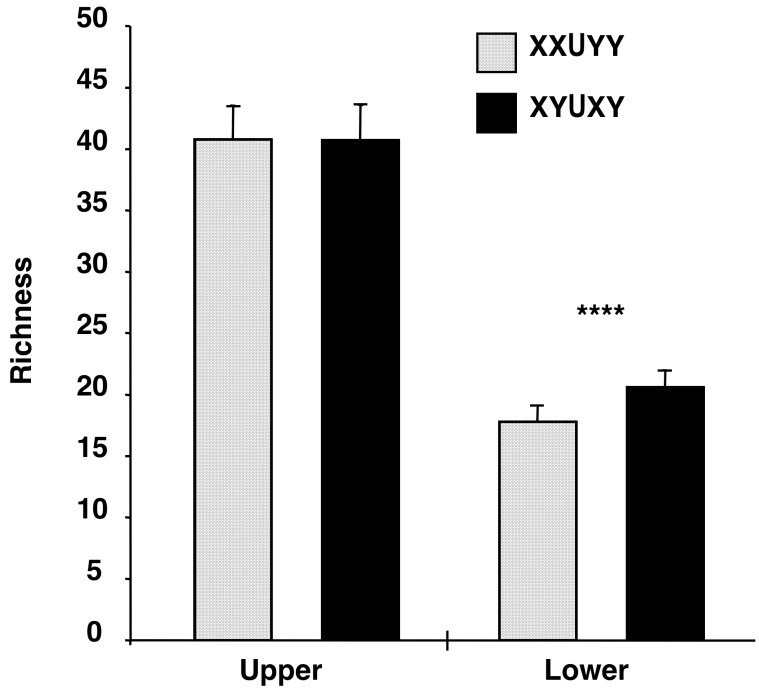

Figure 2.4. Species richness of mites from combined juxtaposed samples (XY∪XY) compared with combined non-juxtaposed samples (XX∪YY), split by horizon.

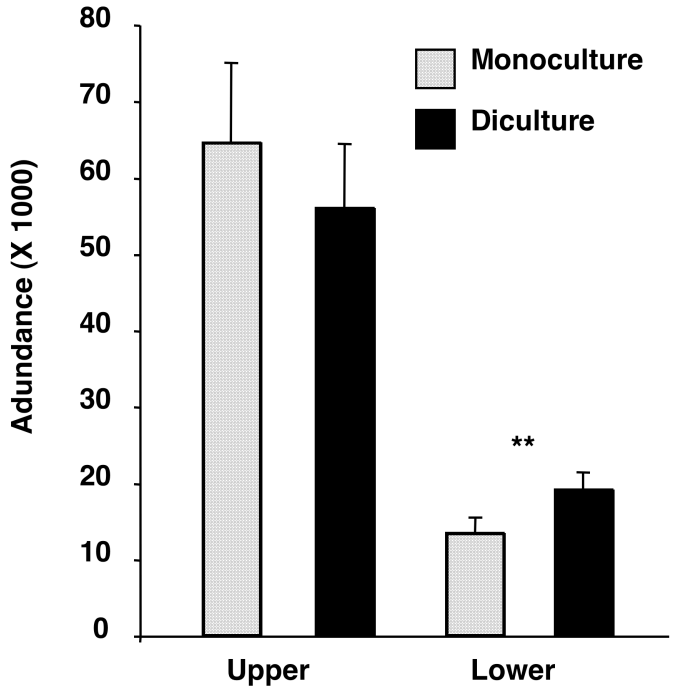

Figure 2.5. Abundance of mites from grass mono- and dicultures, split by horizon.

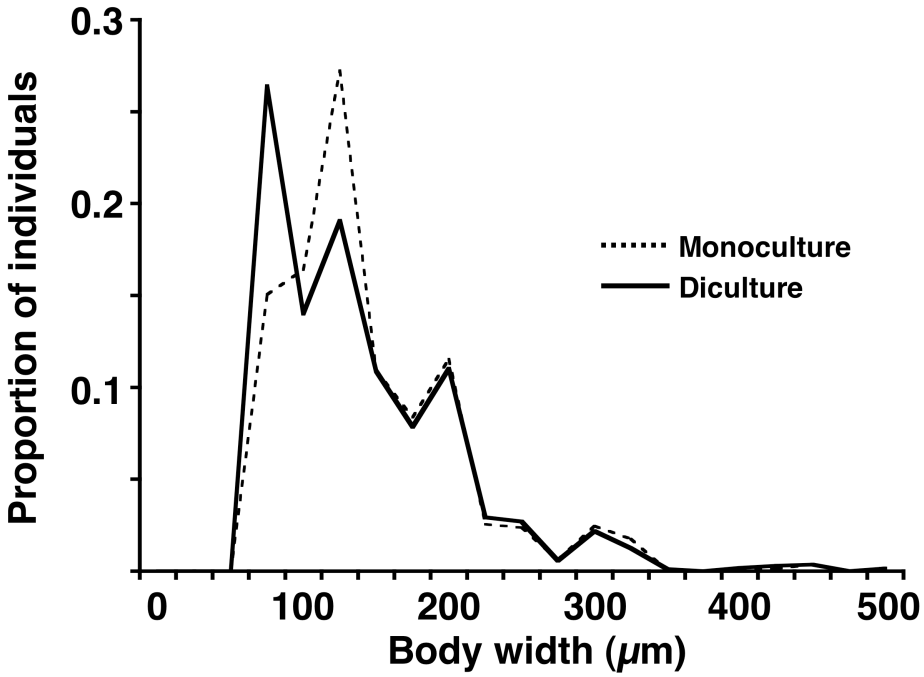

Figure 2.6. Proportion of mites of increasing body width in mono- and dicultures.

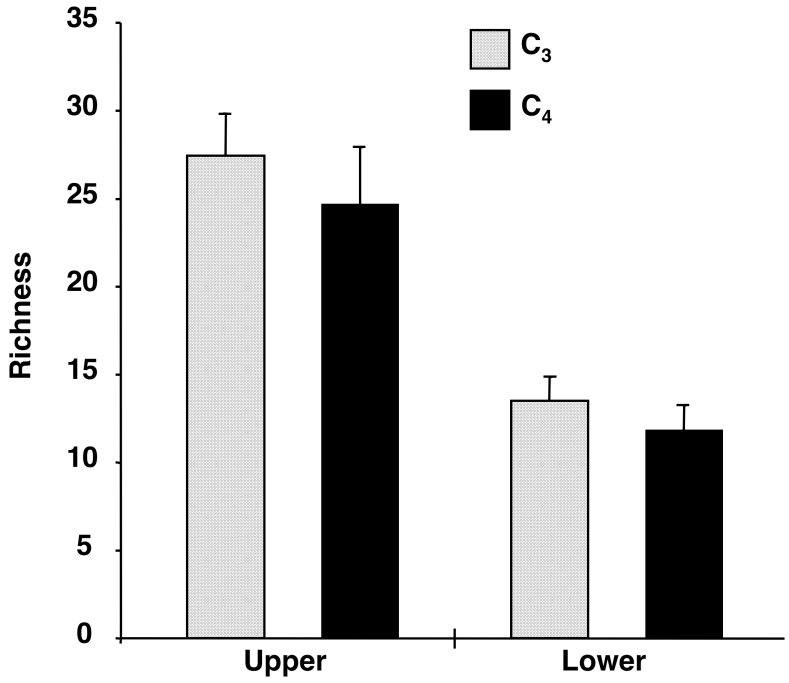

Figure 2.7. Mite species richness from low (C_4) and high (C_3) quality grass samples, split by horizon.

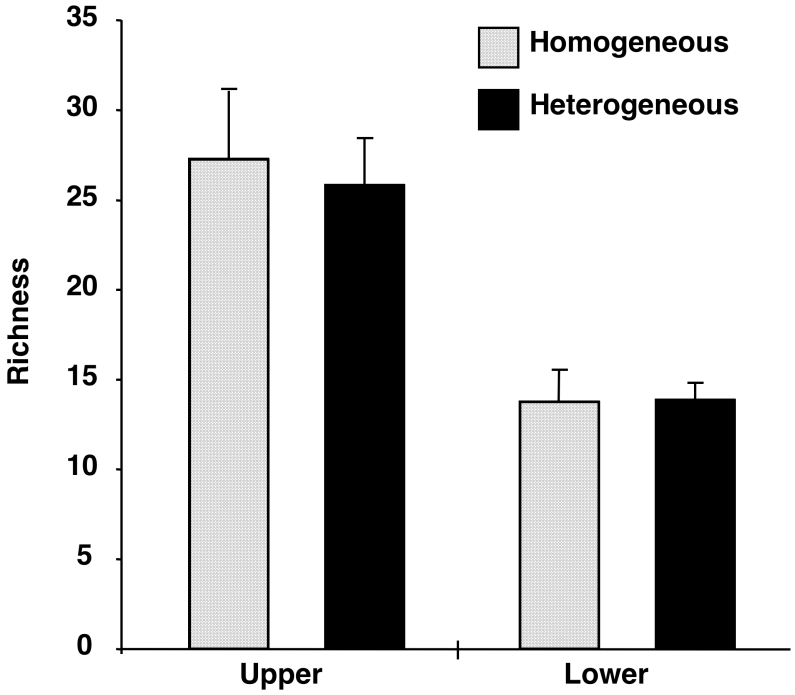

Figure 2.8. Mite species richness from low (C_4) and high (C_3) quality grass samples, split by horizon.

monoculture, demonstrating that the grass diversity effect on mite richness is non-additive. These effects were essentially absent in the topmost 0–5 cm soil layer, but significant at 5–10 cm depth. The mechanisms for these grass diversity effects are not clear since neither grass resource quality nor heterogeneity influenced the soil environment or the mite community in a detectable way.

2.5.1. H1: Grass species richness influences on soil mite richness

On average there were approximately two more mite species where grass species were in diculture than in monoculture at the KPBS (Figures 2.1–4). These findings are consistent with studies showing a modest positive relationship between oribatid mite species richness and the number of dominant tree species of managed forests (Migge et al. 1998), and between nematode and plant species richness in an experimental field study (De Deyn et al. 2004). Most studies, however, show no relationship between aboveground plant diversity and belowground faunal diversity at the species level (Wardle et al. 1999, Korthals et al. 2001, Huhta and Niemi 2003, Salamon et al. 2004). In many of these studies the authors note that "time lags" were evident in their results or at least possible in their experimental design, hence the effects of plant removals or additions on the soil communities may not have been measurable within the time frame of these studies. Since no manipulation of plant diversity was performed in our study the positive relationship between grass and mite species richness was not an experimental artifact.

This relationship was increasingly strong at higher mite taxonomic levels (superfamily > family > genus > species) (Figure 2.2), suggesting that mite species are less related to each other beneath dicultures compared to monocultures. Taxonomic

distinctness (Δ^*) of the soil mite faunas confirmed that mite species were less related, or more phylogenetically diverse, in diculture compared with monoculture soils (Figure 2.3). Thus the richer prairie flora supported both a richer and more phylogenetically diverse soil mite fauna. This result has implications for conservation decisions since given equal species richness it is generally considered a higher conservation priority to conserve for greater phylogenetic diversity (Warwick and Clarke 1995, Faith et al. 2004). These findings also support the practice of using floral inventories as biodiversity assessment tools (Simonson et al. 2001) for soil organisms.

However, soil mite species richness may be underestimated by predictions based solely on grass richness because the relationship between them is non-additive (Figure 2.4). The mechanism for this overyielding of mite richness where grass species were juxtaposed is unknown. Mite richness is known to be positively related to microhabitat diversity (Anderson 1978, Berg et al. 1998, Hansen 2000), and root interspecific interactions affect root architecture, the rhizosphere and hence soil mite habitat (Gordon and Rice 1992). Thus we hypothesize that there was a greater diversity of habitats for mites as a result of root competition where grass species were growing in mixed species combinations compared with monocultures (Figures 2.1, 3, 4). Similar results were found in a grassland experiment where the abundance and species richness of Collembola were found to be positively related to fine root biomass and plant functional group diversity (Salamon et al. 2004).

Also, we found that the influence of grass diversity on soil mite diversity was dependent on soil depth (Figures 2.1–4). In the lower soil horizon (5–10 cm) mites were consistently richer at all taxonomic levels beneath dicultures compared to monocultures,

but differences were not observed in the shallow depths (Figure 2.1). This makes sense in light of evidence that prairie grasses in Kansas tend to avoid rooting just below the surface, a drought tolerance trait (Qian et al. 1997). Any effects of interspecific competition on root architecture, and by extension mite habitat and species richness, will be more pronounced where roots are most active.

Further evidence for this hypothesis was found in the profile of mite abundances (Figure 2.5) and body widths (Figure 2.6) by depth. Soils mites are affected by soil pore size and distribution (Vreeken-Buijs et al. 1998) and their body widths decrease as pore widths decrease with depth in the soil profile (Curry 1971). In our study the proportion of mite body widths less than 125 μm was distinctly skewed favoring smaller mites beneath dicultures compared to monocultures (Figure 2.6). Also, there was a more equitable distribution of mites between the upper and lower horizons of dicultures compared to monocultures (Figure 2.5). These results suggest that the soil associated with dicultures has a more diverse pore structure at depth and a greater abundance of smaller habitable pores than for monocultures; however, this was not measured in the present study.

Mite species were assigned to seven functional groups in order to compare our results with those for taxonomic groupings as well as other studies. Mite functional group richness was positively related to grass species richness as well (Figure 2.1). This may suggest that functional groups are reasonable surrogates for mite species; however, immature and adult mites can have different food sources (Walter 1987, Walter and Ikonen 1989, Siepel and De Ruiter-Dijkman 1993) and less than 20% of the North American soil mite fauna has been described (even fewer have been adequately studied) (Marshall et al. 1987, Walter and Proctor 1999) making generalizations tenuous.

In a parallel collaborative study at KPBS the richness of functional groups of nematodes and protozoa were not influenced by the richness of grasses (Porazinska et al. 2003), although other studies have shown nematode and plant diversity to be related at the generic level (Korthals et al. 2001). There is a lack of data testing the influence of plant diversity on soil mite or arthropod functional diversity but some studies indicate that plant identity and functional role (e.g. legumes) are likely to be more important than plant diversity *per se* (Wardle et al. 1999, Setälä 2002, Hedlund et al. 2003, Salamon et al. 2004).

2.5.2. H2: Grass resource quality influences on soil mite richness

The diversity of aboveground arthropod communities in grasslands was positively related to the nutrient status and productivity of the plants on which they feed (Siemann 1998). However, there was no effect of grass resource quality (C_3 vs. C_4) on soil mite richness (Figure 2.7) at any taxonomic level or functional grouping considered at the KPBS. Similarly, in a parallel study, Porazinska et al. (2003) found no effect of grass resource quality on the diversity of functional groups of nematodes and protozoa. The lack of grass resource quality effect on soil mites was expected since few of grass and soil quality metrics were different between C_3 or C_4 samples (Porazinska et al. 2003, Table 2). The carbon to nitrogen ratio of the C_3 grasses' roots and soil was lower than for C_4 grasses due to elevated nitrogen levels in the C_3 grasses' roots and soil organic matter was also lower under C_3 compared to C_4 grasses.

It is also possible that timing of sampling may have obscured quality differences between C_3 and C_4 grasses. The "cool season" C_3 and "warm season" C_4 grasses have different phenologies (Hartnett and Fay 1998). Larger differences between C_3 and C_4

grasses may have been observed had sampling taken place several times during the season. Also, when compared with forbs, nitrogen fixers and woody plants, the differences between C_3 and C_4 grasses are slight. However, Osler and Beattie (2001) found that even though different tree species had strong effects on the soil environment, these influences were not enough to affect the composition of soil mite communities. Thus it appears that soil and litter fauna are relatively unspecific to the plants and their functional aspects when compared to aboveground fauna.

