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Biodiversity of soil arthropods in a native grassland in Alberta, Canada: obscure associations and effects of simulated climate change

by

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Dedication

For my family, who offered me unconditional love and support throughout the course of this thesis.

Abstract

Soils have traditionally been treated as a “black box” due to the challenges of studying this complex medium. The living component of soil consists of a complex network of roots and mostly very small, highly abundant, and extremely diverse group of microbes, protists, and other invertebrates. In my thesis I explore the diversity of subterranean ants living in a native grassland in Alberta, Canada, and their symbiotic relationship with root-feeding aphids and mealy bugs (Hemiptera: Sternorrhyncha). I identify multiple species of ants and Sternorrhyncha, with varying degrees of specificity of their symbiosis. I also conclude that there is little species-level host-plant specificity.

The latter part of my thesis concerns mites and springtails, which are the most abundant soil micro invertebrates. Biomass of these extremely small organisms is difficult to assess, and as a result many estimation formulae based on body size measurements have been published. However, these estimation methods have rarely been tested. I review published formulae and tested them with newly acquired mite-weight data. While some formulae strongly over- or under estimate mite biomass, other models perform remarkably well.

Using abundance and biomass data, I present the results of the effects of a summer of drought on native grassland soil mites. While drought normally negatively affects most soil arthropod densities, I observed an increase. While the mechanism is not yet clear, this result suggests that some grassland soil mite taxa may be able to benefit from drought conditions.

Finally, I study how changes in environmental conditions, like predicted climate change, may affect native grassland communities. A full-factorial design was used, including a warming, drought, added precipitation, low intensity defoliation, and high intensity defoliation treatments. Results showed that all treatments affected the studied mite assemblages, but the effects differed per mite taxon.

In summary, I have shown that the abundance and diversity of soil biota not only still offer opportunity for discovery, but also react to environmental changes in a way that allows them to be used as biomonitors. These responses vary according to which taxa are being studied, emphasizing the importance of not oversimplifying this rich and complex community.

Acknowledgements

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Chapter 1: Introduction

1.1 Importance of soil

Currently, rates of soil erosion and desertification vastly outpace the relatively slow process of pedogenesis (soil development) (Pimental and Sparks, 2000). Considering that all terrestrial ecosystems, including crop and livestock production, ultimately depend on the soil, these are among some of the biggest threats facing the planet in recent times. While human land use is a large contributor to this soil degradation, global climate change may further exacerbate the problem. One strong contributing factor to soil erosion is the intensity of rainfall (Nearing et al., 2004), which is predicted to increase in certain areas by current climate models (Shen et al., 2005; CCCma, 2012). In general we can expect heavier rainfall over shorter periods, although this is highly dependent on the geographic location. As a result, longer periods of drought are also expected, which can cause desertification. However, climate change affects soil not only through erosion and desertification; changes in precipitation patterns, temperature, and CO_2 enrichment may also directly or indirectly influence soil organisms (Lindberg, 2003; Kardol et al., 2011), disrupting soil processes, and in turn altering above-ground vegetation.

While all terrestrial ecosystems are ultimately dependent on the soil, we still know surprisingly little about the inner workings of this complex matrix. Soil has been called a "black box" (Andren and Balandreau, 1999);we typically apply treatments to a soil surface and observe the effects aboveground, usually from a botanical perspective (e.g. Kardol et al., 2006). However, determining what actually happens within soil has historically been a more infrequent endeavour. In light of climate change, it is imperative that we gain a better understanding of the soil's inner workings, particularly its understudied biota.