This is a recurring theme in the soil literature; belowground food webs tend not to follow patterns established by observations of aboveground food webs (Setälä 2002). Belowground food webs have characteristics that may override differences in resource quality such as separate energy channels (i.e., roots, fungal and bacterial; Hunt et al. (1987)), the commonness of indirect interactions among the fauna, and the high degree of omnivory (Setälä 2002).

2.5.3. H3: Grass resource heterogeneity influences on soil mite richness

There was no effect of grass resource heterogeneity (C_3C_4 vs. C_3C_3 or C_4C_4) on soil mite richness (Figure 2.8) at any taxonomic level or functional grouping considered. This was unexpected given the evidence that heterogeneous mixtures of grass species (diculture; Figure 2.1) did support a richer soil mite fauna compared with monocultures (Figures 2.1–4). Similarly, Migge et al. (1998) found no influence of tree stand type (mixed vs. monoculture) on the diversity of soil oribatid mite communities and Maraun and Scheu (2000) found that oribatids were not influenced by the identity or diversity of plant resources entering the soil system. This was interpreted as a function of the generalist detritivore-fungivore life history of most oribatid mites (Maraun et al. 2003).

Other factors, not measured in our study, may play a more important role in determining soil mite diversity than plant richness or resource quality and heterogeneity. For example Clapperton et al. (2002) found that the abundance and diversity of soil microarthropods was positively related to grassland productivity and hence resource quantity. Currie (1991) showed that at regional scales richness of aboveground animals was highly correlated to potential evapotranspiration, a measure of how much energy is entering the ecosystem, and not plant richness. This suggests that at larger scales than we investigated, patterns in the richness of soil fauna may be similar to those for some aboveground vertebrates. Also potentially important to the diversity of soil mites is the influence and interactions of other soil organisms. Huhta and Niemi (2003) concluded that the influence of earthworms on soil structure and resources was the most significant factor determining the diversity of oribatid mites. Finally, Sulkava and Huhta (1998) found that soil faunal diversity was positively related to the spatial heterogeneity of resources but not the diversity of resources. That is, different resources in patches promoted a richer fauna than the same resource mixed together presumably for reasons of competitive exclusion.

The relationship between above- and belowground diversity in natural systems is certainly complex and dependant upon the organisms studied as well as the scale of the investigation (Currie 1991, Hooper et al. 2000, Ettema and Wardle 2002, Wardle et al. 2004). This study adds to the literature by providing valuable data towards understanding the patterns of this above- belowground relationship and in identifying mechanisms from a field study in a natural system at the species level. This knowledge is invaluable for the

prediction of soil biodiversity, its influence on soil processes and for broader management considerations.

3. ARE SOIL MITE COMMUNITIES SENSITIVE TO THE IDENTITY OF NATIVE AND INVASIVE ALIEN GRASSES?

3.1. ABSTRACT

Associations between plants and animals in aboveground communities are often predictable and specific. The introduction of invasive alien plants into an ecosystem can result in dramatic changes in both the plant and animal communities. Yet many studies of belowground animal communities suggest they are relatively detached from the plant community. The hypotheses that soil mites (Acari) form specific communities associated with different native grass species in an unmanipulated, natural ecosystem and that invasive alien grasses will impact soil mite community composition in this setting were tested.

Soil mites sampled beneath five native and two alien-invasive species of grass at the Konza Prairie Biological Station, Kansas, USA were similarly abundant, species rich, diverse, and taxonomically distinct. There was no evidence that the community composition of soil mites was specific to grass species as a whole, but the oribatid mite sub-community was weakly related to grass identity. No single mite species had affinities for a specific grass species. Canonical correspondence analysis (CCA) suggested that the soil mite community was weakly related to soil environmental conditions (nitrogen

mineralization rate, soil organic matter content and percent clay). Results suggest that soil mite communities were more influenced by characteristics of the plant community as a whole and its effect on prevailing soil conditions. The most recent invasive alien grass did not support a successionally younger mite fauna and neither had influenced mite community structure, possibly because they had not substantially altered the soil environment. These results suggest that extrapolations of soil mite diversity based on assumptions of plant specificity would not be valid.

3.2. INTRODUCTION

The importance of soil organisms to ecosystem functioning and the provision of services to society is unquestionable (Wall 2004). Unfortunately, our knowledge of soil organisms and their diversity lags far behind what is known for aboveground systems (Giller 1996). Vascular plants are relatively easy to census and so they are often used as indicators of more cryptic organisms. For example, Erwin's (1982) much debated estimate of 30 million tropical arthropod species was based on assumptions of tree-host specificity among arboreal herbivorous beetles. This approach has been questioned (Ødegaard 2000, Novotny et al. 2002), and whether plant species are a good indicator of soil dwelling species is still contentious (Hooper et al. 2000, Chapter 2). Plants can influence soil community structure (Bardgett et al. 1999, Yeates 1999, Osler and Beattie 2001, De Deyn et al. 2004, Wardle et al. 2004) and vice versa (De Deyn et al. 2003, Wardle et al. 2004). Some data on belowground herbivores indicate close host specificity (Queneherve et al. 1997, Yeates 1999), but data on non-herbivorous belowground communities suggest no host specificity (Osler and Beattie 2001, Porazinska et al. 2003).

The degree to which the belowground community responds to plant identify, or traits, decreases with increasing trophic levels (Korthals et al. 2001, Porazinska et al.

2003, Wardle et al. 2003, De Deyn et al. 2004). Soil mites (Acari) are typically removed from primary producers by one or more trophic levels (Hunt et al. 1987). Mites in the suborder Oribatida have traditionally been considered *K*-strategist microbivores that feed on a wide variety of fungal substrates (Walter and Proctor 1999), but recent evidence suggests that the Oribatida may span as many as four trophic levels (Schneider et al. 2004) including predators of nematodes (Walter 1987). Mesostigmata are a group of mites which are mostly *r*-strategist top predators in the detrital foodweb, although a few are obligate fungal feeders (Walter and Proctor 1999). The suborder Prostigmata include herbivores, microbivores, predators of nematodes and generalist predators of other microarthropods (Walter and Proctor 1999).

The introduction of invasive alien plants into an ecosystem can cause large changes in its structure and function (Mack and D'Antonio 2003) including in soil communities (Belnap and Phillips 2001, Ehrenfeld and Scott 2001, Evans et al. 2001). The mechanisms of this change involve alteration of the soil physical and chemical environment leading to noticeable changes in soil communities (Belnap and Phillips 2001, Ehrenfeld and Scott 2001, Evans et al. 2001). However, when invasive alien plants have little influence on soil parameters there was no discernable effect on the soil faunal community (Porazinska et al. 2003).

The objective for this study was to determine if grass species impact the diversity and structure of soil mite communities, using soil mites sampled from beneath five native and two invasive alien species of grass at the Konza Prairie Biological Station (KPBS), Kansas, USA (39.1° N, 96.6° W). Specifically, the hypotheses that soil mites form specific communities associated with different grass species in an unmanipulated, natural

ecosystem and that invasive grasses will have an impact on the diversity and structure of soil mite community were tested.

For this purpose a variety of statistical methods were used to obtain a comprehensive understanding of patterns in the soil mite communities, similar to Osler and Beattie's (2001) approach. Univariate and multivariate as well as parametric and non-parametric statistics including canonical correspondence analysis (CCA) (ter Braak 1986) and analysis of similarity (ANOSIM) (Clarke 1993) were used. CCA has proven itself to be a powerful and robust method for visualizing how species are related to ecological gradients, particularly when more than two gradients are involved (Palmer 1993). ANOSIM is a non-parametric method for determining if two or more communities are different. Both of these approaches can yield valuable information in ecological studies; but involve identifying and enumerating every individual in the community. Hyper-diverse communities, such as soil mites, tend to have sparse matrices (most species are only ever sampled once) often leading to low predictive power with CCA and ANOSIM and an increased chance of not rejecting the Null Hypothesis when the Alternative is true (a Type II statistical error) (Osler 2002). To address this a non-parametric test based on presence/absence data, probability of association analysis (POAA) was used as an alternative means to easily detect the presence of community specific associations with treatments (e.g. grass species).

3.3. MATERIALS AND METHODS

3.3.1. Study site description

There are over 300 documented species of plants at the KPBS, though it is dominated by big bluestem (*Andropogon gerardii* Vitm.) and little bluestem

(*Schizachyrium scoparium* (Michx.) Nash), both C_4 perennial grasses (Freeman 1998). Experimental blocks were chosen at two sites within the KPBS: the native plant site (NPS) where invasive alien grasses have not attained a significant presence and the invasive plant site (IPS) where the invasive alien grass, Caucasian bluestem (*Andropogon bladhii* Vitm.), has become dominant since being introduced around 1980.

We chose a watershed (KPBS designation "4B") which is experimentally burned every four years as the NPS, with the last burn occurring the year prior to this study (May of 1998). The IPS was a site adjacent a series of ongoing experiments referred to as the "Belowground Plots" (Rice et al. 1998). For a detailed description of the NPS and the IPS see Porazinska et al. (2003).

3.3.2. Sampling design

On 18 May 1999 four replicate blocks (≈ 20 m × 20 m) were established approximately 100 m apart on the upper side of the NPS slope. Pairs of grasses for each species (Table 3.1) were marked with a pin flag and replicated five times within each block. Selection of grass pairs was non-random: the distance between them was never more than 10 cm and no non-target species of plants were within a 20 cm diameter in order to minimize the influence of non-target plant species' roots. The selected grass

Table 3.1. Sampling design and number of samples positive for the presence of five mite species[1] with significant distributions across grasses.

Grass Species[2]	Site	CeraVirg	RhodSp2	StigVere	PergCurv	SellSp3
AA	NPS	1	2	0	1	0
BB	NPS	0	1	1	3	2
CC	NPS	1	1	1	0	3
DD	NPS	0	0	1	0	0
EE	NPS	0	0	2	2	1
FF	NPS	2	0	0	0	0
IAA	IPS	3	4	4	0	0
IGG	IPS	4	2	3	0	0
Probability		0.012	0.023	0.035	0.039	0.039

Notes: [1](CeraVirg) *Ceratozetes virginicus*, (RhodSp2) *Rhodacarus* sp. 2, (StigVere) *Stigmalychus* nr. *veretrum*, (PergCurv) *Pergalumna curva*, (SellSp3) *Sellnickochthonius* sp. 3. [2](A) big bluestem (*A. gerardii*) (C_4), (B) little bluestem (*S. scoparium*) (C_4), (C) Scribner's panicum (*D. oligosanthes*) (C_3), (D) Kentucky bluegrass (*P. pratensis*) (C_3), (E) prairie dropseed (*S. heterolepis*) (C_4), (F) prairie junegrass (*K. nitida*) (C_3) and (G) Caucasian bluestem (*A. bladhii*)

species were: (A) big bluestem (C_4), (B) little bluestem (C_4), (C) Scribner's panicum (*Dichanthelium oligosanthes* (Schult.) Gould) (C_3), (D) Kentucky bluegrass (*Poa pratensis* L.) (C_3), (E) prairie dropseed (*Sporobolus heterolepis* (A. Gray) A. Gray) (C_4), and (F) prairie junegrass (*Koeleria nitida* Nutt.) (C_3), all native grasses at Konza except for Kentucky bluegrass. At the IPS blocks and grass pairs were selected in a similar manner. Here, big bluestem (A) and the invasive alien, (G) Caucasian bluestem were selected.

3.3.3. Soil mites

Soils for every grass species combination (Table 3.1), from one of the randomly selected 5 replicate pin flag locations within each block, were sampled with a soil corer (4.8 cm in diameter) to a depth of 10 cm in 5 cm increments (Crossley and Blair 1991). Soil samples were carefully wrapped in aluminum foil, placed in coolers and transported to the KPBS soil laboratory within 2 hours of sampling. Mites were actively extracted from the soil cores using a high-gradient modified Tullgren method (Crossley and Blair 1991) into 95% ethanol and stored until identified. All mites—Mesostigmata, Oribatida and Prostigmata—were enumerated and identified to species based on manuals from the Acarology Summer Program (The Ohio State University), Krantz (1978), Dindal (1990), numerous published descriptions and the assistance of mite systematists (Evert E. Lindquist and David E. Walter). Only adult mites were used in statistical analyses since many groups have polymorphic immature stages that cannot be reliably assigned to a species. Data for upper and lower core samples were then added together to determine the abundance (*N*), species richness (*S*) and the inverse of Simpson dominance index (*D*) of mites for each 0–10 cm sample. The inverse of the Simpson dominance index, also

known as Hill's number *N2* is a measure of how many species dominate the sample, thus high dominance implies low evenness (Hill 1973). Taxonomic distinctness (Δ^*), which measures how taxonomically un-related species in a community are to each other, was calculated according to Warwick and Clarke (1995).

3.3.4. Grass and soil covariates

See Porazinska et al. (2003) for procedures used to measure microbial carbon (C) and nitrogen (N), soil C and N mineralization rates, root C and N, total soil moisture, C, N and organic matter (SOM) and soil texture (percent sand, silt and clay).

3.3.5. Data analysis

Statistics were performed and figures generated using R 1.9.1 (R Development Core Team, 2004). Comparisons between grass species of log-transformed response variables were performed by analysis of variance (ANOVA) using a linear mixed effects model (function lme of package nlme) with block entered as a random effect; untransformed data are presented in tables and figures as means ± standard error. Post-hoc comparisons were performed as pairwise t-tests with p-values adjusted for multiple comparisons using the fdr method (Benjamini and Hochberg 1995). Contrasts were used to compare NPS and IPS (function estimable of package gregmisc) also using fdr corrected p-values. A Kruskal-Wallis rank sum test (K-W) was used (function kruskal.test), but no post-hoc comparisons, where suitable transformations of the data could not be found to satisfy the assumptions of ANOVA (Bartlett's test for homogeneity of variance and inspection of residuals).

Analysis of similarity (ANOSIM; function anosim of package vegan) was used to determine if there were differences in the mite communities between grass species,

blocks, or sampling sites (NPS vs. IPS) using Bray-Curtis dissimilarities. Significance of results was determined by Monte Carlo permutations (1000) and reported as the ANOSIM *R* statistic that varies between –1 and 1 (highly significant at extremes), with 0 indicating complete randomness.

A non-parametric test of the hypothesis that mite species associate with particular grass species (probability of association analysis, POAA) was performed using presence/absence data. The probabilities of all possible distributions of positive soil cores (those with one or more individual mites of a given species) among grass species were calculated from multinomial distributions, under the null hypothesis of no association between mite and grass species. Mite species with underdispersed distributions (majority of positive cores associated with particular grass species) were assigned an alpha level equal to the sum of the probabilities of all core distributions with equal or lower probability than the observed distribution. This test sacrifices power in ignoring the numbers of mites in a core, but has the advantage of being free of assumptions about residual errors. The number of mite species with significantly under-dispersed distributions (i.e. found more often in cores from one or more grass species than would be predicted from all possible outcomes) were totaled and compared to a cumulative Poisson distribution (significance level, $\propto = 0.05$; total number of events or mite species, n; mean, $\mu = \propto \cdot n$) to see if it was greater than would be expected by chance alone.

Canonical correspondence analyses (CCA) (ter Braak 1986) was performed (function cca of package vegan) using only the soil parameters which were determined to differ between grasses by ANOVA or K-W. A logarithmic transformation of the data was used to reduce bias of differently scaled parameters (Palmer 1993) and each was checked

for normality by inspection of histograms prior to CCA. Species of grass was also entered as an environmental factor and the effect of blocks was partialled out as a co-variable. Mite species of low occurrence (singletons and doubletons) were removed from the dataset prior to analysis. Three separate CCAs were performed for mite species within the suborders: Mesostigmata, Oribatida and Prostigmata in addition to a CCA of the entire mite community. Significance of results was determined using Monte Carlo permutations (1000). CCA plots were not scaled and only environmental vectors with a significance of $P < 0.1$ are shown.