1.2 Ants

The importance of some soil organisms has long been recognized. One of the most famous early soil ecologists, Charles Darwin (1881, p. 313), stated about earthworms: "It may be doubted whether there are many other animals which have played so important a part in the history of the world, as have these lowly organised creatures." Earthworms are often called ecosystem engineers (Jouquet et al., 2006), but they are not the only invertebrates to fulfill this role in soil. Ants can have extensive effects on terrestrial ecosystems (Hölldobler, 1990). While most ant species can be readily seen foraging aboveground, there are much more poorly studied subterranean ants which only come aboveground as winged reproductive males and females to mate and to establish new colonies (Kishimoto-Yamada et al., 2005). While some of these species are more strictly subterranean than others, it is surprising that so little research has been done regarding their obscure life history. Many of these ant species rely on symbiotic relationships with root-feeding aphids and mealybugs (Hemiptera: Sternorrhyncha) for their carbohydrate and protein needs, and in some cases this symbiosis is mutually obligatory (Kishimoto-Yamada et al., 2005). While this interaction has long been recognized (Lubbock, 1882), there is a paucity of published literature on this topic. This is surprising given that the above-ground equivalent of this symbiosis - ants tending aphids and mealybugs on leaves and stems of plants - is well established in published literature (Buckley, 1987). The activities of both symbionts may have consequences for the above-ground vegetation; ants alter the physical characteristics of the soil, while aphids and mealybugs actively feed on plant roots (Foottit and Richards, 1993). In Chapter 2, I discuss the results of a study that I performed at the University of Alberta Research Ranch in Kinsella, Alberta, on the distribution of subterranean ants and their sternorrhynchan symbionts. I present my observations of which ant species are found together with which aphid and/or mealybug species, further shedding light on these poorly studied, yet common and possibly ecologically important interactions.

1.3 Mites and springtails

While the physical effects of earthworms and ants on soil are much more pronounced and directly visible, other smaller-bodied soil invertebrates also play important roles in belowground ecological processes. This latter group of organisms are easily overlooked as they are dominated by tiny inconspicuous nematodes and microarthropods (Giller, 1996; Coleman et al., 2004). These taxa can either directly contribute to nutrient mineralization by digesting organic detritus, or they may indirectly affect this process through microbivory (feeding on fungi, bacteria, and protists) (Petersen and Luxton, 1982; Coleman et al., 2004). In addition, many soil organisms are predatory, or opportunistically omnivorous, further adding complexity to the soil food web (Anderson, 1973; Moore et al., 1988). The most abundant and undisputedly diverse of these invertebrates are soil mites (Coleman et al., 2004). In grasslands, mites can be found at densities up to 94,700 m^{-2} (Leetham and Milchunas, 1985), while densities up to an astonishing 458,580 m^{-2} have been recorded for a Scots pine forest (Wallwork, 1983). According to Krantz and Walter (2009) mite feeding habits vary widely, but generally, Oribatida are considered fungivores and/or detritivores. A few oribatid families are known to be nematophagous, or microbivorous (some Astigmata) but this seems more an exception than a rule. This is almost the only taxon that can ingest particulate matter; only a few other mite groups can do this, and none are common in soil. Prostigmatid mite species vary too widely in their feeding habits to generalize, but they include predators, plant feeders, fungivores, and omnivores. Endeostigmata includes taxa that are fungivorous, herbivorous, and nematophagous. Finally, Mesostigmata are mostly generalist predators. It should be noted that most mites are considered opportunistic to some extent, making it difficult to confirm true feeding preferences. In addition, little is known about ingestion of protists and bacteria by mites, but these may be indiscriminately ingested on other food such as detritus. Springtails, while not matching mites in diversity, can in some systems equal or exceed mite abundance. Springtails are almost exclusively fungivores. These two taxa, but particularly mites, are the focus of the rest of this thesis.

Because mites are so small, ecologists most often study mite abundance instead of biomass, out of practicality. While abundance is sometimes the most appropriate measure, e.g., in some types of biodiversity studies, studying function (e.g. nutrient cycling, nitrogen fixing, productivity, etc.) of the soil community may require biomass. Mite biomass can be difficult to ascertain for various reasons, but mainly because of the need for very precise balances that are able to measure extremely low weights (< 1 μg). As a result, many formulae have been created to estimate biomass by first estimating body weights based on body size metrics. However, there have been few attempts to compare these estimation methods (Lebrun, 1971; Caruso and Migliorini, 2009). In Chapter 3, I review published studies and compare the accuracy of their bodyweight estimations using newly acquired weights of soil mites.