3.4. RESULTS

Soil conditions were similar between most grass species, except for prairie dropseed (EE, *Sporobolus heterolepis*) that differed from the other grasses for a few parameters (Figure 3.1). Total soil C was different between grass species ($F_{7, 17} = 4.79$, $P = 0.004$), with soils beneath prairie dropseed being higher than most, the remaining grasses were similar as were the NPS and IPS. Total soil N was also highest beneath prairie dropseed, but only soils beneath grasses from the IPS were significantly lower than prairie dropseed. The other grasses had similar soil N concentration. Overall, the NPS had higher soil N than the IPS. Soil C:N was highest beneath prairie dropseed and grasses at the IPS; though this was only marginally significant ($\chi^2_7 = 13.20$, $P = 0.067$). Microbial C, N and C:N were similar for all grass species as was the rate of C-mineralization. N-mineralization rates were related to grass species ($\chi^2_7 = 14.28$, $P = 0.046$). It appeared to be lowest beneath prairie dropseed and grasses at the IPS; however post hoc tests could not be performed to confirm this. There was an effect of grass

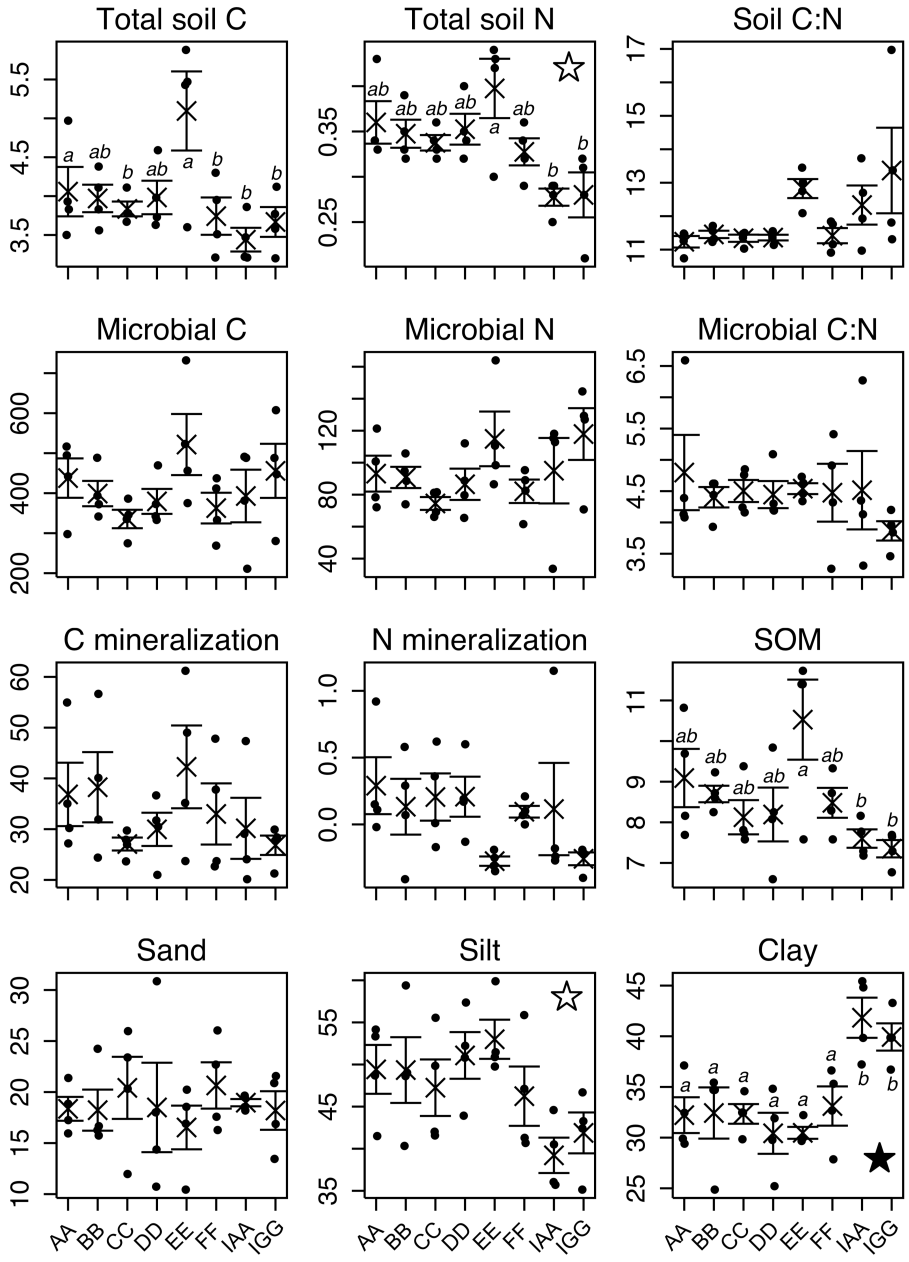

Figure 3.1. Results of soil analyses from beneath grasses at the NPS (AA–FF) and the IPS (IAA, IGG). From left to right, top to bottom, total soil C (% dry soil), total soil N (% dry soil), soil C:N, microbial C (μg · g dry soil^{-1}), microbial N (μg · g dry soil^{-1}), microbial C:N, C mineralization rate (μg · g dry soil^{-1} · day^{-1}), N mineralization rate (μg · g dry soil^{-1} · day^{-1}), soil organic matter (% dry soil), sand (%), silt (%) and clay (%). Data are represented by closed circles. Means (± standard error) bearing the same letter are not significantly different ($\propto = 0.05$). A star symbol above IPS samples (IAA and IGG) indicates differences between NPS and IPS (no star, $P \geq 0.05$; open star, $0.05 > P > 0.01$; solid star, $P \leq 0.01$).

species on SOM ($F_{1, 17} = 4.14$, $P = 0.0079$): it was highest beneath prairie dropseed and lowest beneath grasses at the IPS. Soil textures differed in terms of silt ($F_{1, 17} = 2.63$, $P = 0.049$) and clay ($F_{1, 17} = 4.42$, $P = 0.006$) content. Silt was higher, and clay lower, at the NPS compared to the IPS.

A total of 3361 adult mites comprising 159 species were collected from all samples, with an average density of 58043 ± 6187 mites · m^{-2} in the top 10 cm of soil. All species of grass had similar associated mite abundance (N, $F_{1, 17} = 0.24$, $P = 0.970$), mite richness (S, $F_{1, 17} = 1.09$, $P = 0.409$), Simpson dominance (D^{-1}, $F_{1, 17} = 0.91$, $P = 0.521$), taxonomic distinctness (Δ^*, $F_{1, 17} = 1.20$, $P = 0.352$) and ratio of mesostigmatid to oribatid species richness (M:O, $F_{1, 17} = 1.45$, $P = 0.250$) (Figure 3.2). No differences were found in any of these parameters between the NPS and IPS.

ANOSIM indicated that mite communities sampled from the same grass species were no more similar than those taken from different grass species ($R = 0.036$, $P = 0.312$) indicating a lack of grass species effect on mite community composition (Figure 3.3). Mite communities sampled beneath grasses at the NPS were not distinct from those at the IPS ($R = –0.02$, $P = 0.538$). Mite communities sampled within the same block, regardless of the grass species they were sampled from, were more similar than those sampled from other blocks ($R = 0.23$, $P = 0.005$).

POAA indicated that of the 159 mite species sampled, 80 were frequent enough (occurred in > 2 samples) to have potentially non-random patterns of occurrence between grass species. Of these 80 mite species, only five had significant distributions among the grasses (Table 3.1), which were no more than would be expected by chance ($\mu = 4$, $P = 0.215$). *Ceratozetes virginicus* (Oribatida), *Rhodacarus* sp. 2 (Mesostigmata) and

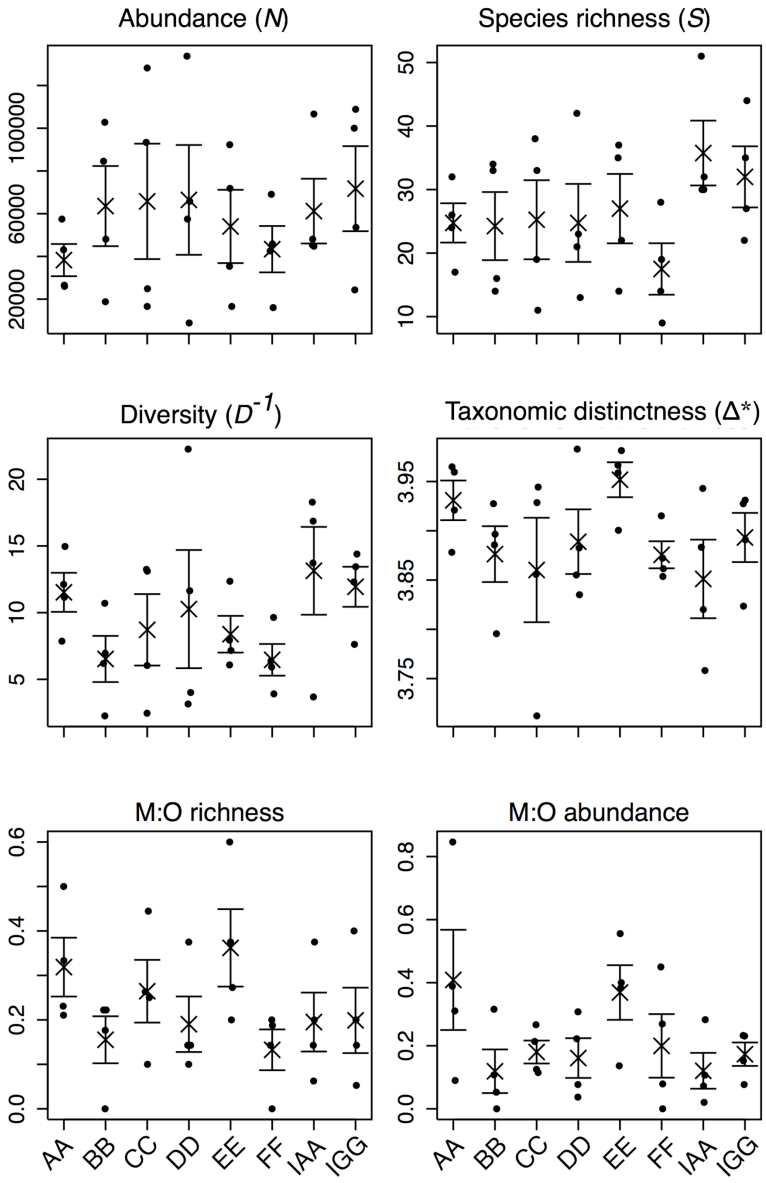

Figure 3.2. From left to right, top to bottom, Soil mite abundance (N, mites · m^{-2}), species richness (S), inverse Simpson's index (D^{-1}), taxonomic distinctness (Δ^*) and ratio of mesostigmatid to oribatid species richness and abundance from beneath grasses at the NPS (AA–FF) and the IPS (IAA, IGG). Symbol descriptions as per Figure 3.1

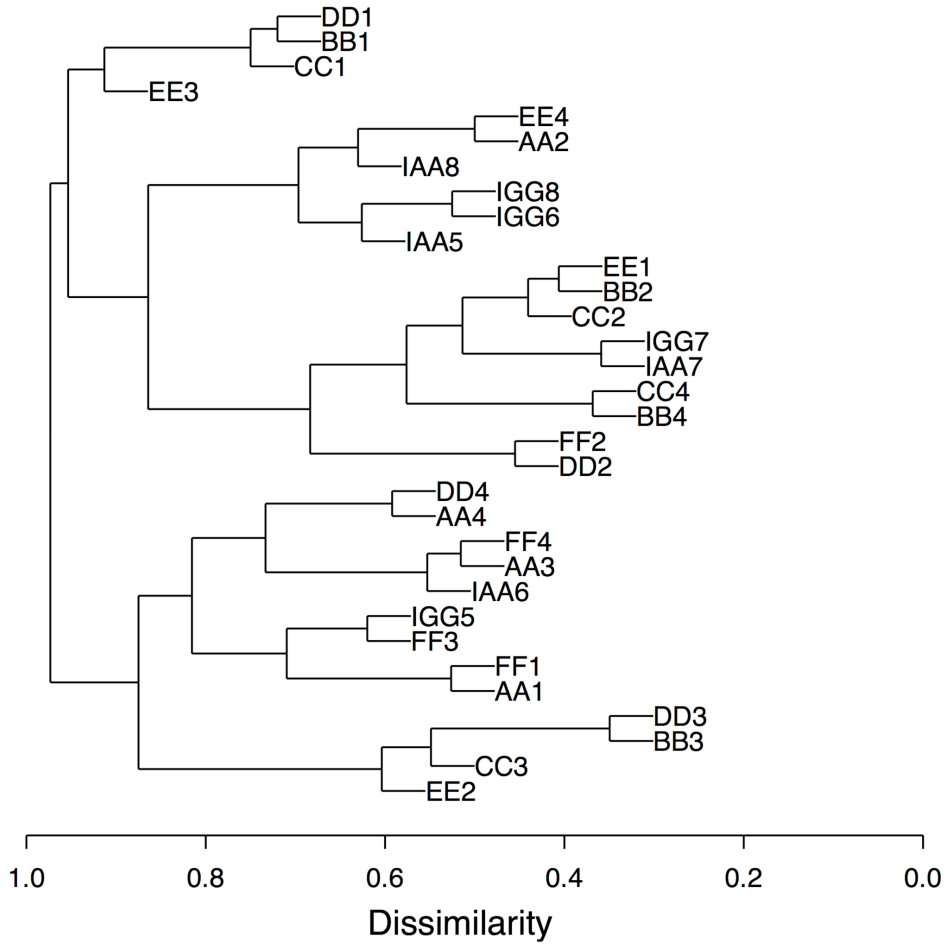

Figure 3.3. Dendrogram representing the dissimilarity of mite communities taken from beneath grasses at the NPS (AA–FF) and the IPS (IAA, IGG). Number suffix indicates blocking structure.

Stigmalychus nr. *veretrum* (Prostigmata) were more frequently found at the IPS than at the NPS. *Pergalumna curva* (Oribatida) and *Sellnickochthonius* sp. 3 (Oribatida) were absent from the IPS. *Pergalumna curva* was sampled six times but never from Scribner's panicum, Kentucky bluegrass or prairie junegrass. *Sellnickochthonius* sp. 3 was sampled six times but never from big bluestem, Kentucky bluegrass or prairie junegrass.

CCA supported the hypothesis that total mite species community composition is related to grass species present, and also certain soil factors (N-mineralization rate, soil C, soil N, SOM and clay) at a marginally significant level ($F_{11, 17} = 1.13$, $P = 0.076$). The first two canonical axes explained only 14.8% of the total variance in the data indicating low explanatory power overall (Figure 3.4). Soil factors significantly correlated ($P < 0.05$) with the first two canonical axes were: N-mineralization rate ($R^2 = 0.51$) and clay ($R^2 = 0.21$). Soil organic matter was marginally related ($P = 0.052$) to the first two axes ($R^2 = 0.18$). Grass species (centroids; Figure 3.4) were related to the soil environmental vectors in a manner expected from results of the ANOVA (Figure 3.1). The first two CCA axes (Figure 3.4) confirm there was little association between grass species and mite species (as shown by ANOSIM and POAA).