Soil microarthropod assemblages are known to be sensitive to different soil characteristics, particularly moisture content (Figure 1.1), where declines in moisture content usually have negative consequences for both taxon richness and abundance (Ford, 1938; Wauthy and Vannier, 1988; Harte et al., 1996; Berg et al., 1998; Lindberg, 2003; Taylor and Wolters, 2005; Tsiafouli et al., 2005; Gergocs and Hufnagel, 2009). However, (semi) arid grasslands may contain taxa specifically adapted to dry conditions (O'Lear and Blair, 1999), and therefore may not show reduction in abundance or diversity when subjected to low moisture conditions. In Chapter 4 I experimentally explore this possibility in a relatively arid locality, situated in a temperate native fescue grassland, by applying one summer of continuous precipitation reduction.

While other environmental factors such as warming have also been considered in the context of testing climate-change effects on soil biota (Hodgson and Convey, 2005; Bokhorst et al., 2008; Briones et al., 2009; Hagvar and Klanderud, 2009), it is uncommon to see both soil moisture and temperature manipulated in a factorial design; rarer still are large scale studies incorporating more than two variables in such an experimental design. In Chapter 5 I present the results of three consecutive summers of climate change and defoliation treatments

on a soil microarthropod community. Figure 1.1 shows the conceptual framework from the perspective of studying soil mites, on which this study is built. This research was also conducted at the University of Alberta Research Ranch in Kinsella, in a native fescue grassland. Grasslands play a vital role in food production, and in Alberta, many grasslands are used for cattle grazing. As such, I tested how lowered and increased precipitation, warming, and different defoliation intensities affected soil mites and springtails.

1.4 Specific research questions and objectives

Chapter 2

1. What subterranean ant taxa and their sternorrhynchan associates can be found at the University of Alberta Research Ranch in Kinsella?
2. Are there any clues, in the shape of particular soil and/or landscape features to determining the presence of subterranean ants that tend root-feeding sternorrhynchans?
3. Are there any specific plant-insect or ant-sternorrhynchan associations, and if so, how exclusive are these associations?

Chapter 3

1. Gather new length, width and weight measurements from a taxonomically and morphologically diverse array of Albertan soil mites.
2. Review all published body weight estimation formulae
3. How well do published weight-estimation models perform when tested with the new data from Albertan mites?

Chapter 4

1. Do short-term drought, warming, and defoliation alter abundance, biomass, taxon richness, and assemblage structure of temperate grassland soil mites in favour of drought-adapted taxa?

Chapter 5

1. What effects do treatments simulating climate change and variation in grazing management (reduced and increased precipitation, warming, defoliation) over three consecutive summers, have on microarthropod assemblages in a temperate grassland community? Specifically, how do these factors, and their possible interactions, affect soil mite diversity, abundance, biomass, and assemblage structure?

In summary, this thesis outlines my different attempts to peer into the dark and obscure realm of soil to study the organisms that live there. As a result I have ventured into three seemingly disparate topics: interactions among ants, aphids, mealybugs and plants; biomass estimation methodology for mites; and soil microarthropod assemblage changes following short-term drought and various treatments simulating climate-change. Together they showcase some of the diversity of the challenges facing soil ecologists today. I also believe that these three topics are tied together under an umbrella of appreciation for the diversity and complexity of soil organisms and the communities that they are part of.

Chapters 2 and 3 have been previously published, and I have maintained their corresponding journal manuscript formats.