The mesostigmatid mite community was marginally related to the environment as a whole ($F_{11, 13} = 0.91$, $P = 0.05$) but no single environmental variable was significantly correlated to the first two canonical axes (Figure 3.5). The oribatid mite community was highly related to environmental conditions ($F_{11, 19} = 1.32$, $P < 0.001$; Figure 3.6). Environmental factors significantly correlated ($P < 0.05$) with the first two axes were: grass species ($R^2 = 0.23$) and N-mineralization rate ($R^2 = 0.21$). Soil organic matter was marginally related to the first two axes ($R^2 = 0.15$, $P = 0.092$). The prostigmatid mite

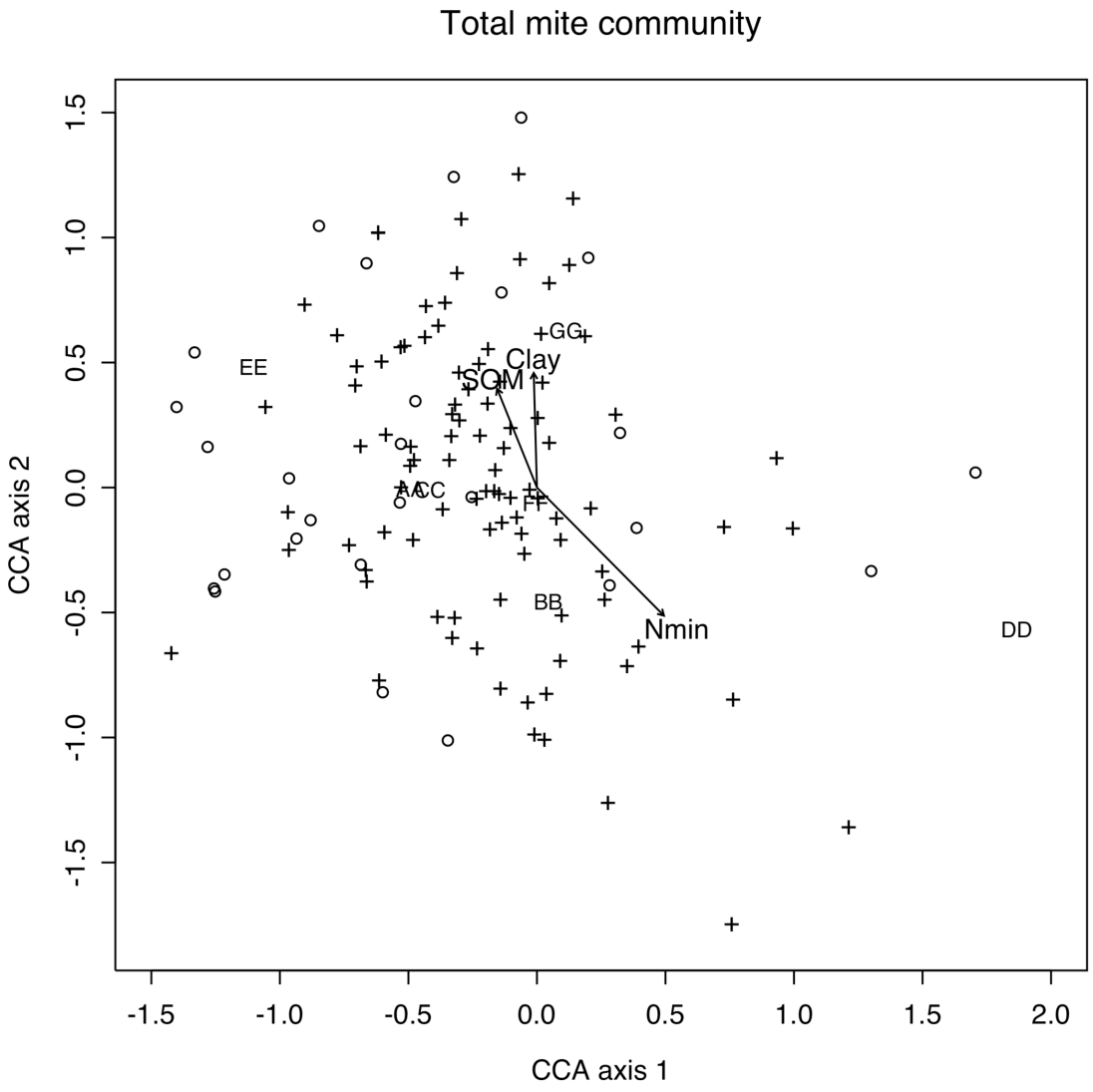

Figure 3.4. Canonical correspondence analysis ordination plot, first two axes. Open circles (○) represent soil samples, mite species are plus symbols (+). Abbreviations for grass species (AA–GG) represent centroids for the grasses' relation to environmental factors. Only environmental vectors significant at $P < 0.1$ are shown.

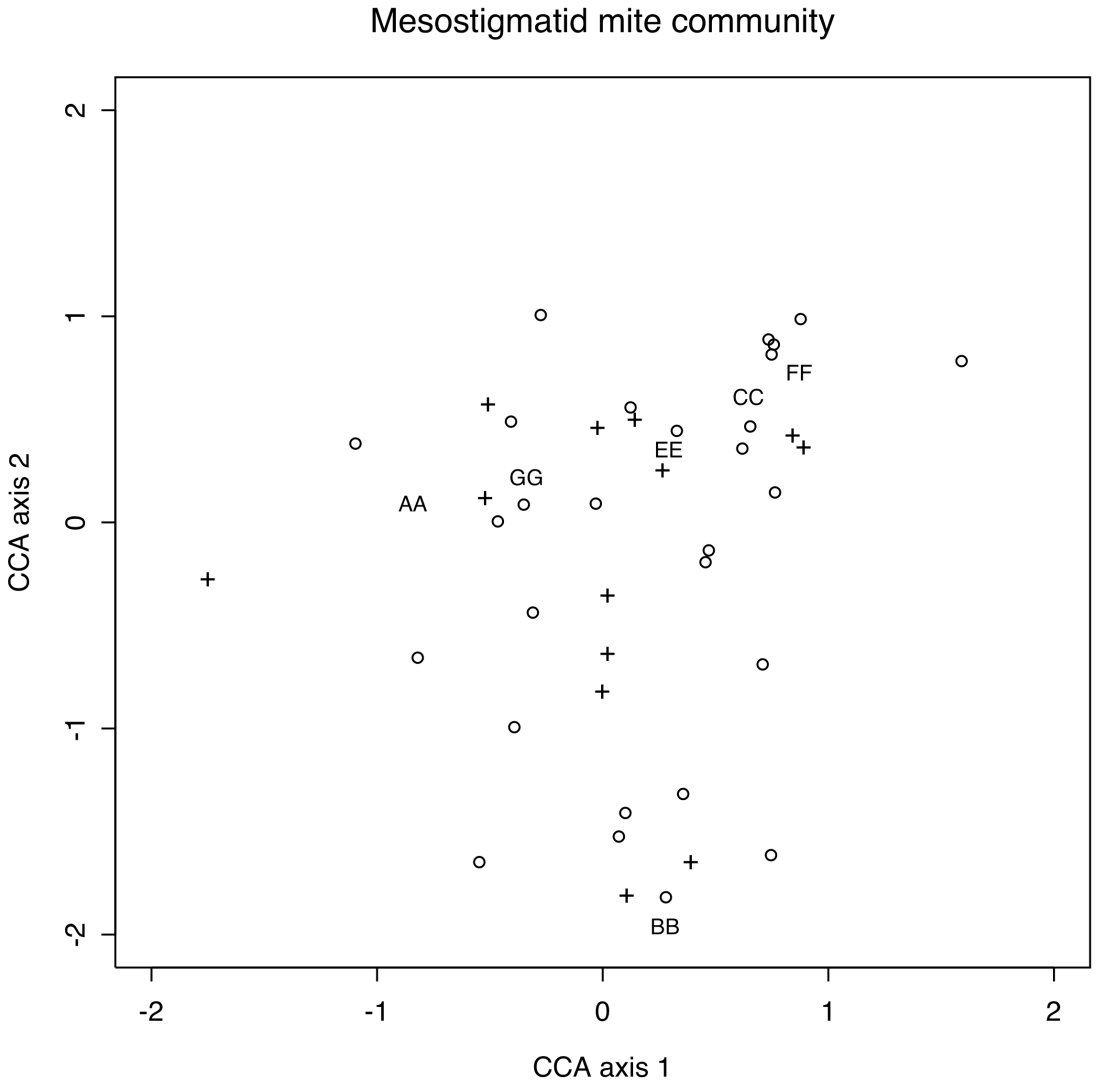

Figure 3.5. Canonical correspondence analysis ordination plots for mite species within the Suborder Mesostigmata. Figure description as per Figure 3.4.

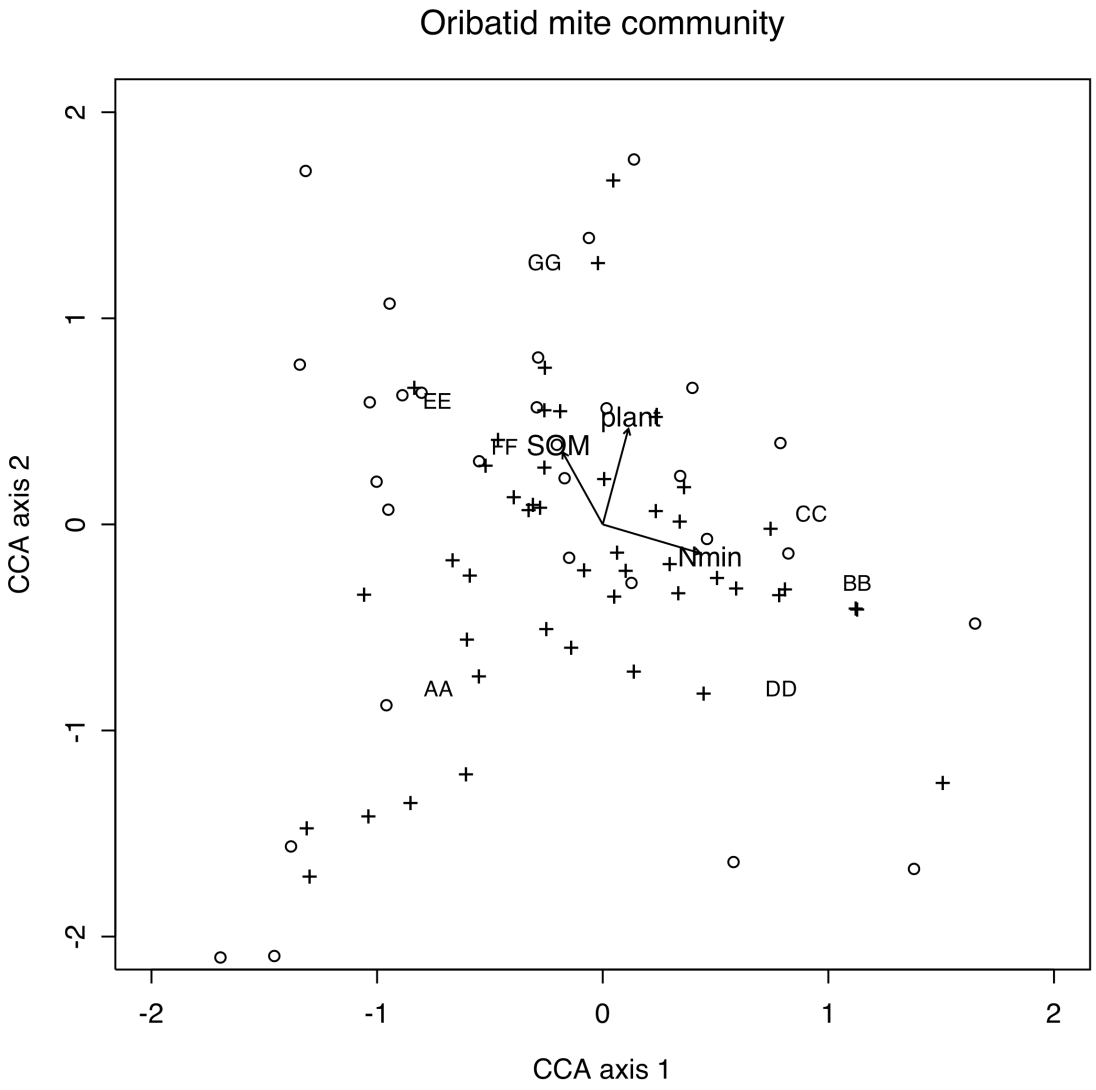

Figure 3.6. Canonical correspondence analysis ordination plots for mite species within the Suborder Oribatida. Figure description as per Figure 3.4.

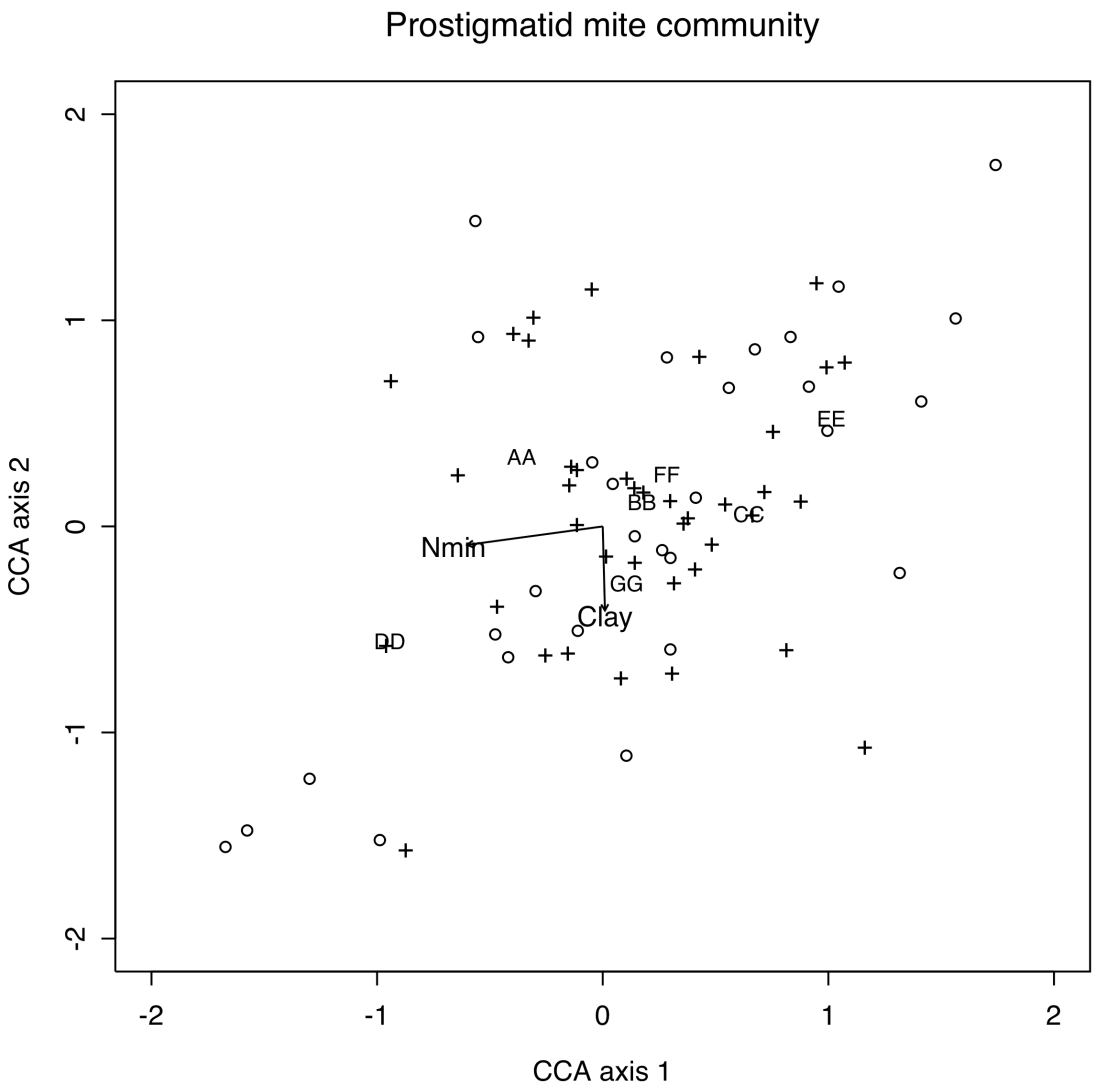

Figure 3.7. Canonical correspondence analysis ordination plots for mite species within the Suborder Prostigmata. Figure description as per Figure 3.4.

community was less related to environmental factors ($F_{11, 19} = 0.99$, $P = 0.470$; Figure 3.7); however, N-mineralization rate was significantly correlated with the first two axes ($R^2 = 0.37$, $P < 0.001$) and clay was marginally significant ($R^2 = 0.17$, $P = 0.058$).

3.5. DISCUSSION

The soil mite community at the KPBS was insensitive to the specific grass species examined. This finding is consistent with that for other soil fauna at the KBPS (Porazinska et al. 2003) and soil mites in a wide range of European forests and fallows (Migge et al. 1998, Maraun and Scheu 2000), and Australian forests (Osler and Beattie 2001). The KPBS soil mite fauna was also insensitive to the presence of an recent invasive alien grass further demonstrating that soil mites are generally non-specific to the identity of grass species present.

3.5.1. Influence of grass identity on soil mites

The lack of soil differences between grass species (Figure 3.1) probably accounts for the similarities in mite abundance (*N*), species richness (*S*), diversity (*D*) and taxonomic distinctness (Δ^*) (Figure 3.2). Other studies have found that even significant influences of different tree species on the soil environment did not influence metrics of associated soil mite communities, and that only the relative abundance of each species was affected (Migge et al. 1998, Maraun and Scheu 2000, Osler and Beattie 2001). It is possible that the removal of some functional groups of soil organisms may have little influence on the abundances of other soil functional groups (Hunt and Wall 2002); although it may be that we have not adequately determined the true functional groupings of soil animals (Schneider et al. 2004) or identified the functional traits of most importance (Heemsbergen et al. 2004). These findings and our data indicate that no one

plant or single resource is a dominant determinant of the richness and abundance of the soil mite fauna in the habitats studied so far. It is more probable that the quantity of resources will influence soil mite abundance and richness (Belnap and Phillips 2001, Clapperton et al. 2002) than the identity of resources. For example the presence of earthworms was the single most important determinant of oribatid mite abundance and richness presumably because they reduce oribatid food resources and habitable soil structure (Huhta and Niemi 2003). Commonness of indirect interactions, polyphagy and multiple resource channels (root, bacteria, fungi) in soil systems (Hunt et al. 1987, Setälä 2002) are possible mechanisms for the soil faunal insensitivity to plant identity.

The multivariate analysis of similarity (ANOSIM) between soil mites communities associated with the different grass species at KPBS (Figure 3.3) confirmed what the univariate metrics of mite *N*, *S*, *D* and Δ^* suggested (Figure 3.2); grass identity was not a determinant of mite community structure. Mite communities were significantly more similar within the same experimental blocks than they were between grasses of the same species suggesting that mechanisms responsible for mite community structure are operating at scales larger than the individual grasses. These mechanisms are probably resource heterogeneity and patchiness, though we did not measure these directly in our study. For example, Sulkava and Huhta (1998) demonstrated that offering heterogeneous resources to soil mites in patches rather than mixed together increased species richness presumably by allowing different communities of mites to form on the different resources, thus avoiding competition. This suggests that the experimental blocks captured differing resource mixes, either from the plant community, the soil microbial community, or both, and that this promoted different soil mite faunas.

This supposition is supported by canonical correspondence analysis; the soil mite community was weakly related to soil environmental conditions including N-mineralization rate, SOM content and percent clay (Figure 3.4). Higher N-mineralization rates and SOM may be indicative of more resources for the soil mite community (St. John et al. 2002) while soils with a higher clay content may have fewer habitable pores of sufficient size for larger mite species (Curry 1971). Separate ordinations of mite species within the three Suborders, Mesostigmata, Oribatida and Prostigmata uncovered trends that were predictable based on life histories traits of these groups. Oribatida were the most influenced by soil environmental conditions and were marginally influenced by the species of grass present (Figure 3.6), in contrast, mesostigmatids (Figure 3.5) and prostigmatids (Figure 3.7) were not influenced. Though recent evidence suggests that there is more niche separation between oribatid species than previously known (Schneider et al. 2004), they tend to occupy lower trophic levels than mesostigmatid and prostigmatid mites, which may explain why they are most sensitive to environmental conditions and grass identity.

These results agree with other studies suggesting that the influence of plants on soil organisms decreases with trophic distance (Korthals et al. 2001, Porazinska et al. 2003, Wardle et al. 2003, De Deyn et al. 2004). Mesostigmatid mites are generalist predators and predictably were less influenced by environmental conditions and grass identity than the Oribatida. In comparison, communities of Collembola (fungal feeding microarthropods) and oribatid mites demonstrated a significant degree of specificity to the identity of plants in the arctic (Coulson et al. 2003). These results also suggest that context may play a large role in determining the relationship between aboveground plant

identity and the soil community. For example 159 species of mites from several trophic levels were identified in the KPBS samples compared with only 13 species of fungal feeding microarthropods in the arctic samples.

There was no evidence that mites formed specific communities with grasses as determined by POAA. Of the five mite species with significant distributions no pattern in their life histories could be found (Table 3.1). *Ceratozetes virginicus* and *Pergalumna curva* are oribatids in genera considered to be omnivorous, feeding on plant and fungal matter, carrion and opportunistically on nematodes (Walter 1987, Schneider et al. 2004). *Sellnickochthonius* sp. 3, belongs to the oribatid family Brachychthoniidae of which almost nothing is known of their food habits except that several species have been cultured on unicellular algae (RA Norton *personal communication*). *Stigmalychus* nr. *veretrum* is a prostigmatid omnivore feeding mainly on fungal hyphae, spores and soft-bodied invertebrates including nematodes (DE Walter, *personal communication*). *Rhodacarus* sp. 2 is a small bodied, predatory mesostigmatid that feeds almost exclusively on nematodes (EE Lindquist *personal communication*). These five mite species had non-random distributions because they were more commonly encountered at either the NPS or the IPS rather than with any particular grass species (Table 3.1). As oribatids are not typically vagile relative to mesostigmatid and prostigmatid mites, finding differences in species' distributions between two similar sites only ~1 km apart is not unusual (St. John et al. 2002). Conversely, *Stigmalychus* nr. *veretrum* and mites in the genus *Rhodacarus* are effective colonizers (Walter 2001, St. John et al. 2002), and the results from POAA may indicate a preference for the IPS over the NPS perhaps relating to soil N and texture (Figure 3.1).

3.5.2. Invasive alien grass influence on soil mites

The recent invasive alien grass, Caucasian bluestem (GG), had no influence on mite community structure (Figures 3.3–7). We hypothesize that it had not yet altered the soil environment sufficiently to significantly influence the mite community (Figure 3.1). Similarly, Porazinska et al. (2003) found no influence of Caucasian bluestem on the abundances of several trophic groups of nematodes in a parallel study at the KPBS. It is probable that the legacy of the pre-invasion grass community is still a major driver of the soil environment, fauna and processes where Caucasian bluestem has established (Anderson 2000, Burkins et al. 2000, Bardgett et al. 2001). Porazinska et al. (2003) found evidence that the microbial community was more diverse under the native Big bluestem compared to Caucasian bluestem suggesting that changes in the community structure of bacterial or fungal components have begun. Klironomos (2002, 2003) demonstrated that successful invasive plants benefit from interactions with arbuscular mycorrhizal fungi while being released from the effects of phytopathogenic fungi. It is possible that absence of phytopathogenic fungi associated with Caucasian bluestem may explain some of the microbial diversity differences that Porazinska et al. (2003) found at the KPBS, but we found no evidence that this affected resources for mites (Figure 3.1). Just as aboveground herbivore communities may be unaffected by invasive alien plants closely related to the native plant being displaced (Frenzel and Brandl 2003), most soil mites may be insensitive to the original plant source as long as similar amounts of resources are entering the fungal and bacterial pathways. This suggests that invasive alien plants would need to cause large scale alterations of the environment before the trophic levels mites occupy are impacted (Belnap and Phillips 2001). However, the KPBS mite community

may be impacted over time, as there is evidence that Caucasian bluestem has raised the C:N ratio of the soil (H. Reed *personal communication*), which discourages bacterial activity and slows community respiration.

It was expected that given the relatively shorter evolutionary time to form associations, compared with native grasses and Kentucky bluegrass, Caucasian bluestem would have a significantly poorer and successionally younger associated mite fauna than big bluestem; however, this was not the case (Figure 3.2). Using the ratio of mesostigmatid to oribatid species as a sensitive indicator of relative successional age for a community (St. John et al. 2002) we found no difference in this ratio between Caucasian and big bluestem. It appears that at the KPBS Caucasian bluestem has displaced the native flora while adopting its soil mite community. This interpretation makes sense in light of findings that most KPBS soil mites are insensitive to grass identity (Figures 3.3–4). However, given more time Caucasian bluestem may continue to alter the soil environment and displace mite species not adapted to the differing resources and conditions.

Soil mite species were not specific to individual species of grasses at the KBPS, but are possibly more influenced by characteristics of the plant community as a whole and/or prevailing soil conditions. This lack of congruence between soil mite species associations and plant species indicates that any extrapolation of soil mite richness based on plant specificity may not yield valid results.

4. SOIL MITE DIVERSITY AND DECOMPOSITION IN A TALLGRASS PRAIRIE: A CONTEST AMONG MODELS

4.1. ABSTRACT

Whether biodiversity relates to ecosystem function, or not, is hotly debated and present results are based on data from laboratory or highly manipulated field studies. This makes applicability of findings to natural conditions, both above- and belowground, difficult. Rates of cotton strip decomposition (% cotton strip tensile strength loss per day, *CTSL*), and soil mite abundance and species richness were measured at high and low fire frequency sites in an uncultivated tallgrass prairie, the Konza Prairie Biological Station, Kansas, USA. Likelihood-based and information theoretic approaches were used to examine strength of evidence in data for models of *CTSL* representing the Null, Rivet and Redundant hypotheses of biodiversity and ecosystem function (BEF). The Null model including temperature, moisture and saturating effects in the total abundance of predatory mites (Mesostigmata) had more support in the data than any other models (Akaike weight, $w_i = 0.49$). Models representing Rivet and Redundant patterns of BEF settled on

parameter values distinct from the Null models but had less support in the data regardless of which mite group was being considered.

A significant trend was observed in the models' residuals from low fire frequency sites; trends not observed in high fire frequency sites. Annually burned sites may more closely emulate the agricultural system the models were originally designed for than low fire frequency sites, accounting for differences in model performance. Biophysical properties on low fire frequency sites such as increased litter cover, different soil carbon constituents or a different microbial community may regulate decomposition in a manner not accounted for by only soil temperature and moisture driving variables.

4.2. INTRODUCTION

Considering ecosystem function as a product of biodiversity is an emerging paradigm in community ecology (Naeem 2002). Several relationships between biodiversity and ecosystem function (BEF) have been proposed (Ehrlich and Ehrlich 1981, Walker 1992, Lawton 1994, Naeem et al. 1995, Giller and O'Donovan 2002, Naeem et al. 2002) most centering on three patterns represented by the Null, Rivet, and Redundant hypotheses. The Null hypothesis suggests that no BEF relationship exists, and that function will be the same for all levels of biodiversity. The Rivet hypothesis says each species in a system is responsible for a discrete amount of ecosystem function up until full function is achieved. The Redundant hypothesis asserts that a minimal number of species are required for ecosystem function and that additional species have little or no influence. The inverses of these hypothesis may also represent BEF relationships (Giller and O'Donovan 2002).

Many experimental and observational approaches to studying BEF are required before we can realize a synthetic understanding of patterns and mechanisms (Mikola et al. 2002, Diaz et al. 2003). Experimental, laboratory and field tests of BEF have demonstrated relationships (Naeem et al. 1996, Tilman et al. 1996, Klironomos et al. 2000, Lambers et al. 2004, Setälä and McLean 2004), usually at low levels of species richness (< 10 species), supporting the Redundant hypothesis.

Most BEF experiments have measured plant species richness as 'biodiversity' and net primary productivity (NPP) as the 'ecosystem function.' The applicability of conclusions from these experiments to belowground systems is questionable (Wardle et al. 2000, Setälä 2002, Moore et al. 2003, Wardle et al. 2004) as is the assumption of one ecosystem function behaving the same as another. Decomposition has been shown to be positively related to the diversity of litter feeding macro-invertebrates (Hättenschwiler and Gasser 2005) but few data exist for the more abundant and diverse mesofauna such as nematodes an microarthropods (e.g. mites).

Decomposition in soil systems is most directly controlled by microorganisms (and the quality of their food resources) which in turn are largely controlled by microclimatic factors (Gonzalez et al. 2001, Gestel et al. 2003). Predictive modeling of litter decomposition and nutrient cycling in agricultural soils is possible using only a few abiotic inputs such as temperature and moisture (Andrén and Paustian 1987) and may not require information on the soil fauna (Andrén et al. 1995, Nannipieri et al. 2003). Yet studies in natural systems have attributed 4 to 70 % of decomposition rates to the presence of soil mites, in combination with other less abundant microarthropods, due to their indirect influence on decomposition (Seastedt 1984c). Hunt et al. (1987) estimated

that soil fauna, including protozoa and nematodes, were directly responsible for 37% of the mineralized nitrogen in the short grass steppe.

Belowground BEF studies have either been theoretical (Hunt and Wall 2002), simplified microcosm experiments (Cragg and Bardgett 2001, Bradford et al. 2002, Liiri et al. 2002, Heemsbergen et al. 2004, Setälä and McLean 2004) or highly manipulated field studies (Andrén et al. 1995, Wardle et al. 1999, Zak et al. 2003), and suggest a high degree of redundancy in soil organisms with respect to ecosystem functions such as decomposition and NPP (Setälä 2002, Nannipieri et al. 2003, Heemsbergen et al. 2004). A difficulty for interpretation of these results, however, is that experimental manipulations of species richness on ecosystem functioning may be masked by influences of the legacies of the species removed (e.g. soil structure, carbon, nitrogen, organic matter) (Anderson 2000, Bardgett et al. 2001). BEF experiments in natural soil ecosystems, incorporating species richness of soil organisms have not been attempted previously.

Unplowed, but fire manipulated, tallgrass prairie at the Konza Prairie Biological Station (KPBS) a Long Term Ecological Research (LTER) site near Manhattan, Kansas (39.1˚ N, 94.6˚ E.) was chosen for study. Species richness and abundance of soil mites at the KPBS are represented by the three major suborders, Mesostigmata, Oribatida and Prostigmata (Chapters 2, 3). We used the species richness of Mesostigmata and Oribatida in our models as their life history traits and feeding habits are relatively predictable. Most oribatid mites have *K*-style life history traits and are microbivores and litter shredders (Walter and Proctor 1999). Mesostigmatid mites have *r*-style life history traits and are predators of nematodes and/or other microarthropods (Walter and Proctor 1999).

The study objective was to determine which of the BEF hypotheses (Null, Rivet, Redundant and their inverses) is most likely belowground under natural conditions. Models representing the BEF relationships were developed and confronted with decomposition rate data from a standardized substrate (cotton strips) as a measure of ecosystem function, and soil mite species richness as a measure of biodiversity. Since most models of decomposition that include soil fauna typically only consider abundance or biomass (Seastedt 1984c, Hunt et al. 1987) similar models were developed using abundance instead of species richness.

4.3. MATERIALS AND METHODS

4.3.1. Site and climate

Monthly mean temperatures at the KPBS range from –2 °C in January to 27 °C in July, and 75 % of the annual average precipitation (835 mm) falls during the growing season (Hayden 1998). The soils at the KPBS have textures of silty loam or silty clay loam and range in clay content from 26–34 % (Ransom et al. 1998, Porazinska et al. 2003, Chapter 3). These soils are 3–7 % organic carbon in the top 20 cm (Knapp et al. 1998, Porazinska et al. 2003, Chapter 3) and 60–80% of net primary production is allocated belowground (Rice et al. 1998). Extensive data on soil chemistry (Ransom et al. 1998), C and N dynamics (Blair et al. 1998), soil invertebrates (Seastedt 1984b, a, Ransom et al. 1998, Porazinska et al. 2003, Chapter 2, Chapter 3), and plant species diversity (Freeman 1998) are available through the KPBS on-line database (http://www.konza.ksu.edu/).