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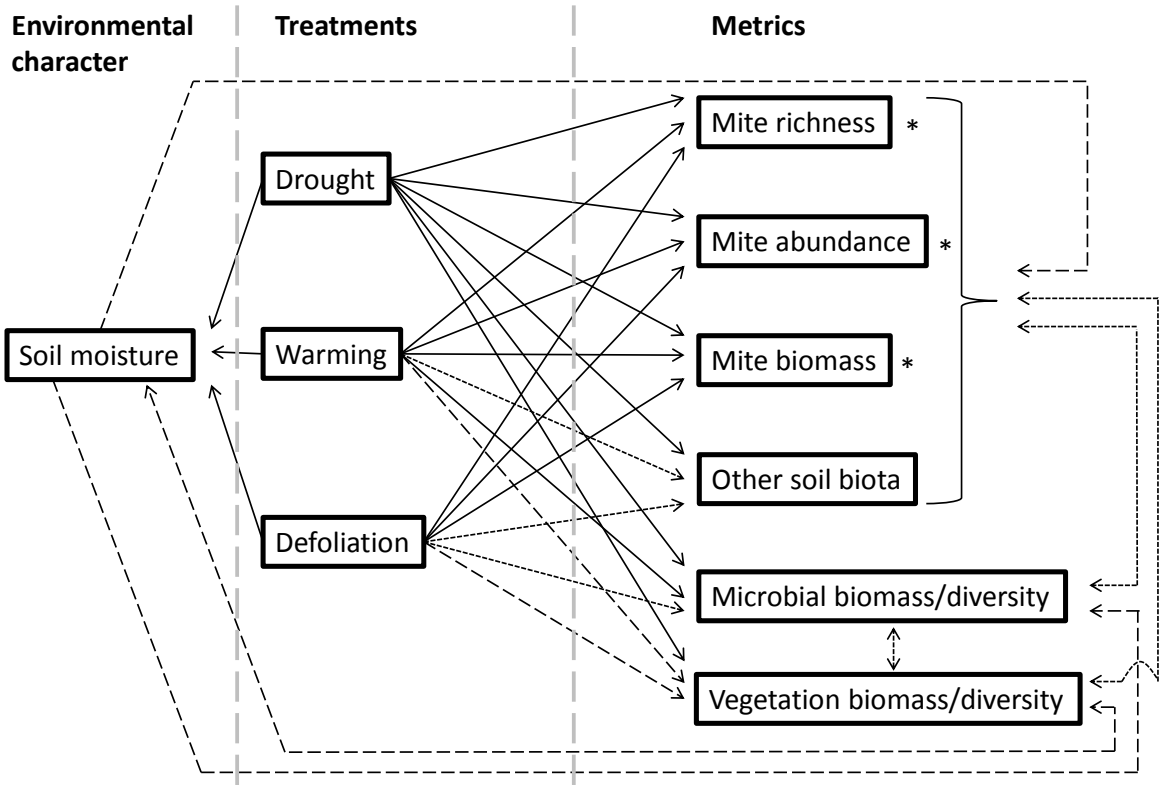

Figure 1.1: Conceptual framework which shows interactions of soil fauna with important aspects of their environment and climate-change simulating /defoliation treatments. Solid lines represent a negative effect (reduction), long-dashed arrows signify a positive effect, and dotted arrows signify variable responses. Asterisks (*) indicate the focus of my study.

Chapter 2: Ants and subterranean Sternorrhyncha in a native grassland in east-central Alberta, Canada[1]

2.1 Introduction

Ants (Hymenoptera: Formicidae) and various Sternorrhyncha (Hemiptera) have a long history of close association (Johnson *et al*. 2001). Their relationship is mostly mutualistic whereby the ants benefit from "honeydew" (carbohydrate-rich secretions) produced by the sternorrhynchans and the sternorrhynchans are protected from predators. Four families of Sternorrhyncha commonly exhibit this 'trophobiotic' form of mutualism with ants: Aphididae (Aphidoidea) and Coccidae, Pseudococcidae, and Stictococcidae (Coccoidea) (Delabie 2001). Most research has focused on this interaction aboveground (reviewed by Way 1963; Buckley 1987; Stadler and Dixon 2005; Styrsky and Eubanks 2007) and has shown that the association of the tending ants and their symbionts ranges from facultative to obligate (Hölldobler and Wilson 1990; Lapolla *et al.* 2006). Interactions of tending ant species and root feeding aphids and mealybugs are poorly understood, even though this phenomenon has long been recognized (*e.g.*, Lubbock 1882).

In a study conducted near Kinsella, Alberta, Canada, Coupe (2003) suggested that the ants *Tapinoma sessile* (Say), two species of *Lasius* F., and a species of *Myrmica* Latreille were possibly tending unidentified aphids. In this study we followed up on Coupe's observations to determine plant/insect associations, the specificity of interactions, and whether particular soil and landscape features provide clues to the presence of ants tending root-feeding sternorrhynchans.