The KPBS has watershed-level manipulations of fire frequency (1-, 2-, 4-, and 20-year intervals) and grazing activities (*Bos bison)* (Knapp and Seastedt 1998). Burning

regimes modify the diversity of plant communities with the highest plant diversity occurring in the watersheds with the longest interval between fires (Collins and Steinauer 1998).

In November 2000, three plots approximately 1.5 × 1.5 m were established on tully soils (Ransom et al. 1998) of two un-grazed watersheds burned annually (1C, 1D-1, 1D-2) and three plots on tully soils of two un-grazed watersheds burned every 20 years (20B, 20C-1, 20C-2). Plot names were those designated by the KPBS. The leading 1 or 20 indicates the period of burns in years and the following letter indicates a particular watershed replicate. The "-1" or "-2" suffix indicates where two plots, greater than 100 m from each other, were established on the same watershed.

4.3.2. Field measurements

4.3.2.1. Cotton Strips

On each sampling date, up to three 8 × 20.5 cm strips of Shirley burial testing cloth (Shirley Dyeing & Finishing Ltd, Cheshire, UK) were prepared and inserted to 15 cm depth into soils of each plot according to standard protocol (Harrison et al. 1988). Strips were harvested and new strips inserted approximately every 20 days (range 18–24 days) in the summer months (June–September) for the years 2000 and 2001. Insertion control cotton strips were harvested immediately after insertion to the soil. Harvested strips were wrapped in aluminum foil, placed in sealed plastic bags, refrigerated at 4 °C, until returned within 24 hrs to the Natural Resource Ecology Laboratory at Colorado State University (NREL) for washing. Washed strips were stored at –7 °C until analyzed at the end of the experiment. Strips were cut into 20 mm sections by depth and measured for tensile strength (kg) on an Instron 4442 (Instron Corporation, Canton, MA, USA).

Decomposition of strips was assumed to be 99 % where strips were too decomposed to be measured. Percent tensile strength loss per day, *CTSL* (% · day^{-1}) was calculated as the average for all depths (0–15 cm) from both strips, unless only one was intact. Data were corrected for number of days the strips were left in the field after regression of *CTSL* against number of days indicated there was a slight positive relationship (data not shown).

4.3.2.2. Soil texture and carbon

Soil samples from each plot were collected 0.5 m from the cotton strips on September 17th, 2000 using a 5 cm diameter core tool to 10 cm depth. Samples were emptied into plastic bags, refrigerated at 4 °C until returned within 24 hrs to NREL for processing. A 40 g sub-sample was used for determination of sand, slit and clay content (Gee and Bauder 1986): sand was determined gravimetrically as particles > 53 μm, clay was determined with a hydrometer after suspension in 5 % sodium hexametaphosphate, and silt was determined by subtraction.

Soil C was determined on air-dried soil that were passed through a 2 mm sieve and finely ground with a ball-mill. A 0.2 g sub-sample of the finely ground soil was analyzed for C on a LECO CHN-1000 elemental analyzer (LECO Corporation, St. Joseph, MI, USA).

4.3.2.3. Soil moisture

Approximately once every two to three weeks in the summers of 2000 and 2001 soil moisture on each plot was measured using Time Domain Reflectometry (TDR) probes. Each plot contained two TDR probes (Taylor and Seastedt 1994), connected to a Tektronics 1502B cable tester (Tektronics, Inc., Redmond, OR). Individual waveforms

were analyzed to determine the dielectric constant. The dielectric constants were then used to derive volumetric soil moisture (Topp et al. 1980). If both probes returned positive soil moisture values the average was used, negative values were assumed to result from instrument error. If no reliable results were recorded then soil moisture values were estimated from adjacent plots involved in a related experiment (unpublished data).

Soil water potentials (MPa), required for use in the competing models (Andrén and Paustian 1987), were estimated using Model 4 (Vereecken et al. 1989), since it was found to perform well with the fewest parameters—soil moisture, texture, C and bulk density. Soil bulk density values for each plot were obtained from KPBS on-line dataset NSC01. If no bulk density data were available for a given watershed values from the closest adjacent watershed were used.

4.3.2.4. Temperature

Average temperatures for the time each cotton strip was in the field were measured with RL100 temperature data loggers (Ryan Instruments, Redmond, WA) at 7 cm depth. Missing temperature values, resulting from equipment failures, were estimated by regressing known temperature values from our plots against soil temperature data collected nearby (KPBS on-line data set AWE01). In all cases there was good fit ($R^2 >$ 0.7) between the data sets. Temperatures at sites 1D-1 and 20C-1 were assumed to adequately represent conditions for 1D-2 and 20C-2 respectively.

4.3.2.5. Soil mites

Soil samples for mite analysis were collected once in September 2000 with a soil corer (4.8 cm in diameter) at 5 cm increments to 10 cm depth (Crossley and Blair 1991). Two samples were taken from each plot, one within 0.5 m of the cotton strips and another

1 m away. Soil samples were carefully wrapped in aluminum foil, placed in coolers and transported to the KPBS soil laboratory within 2 hours of sampling. Microarthropods were actively extracted from soil cores using a high-gradient modified Tullgren method (Crossley and Blair 1991) into 95% ethanol for storage until identifications could be performed. All soil mites belonging to the Suborders Mesostigmata and Oribatida were enumerated and identified to species based on manuals from the Acarology Summer Program (The Ohio State University) as well as numerous published descriptions and the assistance of mite systematists (Valerie M. Behan-Pelletier, Evert E. Lindquist and David E. Walter). Only adult mites were used in analyses since many groups have polymorphic immature stages that cannot be reliably assigned to a species.

4.3.3. Competing models

Andrén and Paustian (1987) presented a simple model of barley straw decomposition in a barely cropping system. It had excellent fit to observed data ($R^2 \approx 0.99$) using only soil temperature and water potential as driving variables and four compartments to account for different decomposition rates of the various constituents of straw. We used their model but assumed only one compartment and zero-order kinetics of decomposition. This was possible since cotton strips are nearly 100 % cellulose, are left in the field for short periods of time (days to weeks in grassland systems) (Gestel et al. 2003) and our main interest was in comparing differences in the decomposition rate constant, k, not the prediction of mass loss.

We modeled the effects (E) of soil temperature (T) and moisture (ψ), and mite species richness (S) and abundance (N) as modifiers of the decomposition rate constant (k) ranging from 0 to 1 (Andrén and Paustian 1987). Thus k represents the decomposition

rate at optimal conditions of the driving variables (i.e., $E = 1$; Figure 4.1). The models were developed in a nested fashion starting with the simplest of Null models with temperature and/or moisture influences. We then took the most likely of these and added effects of mite species richness in Rivet and Redundant models or mite abundances as an alternative in the Linear-*N* or Asymptotic-*N* models described below.

4.3.3.1. Null-temperature model, Null_T

This model predicts that *CTSL* is entirely dependant on soil temperature:

$$CTSL = k \cdot E_T \tag{1}$$

where k is the decomposition constant (%·day^{-1}) and E_T is the effect of temperature expressed as a Q_{10} relationship:

$$E_T = Q_{10}^{(T_i - T_{\max})/10} \tag{2}$$

T_i is the ith soil temperature, $T_{\max}$ is the highest temperature recorded in the study and Q_{10} is a parameter optimized in the model and represents the multiplicative increase in E_T for every 10 °C increase. Negative effects of freezing were not considered since temperatures for the entire study were well above 0 °C (Table 4.1).

4.3.3.2. Null-moisture model, Null_ψ

The Null_ψ model predicts that *CTSL* will be affected only by soil water potential, ψ:

$$CTSL = k \cdot E_\psi \tag{3}$$

where E_ψ is the effect of soil water potential. Andren and Paustian (1987) assumed E_ψ to be a log-linear function of ψ. Since the range of ψ values recorded in this study (Table

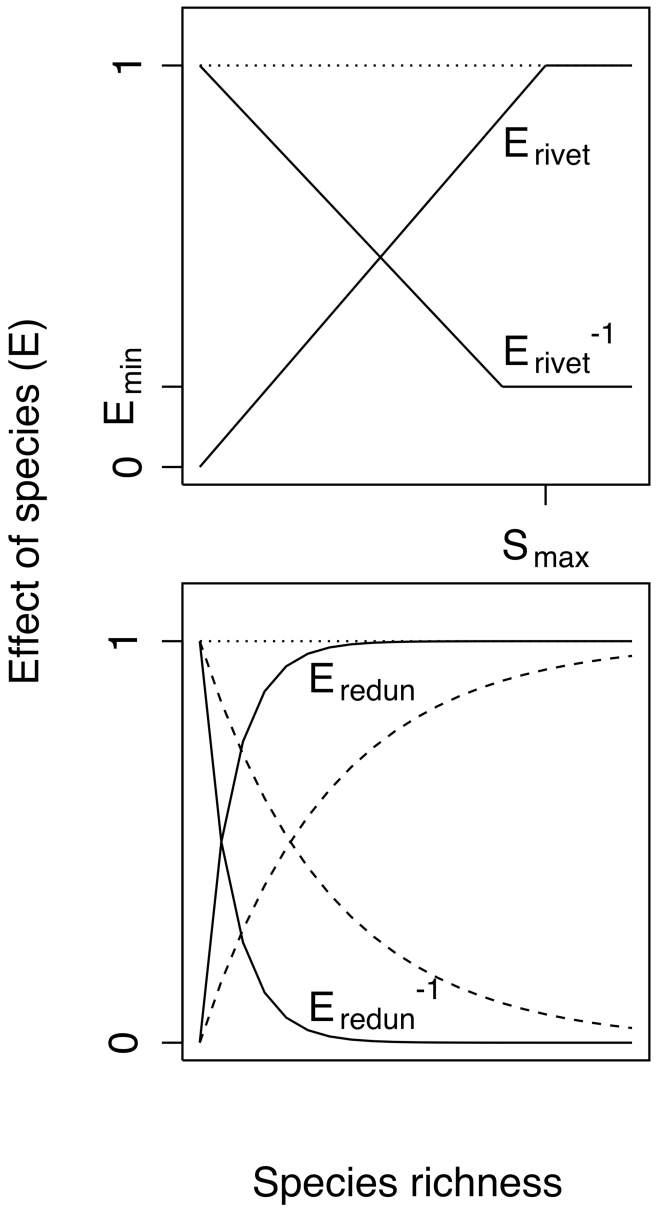

Figure 4.1. BEF model representations. The relationship between species richness (S) and its effect (E) on decomposition were modeled by either a 2-stage linear function (top panel) for the Rivet (E_{rivet}, Eq. 7) and Inverse Rivet (E_{rivet}^{-1}, Eq. 8) hypotheses or an asymptotic function (bottom panel) for the Redundant (E_{redun}, Eq. 10) and Inverse Redundant (E_{redun}^{-1}, Eq. 11) hypotheses. See model descriptions for the definitions of the parameters S_{max} and E_{min}. Solid and hatched lines in the bottom panel represent the function E_{redun} and E_{redun}^{-1} where the value of $\beta_{solid} > \beta_{hatched}$ (i.e., the solid line represents greater redundancy than the hatched line). The horizontal dotted line at $E = 1$ in both panels represents the Null hypothesis of BEF.

4.1) fell into the range best described by a linear function (Bunnell and Tait 1974, Paul and Clark 1996) we felt it justified to use the linear relationship:

$$\begin{aligned} E_\psi &= 1; \ \psi > \psi_{\max E} \\ E_\psi &= \frac{\psi - \psi_{\min E}}{\psi_{\max E} - \psi_{\min E}} \\ E_\psi &= 0; \ \psi < \psi_{\min E} \end{aligned} \tag{4}$$

$\psi_{\max E}$ and $\psi_{\min E}$ are boundary values for wet and dry soils respectively, optimized by fitting the model to data. Negative effects of high soil moisture (saturation) were not considered.

4.3.3.3. Null-temperature-moisture model, $\text{Null}_{T\psi}$

The $\text{Null}_{T\psi}$ model builds on Eqs. 1 and 3 by including effects of both soil temperature and water potential:

$$CTSL = k \cdot E_T \cdot E_\psi \tag{5}$$

4.3.3.4. Rivet and Inverse Rivet models

The Rivet model builds on Eq. 5 by adding an effect of the soil mite fauna, E_{rivet}:

$$CTSL = k \cdot E_T \cdot E_\psi \cdot E_{\text{rivet}} \tag{6}$$

where E_{rivet} is a two-stage, linear function with a maximum effect of richness at $S_{\max}$ (Figure 4.1). $S_{\max}$ is optimized by fitting the model to data. The effect of species richness, S, of the ith sample is given by:

$$E_{\text{rivet}} = \frac{S_i}{S_{\max}}; \ 0 \le E_{\text{rivet}} \le 1 \tag{7}$$

Thus, $S_{\max}$ represents the level of species richness at which the effect of species loss from that point will be a steady decline in ecosystem function but above which the effect of species addition will be negligible. If the optimized value of $S_{\max}$ falls at or

below the lowest value of S measured in the study, this model cannot be distinguished from the Null_{T_ψ} model. The Rivet model was divided into three sub-models: $\text{Rivet}_{\text{meso}}$, $\text{Rivet}_{\text{orib}}$, and $\text{Rivet}_{\text{total}}$. These sub-models use species richness data for only Mesostigmata, Oribatida or both, respectively.

The Inverse Rivet model is given by substituting:

$$E_{\text{rivet}^{-1}} = \frac{S_{\max} - S_i}{S_{\max}};\ E_{\text{rivet}^{-1}} \geq E_{\min} \tag{8}$$

for E_{rivet}. In this model $E_{\min}$, is the corollary to $S_{\max}$ in Eq. 7 (Fig 1). It is the level above which loss of species richness increases ecosystem function but below which increasing richness does not reduce ecosystem function any further. If the optimized value of $E_{\min}$ reaches 1 than the inverse rivet model can be rejected for being no different from the Null_{T_ψ} model.

4.3.3.5. Redundant and Inverse Redundant models

The Redundant model represents the hypothesis that as species richness increases, the effect of each added species is a saturating function (Figure 4.1).

$$CTSL = k \cdot E_T \cdot E_\psi \cdot E_{\text{redun}} \tag{9}$$

A characteristic of the Redundant pattern is that only a few species are required for a given ecosystem function and so we chose an exponential form to best describe this:

$$E_{\text{redun}} = 1 - \beta^{-S_i} \tag{10}$$

The parameter β represents the multiplicative decrease in the influence of each additional species and is optimized by fitting the model to data. Thus, β can be used as a measure of redundancy. If the optimized value of β is so large that it describes a curve that is saturated ($E_{\text{redun}} \approx 1$) for all measured values of S then the Redundant model can be

rejected for being no different than the Null$_{T_\psi}$ model. An advantage of Eq. 10 is that it also represents the Modified Rivet pattern (Giller and O'Donovan 2002) at lower values of β (Figure 4.1); however, the delineation of high and low levels of redundancy can be subjective. The Redundant model was divided into three sub-models: Redundant$_{meso}$, Redundant$_{orib}$ and Redundant$_{total}$. These sub-models use species richness (S) data for only oribatids, mesostigmatids or all mites, respectively.

The Inverse Redundant model is given by substituting:

$$E_{\text{redun}^{-1}} = \beta^{-S_i} \tag{11}$$

for E_{redun} (Figure 4.1). In this model, larger β values imply that ecosystem function will reach a minimum as only a few species are added. Similar to above, this equation can also represent the Inverse Modified Rivet pattern at lower values of β. If the optimum value of β (by fitting to data) is 1, the Inverse Redundant model cannot be distinguished from the Null$_{T_\psi}$ model.

4.3.3.6. Abundance models: Linear-*N* and Asymptotic-*N*

Abundance models were identical to the Rivet and Redundant models, except that abundances of mites were used instead of species richness. These models are another form of the Null pattern of BEF but incorporate more biological information. They represent the hypothesis that abundance, not species richness, of mites is important to decomposition. Abundance analogues to the Rivet models were Linear-N_{meso}, Linear-N_{orib} and Linear-N_{total} and Redundant analogues were Asymptotic-N_{meso}, Asymptotic-N_{orib} and Asymptotic-N_{total}.

4.3.4. Statistical analyses

Statistics and figures were generated using R 1.9.0 (R Development Core Team 2004). Analysis of variance was used to determine differences in measured soil moisture and temperature and *CTSL* between with plots and fire frequency.

We used likelihood-based methods and information theoretics (Akaike's Information Criterion, AIC_C) to quantify the strength of evidence for alternative models and to estimate their parameters (Burnham and Anderson 2002). Maximum-likelihood estimates of model parameters and AIC_C values were obtained by non-linear fitting of model predictions with observations using Newton's gradient search method and multiple starts in Excel Solver (Microsoft 2002). The model with the lowest AIC_C score was chosen as the most likely given the data (Burnham and Anderson 2002). Subtracting the AIC_C score of the best model, i, from a given model, j, determines the distance a model is from the best model, Δ_i. Generally, models with $\Delta_i > 3$ are not considered valid, models with $3 > \Delta_i > 2$ lack support in the data relative to the best model, and those with $\Delta_i < 2$ are considered candidates. Normalized Akaike weights (w_i) were also calculated to evaluate the differences between a given model and the most likely model (Burnham and Anderson 2002). Relative likelihoods, or evidence ratios, of model j given the model i were calculated as w_i/w_j. Unadjusted R^2 values of model predictions versus observations are presented for comparison to likelihoods, not as a means of discrimination.

4.4. RESULTS

No significant differences were found in soil temperature, soil moisture and *CTSL* between study plots and burn treatments (Table 4.1). All three Null models and the best

Table 4.1. Means of model input data for each study plot. Abundances (m^{-2}) and species richness of Oribatida (orib) and Mesostigmata (meso) are the totals for two samples each taken within 1.5 m of the cotton strip sampling plots, September 2001. Soil temperatures (°C), water potential (MPa) and cotton strip decomposition rates (% · day^{-1}) are expressed as means (standard deviations in parentheses) for the eight sample dates in the summers of 2000 and 2001. No significant differences in T, ψ or $CTSL$ were found between plots or burn treatments ($\alpha = 0.05$). See Appendix Table 5.1 for raw data.

Plot	Abundance (N)		Species richness (S)		Temperature (T)	Water potential (ψ)	Decomposition rate ($CTSL$)
	orib	meso	orib	meso			
1C	16302	4974	17	7	24.02 (2.92)	–0.0204 (0.0215)	3.22 (0.77)
1D-1	25144	2487	19	5	24.78 (3.14)	–0.0296 (0.0327)	2.69 (0.87)
1D-2	24868	2210	24	4	24.78 (3.14)	–0.0289 (0.0328)	2.85 (0.53)
20B	40341	4420	25	6	22.90 (2.27)	–0.0198 (0.0182)	3.08 (0.54)
20C-1	19065	3868	21	5	24.07 (2.76)	–0.0307 (0.0307)	3.00 (0.42)
20C-2	33157	9118	22	10	24.07 (2.76)	–0.0297 (0.0271)	2.99 (0.62)

models incorporating effects of mite species richness and abundance models are re
in Table 4.2 and Figures 4.2 and 4.4.

4.4.1. Null pattern models

The Null_T model had the poorest fit of all models, scoring a Δ_i value of 66 (
4.2, Figure 4.2), and failed to predict a significant amount of variance in the data. T
Null_ψ model scored significantly better than Null_T but did not rank as a candidate m
($\Delta_i = 4.17$) or adequately predict *CTSL* values above 3.16 % · day^{-1} (Figure 4.2).
Combining temperature and moisture effects into the $\text{Null}_{T\psi}$ model was a significa
improvement on both the Null_T and Null_ψ models taken separately. Model fit for N
increased to $R^2 = 0.58$ and *CTSL* values above 4 were more accurately predicted.
However, this model lost in competition ($\Delta_i = 2.10$) to Asymptotic-N_{meso}.

4.4.2. Rivet, Redundant and abundance models

The most likely model in the competition, Asymptotic-N_{meso}, indicated that co
strip decomposition in the field is related to not only microclimate factors but also
abundance of the mostly predatory mesostigmatid mites. This model, using temper
moisture and the abundance of soil mesostigmatid mites as driving variables had th
support in the data out of all the competing models considered ($w_i = 0.49$, Table 4.
Figure 4.2). The value of β in this model (1.0009) corresponds with a density of 51
mites · m^{-2} at near maximum effect of the mites $E_{\text{redun}} = 0.99$ (Figure 4.3).

$\text{Rivet}_{\text{total}}$, $\text{Redundant}_{\text{meso}}$ and $\text{Redundant}_{\text{total}}$ models had some support in the
($w_i = 0.06$–0.11), but none ranked as candidates for consideration relative to the
mesostigmatid abundance model (Asymptotic-N_{meso}) and they were also out-compe
the simpler $\text{Null}_{T\psi}$ model (Table 4.2, Figure 4.2). The $\text{Rivet}_{\text{total}}$ model had a maxim

Table 4.2. Results of model optimizations. Maximum-likelihood values of model parameters (see model descriptions) are given as well as the distance (Δ_i) each model is from the most likely model ($\Delta_i = 0$). Only Null models and the most likely of the biotic models are shown. All others had Δ_i values much higher than 4.

Model	k	Q_{10}	$\psi_{\min E}$	$\psi_{\max E}$	$S_{\max}$	β	Δ_i
Null_T	3.07	0.82	–	–	–	–	66.02
Null_ψ	3.16	NA	–0.1393	–0.0340	–	–	4.17
$\text{Null}_{T\psi}$	4.05	1.37	–0.1457	–0.0116	–	–	2.10
Asymptotic-N_{meso}	4.44	1.45	–0.1477	–0.0087	–	1.0009	0.00
$\text{Rivet}_{\text{total}}$	4.22	1.40	–0.1455	–0.0107	26	–	3.07
$\text{Redundant}_{\text{meso}}$	4.31	1.41	–0.1469	–0.0104	–	1.7573	3.07
$\text{Redundant}_{\text{total}}$	4.17	1.38	–0.1458	–0.0116	–	1.1400	4.05

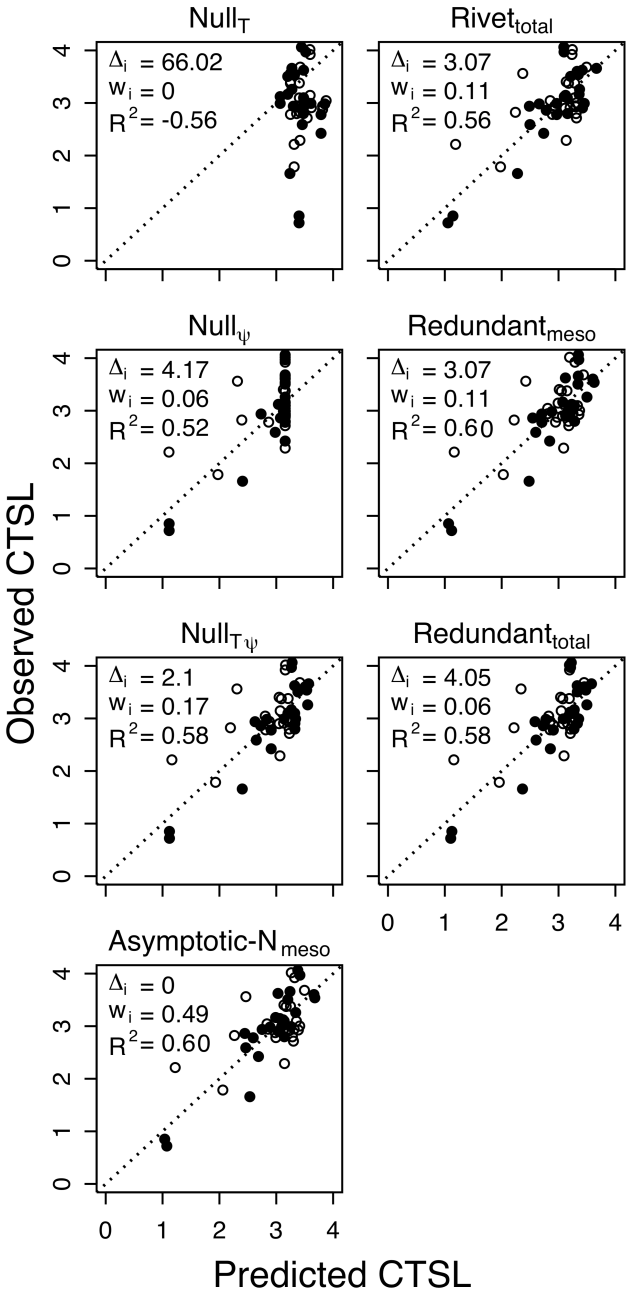

Figure 4.2. Observed vs. model predicted values of cotton strip tensile strength loss rate (*CTSL*, % · day^{-1}) for each of the distinct competing models. Open symbols represent 20-year burn sites, closed symbols are annual burn sites. Dotted lines represent 1:1 values. Null$_{T\psi}$ was the most likely of the Null models and serves as the basis for (i.e., it is nested within) the subsequent models incorporating mite species richness and abundance.

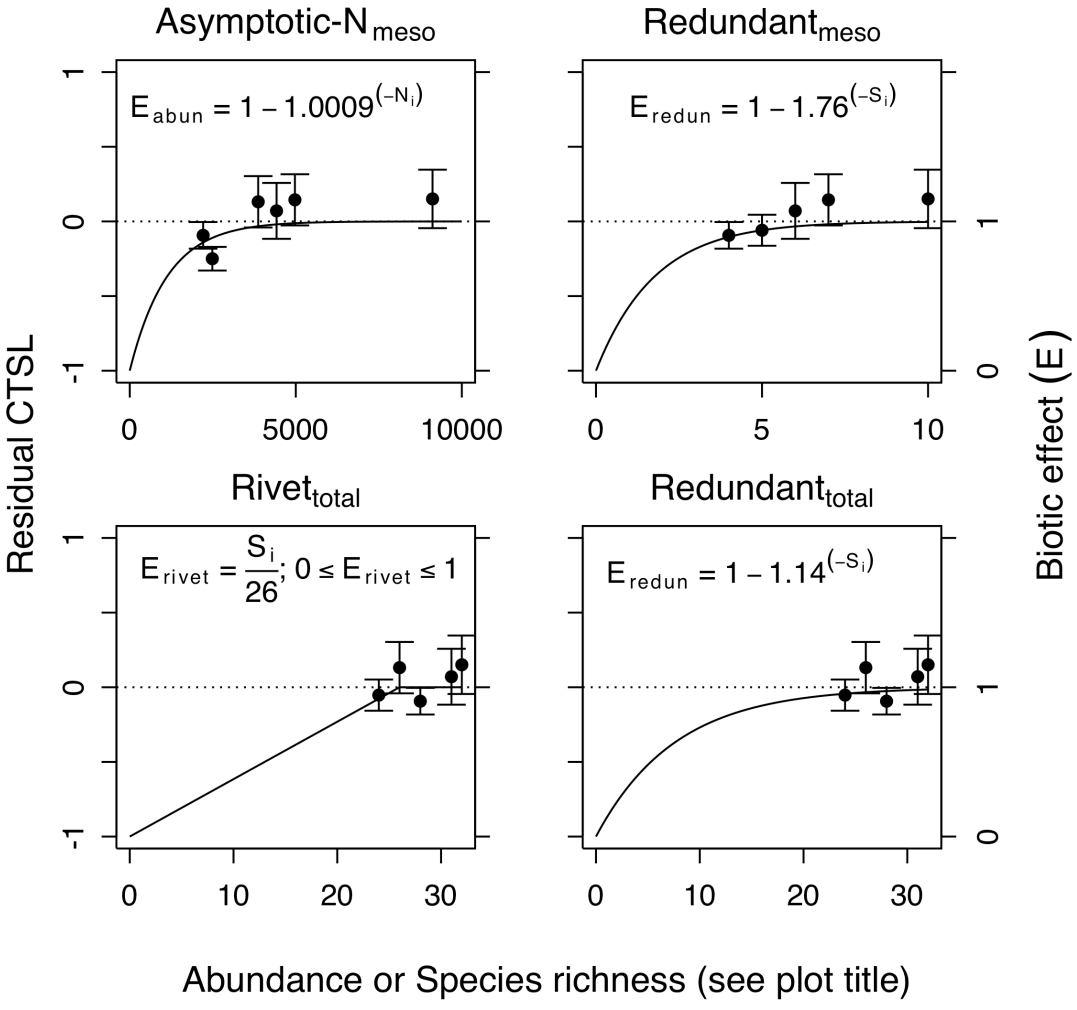

Figure 4.3. Mean residuals (± S. E.) from the Null$_{T_\psi}$ (observed–predicted values) vs. either the abundance (Asymptotic-N_{meso}) or species richness (remaining panes) of components of the soil mite fauna. Overlaid curves (solid lines) are the maximum-likelihood effects functions (E) for the best biotic models with their equations annotated to each plot. Dotted lines are at residual = 0.

likelihood estimate of S_{max} = 26 suggesting that there was linear, positive effect of species richness up to 26 species of oribatid and mesostigmatid mites (Figure 4.3). Because all plots sampled had more than 24 species (Table 4.1) few inferences could be drawn from this model. Similarly, the Redundant_{total} model was optimized at a high maximum-likelihood value of $\beta = 1.14$ implying that there is a modest saturating trend in the influence of species richness on decomposition; however, support in the data for the model was lacking ($\Delta_i = 4.05$) as were data for richness values below 24 species (Figure 4.3). Species richness of the mesostigmatid fauna (Redundant_{meso}) appeared to be a better ($\Delta_i = 3.07$) indicator of decomposition rate (Figure 4.2–3) than the species richness of oribatid and mesostigmatid mites combined. Models representing the Inverse Rivet and Inverse Redundant hypotheses optimized at parameter values of S_{max} and β, respectively, that made them indistinguishable from the Null_{T_ψ} model and thus were rejected.

4.4.3. Characteristics of most likely models

Both of the most likely models (Null_{T_ψ} and Asymptotic-N_{meso}) and many of the others incorporating E_ψ had maximum-likelihood estimates of ψ_{minE} and ψ_{maxE} approximately –0.15 and –0.01 MPa , respectively. Maximum-likelihood estimates of Q_{10} were about 1.5, indicating approximately a 50% increase in *CTSL* per 10 ºC increase. The models' abilities to predict *CTSL* varied according to the burn regime of watersheds (1 vs. 20 years). Observed vs. predicted values from annually burned watersheds fell well along the 1:1 line (Figure 4.2) indicating good model fit to data for most models (R^2 = 0.85 for Asymptotic-N_{meso}). Watersheds burned every 20 yrs had considerably more scatter about the 1:1 line (R^2 = 0.60 for Asymptotic-N_{meso}). Inspection of residuals (Figure 4.4) confirmed that there was no significant trend in the residuals for both burn regimes

together, or for annual burns separately, but there was a trend in the residuals from 20 year burn sites ($F_{1, 22} = 9.11$, $P = 0.006$). This separation in trends was consistent for all models that were capable of explaining reasonable amounts of variance ($R^2 > 0.3$) in the data (Figure 4.4).

4.5. DISCUSSION

Results of the model competition supported the Null pattern of BEF in this natural soil system with the caveat that the abundance of predatory mites was related to cotton strip decomposition (Table 4.2, Figure 4.2). Models representing the Rivet (including the Modified Rivet), and Redundant hypotheses (and their inverses) were not supported by the data.

These results are consistent with experimental studies showing little influence of soil faunal richness on ecosystem functions such as decomposition and NPP (Andrén et al. 1995, Cragg and Bardgett 2001, Setälä 2002, Heemsbergen et al. 2004). The indirect role of soil mesofauna such as mites and Collembola on decomposition, in contrast to aboveground studies where plants and NPP are commonly studied (Naeem et al. 1995, Tilman et al. 1996, Lambers et al. 2004), likely explains why their diversity seems unimportant to ecosystem functioning. The complexity of relationships between soil species directly and indirectly involved in decomposition, as well as the many possible trophic interactions involved (Hunt et al. 1987, Moore et al. 1993, de Ruiter et al. 1994, Moore et al. 2003), remains a challenge for soil ecologists in making generalizations about the role of soil diversity in ecosystem functioning. It is possible that soil systems are capable of huge losses in diversity, even the loss of entire functional groups (Hunt and Wall 2002) with little effect on ecosystem functioning.

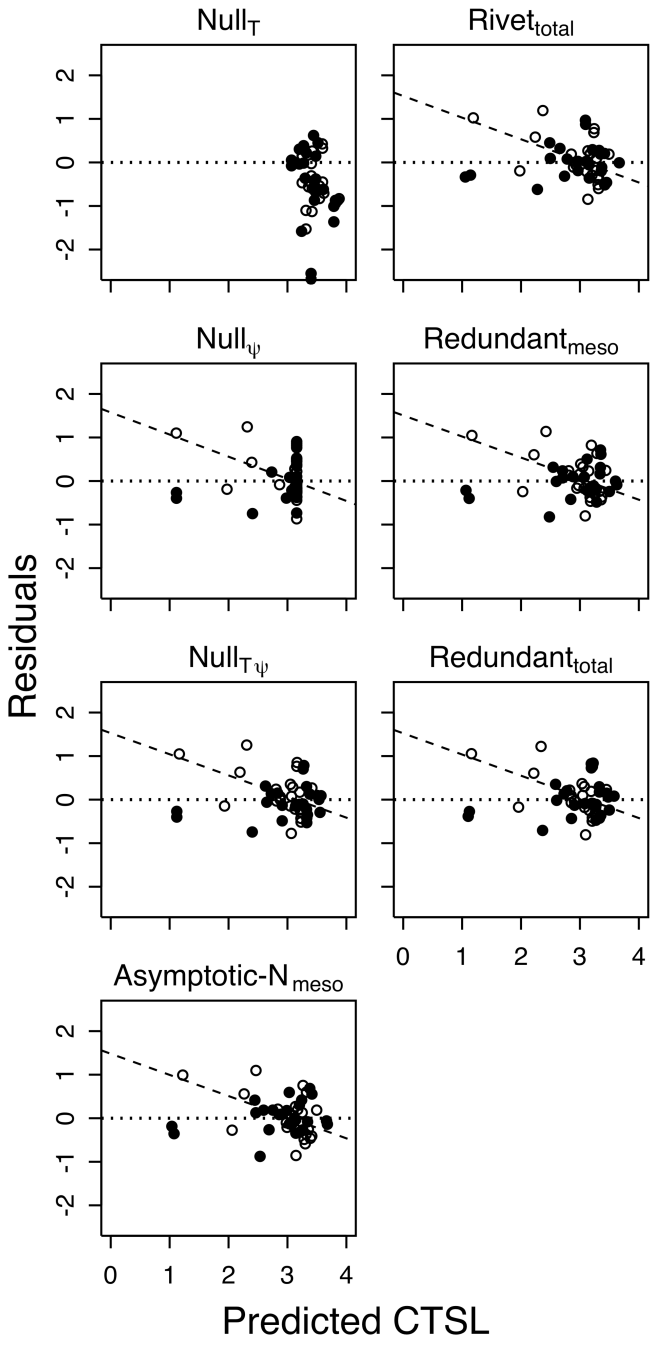

Figure 4.4. Residuals (observed–predicted values) vs. model predicted values. Open symbols represent 20 year burn sites, closed symbols are annual burn sites. Dotted lines are at residual = 0. Hatched lines represent significant regressions ($\alpha = 0.05$) for the 20 year sites only. No significant trends were found for annual burn sites.

4.5.1. Competing Models

The $\text{Null}_{T\psi}$ model using only temperature and moisture as driving variables had > 1.5 times more support in the data (evidence ratio) than models representing the Rivet and Redundant hypotheses for the total mite community (Table 4.2, Figure 4.2). The model considering only soil moisture as a driving variable (Null_{ψ}) produced a decent fit to the data ($R^2 = 0.52$), but only managed to do so by predicting an unacceptably low value of soil moisture of maximum effect on decomposition ($\psi_{\max E}$). The model effectively maximized the value of the decomposition constant, k, close to the average observed decomposition rate (Table 4.2). The Null_{T} model completely lacked support in the data (Table 4.2). Had the study included colder seasons, it is likely that the Null_{T} model would have performed at least marginally better.

The models representing the Rivet and Redundant hypotheses for the total mite communities (S_{total}) did not rank as candidates ($\Delta_i = 3.07$ and 4.05 respectively; Figure 4.2). Inspection of their effects functions (E_{rivet}, E_{redun}) versus species richness, S, superimposed on the residuals from the $\text{Null}_{T\psi}$ model (Figure 4.3) demonstrates a limitation of the natural experiment approach we used. Species richness values measured in this study were relatively high compared to those used in manipulative studies (Naeem et al. 1996, Tilman et al. 1996, Klironomos et al. 2000, Cragg and Bardgett 2001, Liiri et al. 2002, Lambers et al. 2004, Setälä and McLean 2004) and there were few to no data in the critical range of S near the origin. Since there were no data for sites with $S_{\text{total}} < 24$ the true shape of the function in the range $S = 0$ to 24 cannot be predicted and the validity of these models would be questionable even if they did perform better in the model competition.

The model representing the Redundant hypothesis among mesostigmatid mites, $\text{Redundant}_{\text{meso}}$, performed well but did not rank as a candidate ($\Delta_i = 3.07$; Figure 4.2). The maximum-likelihood value of β, which describes the multiplicative decrease in the effect of mesostigmatid species richness on decomposition, was 1.76 implying high redundancy in the mesostigmatid fauna (Table 4.2, Figure 4.3).

The most likely model, Asymptotic-N_{meso}, included temperature and moisture as abiotic driving variables and abundance of adult mesostigmatid mites as the biotic driving variable (Table 4.2, Figure 4.2). The maximum-likelihood estimate of parameter β, which describes the multiplicative decrease in the effect of mesostigmatid abundance on decomposition corresponded with a density of roughly 5200 mites $\cdot$ m^{-2} near the maximum effect on decomposition ($E_{\text{Asymptotic-}N\text{meso}} = 0.99$; Figure 4.3). Adult mesostigmatid mite densities averaging 4100 and as high as 12700 mites $\cdot$ m^{-2} have been recorded from the Konza Prairie (Chapter 2), which provides validation for the mechanisms represented by the Asymptotic-N_{meso} model.

4.5.2. Validity of maximum-likelihood parameter estimates

Maximum-likelihood estimates of the soil moisture value of minimum influence on decomposition ($\psi_{\min E}$, Table 4.2) seem too high compared to expectations of microbial performance in the field (Wilson and Griffin 1975, Paul and Clark 1996) but were a consequence of the linear model chosen for E_ψ. Had we modeled a wider range of moistures, a log-linear model would have been more appropriate. Substituting a log-linear relationship for E_ψ (Eq 6c: Andrén and Paustian 1987) in all the competing models decreased the maximum-likelihood estimate of $\psi_{\min E}$ to –1.5. This water potential is known as the permanent wilting point of plants, a measure of extremely dry soil

conditions and low biological activity. This provided validation that the models presented here would perform well over a wider range of soil moistures by using either linear or log-linear relationships for E_ψ depending on the value of ψ, as suggested by Bunnell and Tait (1974). Maximum-likelihood estimates of $\psi_{\max E}$ (Table 4.2) were a good match for observations of optimal soil moisture conditions for microbial decomposition (Wilson and Griffin 1975, Paul and Clark 1996) lending further support to the mechanisms implied by the models.

Maximum-likelihood estimates of Q_{10} were about 1.5 (Table 4.2), representing a 50 % increase in *CTSL* per 10 ºC increase. These values seem reasonable compared to other studies (Andrén and Paustian 1987) especially since the data were collected during the hottest months of the year, temperatures were all about optimal (Parton et al. 1993, Paul and Clark 1996) and ranged less than 12 ºC over the course of the study (Table 4.1).

4.5.3. Mite community influences in models

Both feeding habits and life-history traits of mesostigmatids and oribatids differ (Walter and Proctor 1999), thus differences in their importance to decomposition rates (Table 4.2) was predictable. Richness and abundance of the Mesostigmata are more likely to be closely associated with short-term, high-rates of soil biological activity, of the type measured with cotton strip decomposition (Gestel et al. 2003), because they are drawn to nematode prey feeding on decomposer bacteria and fungi (Walter 1988, St. John et al. 2002).

Laboratory studies have shown that richness of microarthropods in soils, including mites, does have an influence on the growth rate of plants (an indirect measure of decomposition through nutrient cycling) (Liiri et al. 2002, Setälä 2002), but that this

influence is maximized at about 4–6 species (supporting the Redundant hypothesis), and it is more important to have all functional groups represented than many species within a single functional group. Soil mite species richness in our study was well above six per plot (Table 4.1). Thus it is possible that the redundant model is applicable to the total soil mite fauna, but we were only able to measure their influence near the asymptote and not where the maximal rate of change takes place close to the origin.

4.5.4. Annual burn vs. 20-year burn

Plots of residuals versus model predictions demonstrated that sites with low fire frequency had a significant trend not accounted for by the models (Figure 4.4) whereas annually burned sites were highly predictable ($R^2 = 0.85$) with only temperature, moisture and a single biotic driving variable, N_{meso}. The competing models may have performed better on annually burned sites because they more closely emulate the highly manipulated crop systems for which they were originally developed (Andrén and Paustian 1987). It is possible that annual burning of sites led to a reduction in the diversity of soil's biophysical properties (Anderson 2000, Bardgett et al. 2001) and that soil temperature and moisture, have become overly dominant determinants of decomposition on these sites. A more diverse set of biophysical properties possibly buffered the 20 yr burn sites against fluctuations in soil temp and moisture, decreasing the performance of the competing models for these sites (Figure 4.4). The biophysical properties of importance could include increased standing dead biomass, soil carbon, heterogeneity of soil organic matter or more abundance and richness of the soil microbial fauna for sites with less frequent fires.

4.5.5. BEF models not considered

The BEF models presented here for competition form the basis for many of the BEF hypotheses discussed by researchers (Naeem et al. 2002) . This study provides evidence for rejecting Rivet and Redundant concepts for soil mite effects on rapid decomposition of a cellulose rich source in tallgrass prairie; however, the relatively superior performance of the Null_{T_ψ} model does not discount other possible mechanisms. It is possible that the true BEF relationship between mites and decomposition at the KPBS is the Idiosyncratic, or Keystone or Discontinuous pattern, but their analysis generally require intimate knowledge of each species' life history characteristics and an experimental method to test.

It has been argued that experimental tests of BEF are invalid due to artifacts of their design being confounded in the hypotheses being tested: sampling and removal effects (Huston 1997, Mikola et al. 2002, Diaz et al. 2003). Sampling effects are the increased probability of including species of large influence as the number of species in a treatment increases (Huston 1997, Mikola et al. 2002) while removal effects are those that result form the removal of species from a plot rather than the intended effect of species reductions (Diaz et al. 2003). Separating real, biological mechanisms from sampling and removal effects is difficult.

A strength of the current study was that by using confrontation modeling based on an experiment in a tallgrass prairie, natural levels of diversity were used, avoiding complicating removal effects. Confrontation modeling has potential to improve interpretation of results from experimental tests of BEF relationships as well. Models

representing sampling and removal effects could compete with models of BEF patterns to see which is most likely.

It was anticipated that the Null$_{T\psi}$ model would out-compete the Rivet and Redundant models because in this experiment the inherent level of species richness could be considered to be optimal at each site. That is, species evolved to function optimally in these natural conditions, whereas experimental manipulations of species richness attempt to model extinction scenarios. However, species richness and abundance in any one area fluctuates naturally for a multitude of possible reasons both predictably (e.g. seasonally, successionally) and through random events (e.g. extreme weather events). Such natural variability may lead to experimentally exploitable ranges biodiversity in natural ecosystems.

5. APPENDIX A: CHAPTER 4 DATA

Appendix Table 5.1. Model input data and observed rates of decomposition for each study plot. Soil temperatures (°C) are the means calculated for the entire time the cotton strip was in the field. Water potential (MPa) were determined from single TDR measurements taken close to the harvest date of each cotton strip. Cotton strip decomposition rates (% · day^{-1}) are presented as the rate for the time each strip was in the field.

Plot	Cotton strip harvest date	Temperature (T)	Water potential (ψ)	Decomposition rate ($CTSL$)
1C	20000627	22.91	-0.0069	3.97
1C	20000719	25.75	-0.0131	3.54
1C	20000812	26.08	-0.0482	2.94
1C	20000902	26.97	-0.0591	1.66
1C	20010606	18.43	-0.0022	2.98
1C	20010630	21.65	-0.0012	2.99
1C	20010718	23.98	-0.0156	4.06
1C	20010808	26.37	-0.0167	3.60
1D-1	20000627	23.45	-0.0081	3.10

1D-1	20000719	26.45	-0.0154	3.26
1D-1	20000812	23.77	-0.0399	2.59
1D-1	20000902	24.59	-0.1021	0.72
1D-1	20010606	19.28	-0.0033	2.42
1D-1	20010630	23.49	-0.0037	2.80
1D-1	20010718	27.56	-0.0260	3.51
1D-1	20010808	29.65	-0.0380	3.12
1D-2	20000627	23.45	-0.0073	3.62
1D-2	20000719	26.45	-0.0148	3.66
1D-2	20000812	23.77	-0.0368	2.86
1D-2	20000902	24.59	-0.1021	0.85
1D-2	20010606	19.28	-0.0022	2.78
1D-2	20010630	23.49	-0.0025	2.91
1D-2	20010718	27.56	-0.0301	3.17
1D-2	20010808	29.65	-0.0351	2.99
20B	20000627	21.90	-0.0072	4.02
20B	20000719	24.30	-0.0116	3.68
20B	20000812	23.87	-0.0243	2.90
20B	20000902	24.28	-0.0595	2.82
20B	20010606	18.13	-0.0051	3.04
20B	20010630	21.55	-0.0040	2.91
20B	20010718	24.36	-0.0255	2.29
20B	20010808	24.77	-0.0208	2.94

20C-1	20000627	21.85	-0.0153	3.15
20C-1	20000719	24.52	-0.0205	3.38
20C-1	20000812	25.21	-0.0225	2.80
20C-1	20000902	25.86	-0.1022	2.21
20C-1	20010606	18.93	-0.0100	2.94
20C-1	20010630	22.56	-0.0062	2.72
20C-1	20010718	26.83	-0.0337	3.37
20C-1	20010808	26.82	-0.0351	3.40
20C-2	20000627	21.85	-0.0087	3.92
20C-2	20000719	24.52	-0.0207	3.10
20C-2	20000812	25.21	-0.0227	2.93
20C-2	20000902	25.86	-0.0735	1.79
20C-2	20010606	18.93	-0.0034	2.88
20C-2	20010630	22.56	-0.0032	3.00
20C-2	20010718	26.83	-0.0437	2.78
20C-2	20010808	26.82	-0.0620	3.56

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