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2.2 Methods

The study site (centered around 53°01.1'N, 111°32.1'W) is located at the University of Alberta Research Ranch in Kinsella, Alberta, Canada. The ranch is situated in native fescue grassland within aspen parkland, which is geographically positioned between grasslands to the southeast and boreal forest to the northwest. The landscape consists of knob and kettle topography with short slopes interspersed with intermittent wetlands. Soils are characterized as orthic black and dark brown chernozems (Howitt 1988). The vegetation is dominated by graminoids (*Festuca hallii* (Vasey) Piper and species of *Bromus* L., *Elymus* L., *Hesperostipa* (Elias) Barkworth, and *Poa* L. (Poaceae) and species of *Carex* L. (Cyperaceae)), low growing forbs and shrubs (*Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem. and *Rosa arkansana* Porter (Rosaceae), *Artemisia frigida* Willd. (Asteraceae), *Elaeagnus commutata* Bernh. ex Rydb. (Elaeagnaceae)), and patches of trembling aspen (*Populus tremuloides* Michx. [Salicaceae]) (S.R. White, University of Alberta, pers. comm.).

In mid June and late July 2009, 230 soil cores were taken from a variety of locations at the ranch over an area of approximately 50 ha. Nineteen transects of 50 m or 100 m were selected within this area to maximize plant diversity and variation in aspects and slopes but avoided aspen stands. A 1 m^2 quadrat was sampled every 10 m along each transect resulting in a total of 115 quadrats. To avoid visual bias, each quadrat was blindly placed approximately 1-3 metres away from the transect, alternating between left and right.

Percent cover of "grasses", "forbs", "shrubs", and "bare ground" in each quadrat were determined by rough visual estimation. Other measures taken were soil moisture content (Theta probe type ML2x, Delta-T Devices, Cambridge, England), slope category (none, shallow, steep), aspect, and number of visible entrances to ant nests. Two soil cores approximately 15 x 20 cm wide and 15 cm deep were collected per quadrat using a spade and a hand shovel, placed into plastic bags, and returned to the laboratory for examination. We attempted to maximise the number of plant species included within each coring site.

Each core was manually broken apart in a white tray and carefully inspected for ants, aphids, and mealybugs. Cores that had gone through ant nests were recognized by the presence of chambers, ant eggs, pupae, and a relatively high abundance of ants. Plants with sternorrhynchans on their roots or root crowns were identified to the lowest level possible with the aid of local botanists. Ants were identified using Wheeler and Wheeler (1963), Bolton (1995), and unpublished keys to Albertan species created by JG. Sternorrhynchans were identified by HELM using reference collections at the Canadian National Collection, Agriculture and Agri-Food Canada, Ottawa. Ant/sternorrhychan associations were categorized as "direct" (sternorrhynchans found in an ant nest or observed being carried by ants) or "indirect" (sternorrhynchans and ants simply found in the same quadrat or soil core). We looked for evidence of associations among insects, plants, and environmental variables using bivariate correlation tests in SPSS 17.0.0 (SPSS Inc. 2008).

2.3 Results

A total of 23 of the 87 species of ants reported for Alberta (Glasier 2011) were collected. Eleven of these were not observed in association with sternorrhynchans: *Camponotus modoc* Wheeler, *Formica hewitti* Wheeler , *F. lasioides* Emery, *F. limata* Wheeler, *F. neogagates* Viereck, *F. neorufibarbis* Emery, *F. obscuriventris* Mayr, *F. oreas* Wheeler, *F. podzolica* Francoeur, *Leptothorax muscorum* (Nylander), and *Myrmica brevispinosa* Wheeler. The remaining 12 species (Table 2.1) were considered to be directly or indirectly associated with subterranean Sternorrhyncha. Most of the ants listed in Table 2.1 were found in association with more than one species of root feeding sternorrhynchan, sometimes with more than one species of Sternorrhyncha in the same ant nest.

Eight species of Aphididae were collected, the most common being *Forda marginata* Koch and a member of the *Geoica utricularia* (Passerini) species complex. Specimens of *Anoecia* Koch collected from *Elymus* roots differ from all described species in this genus but match specimens previously known only from roots of *Hordeum jubatum* L. (Poaceae) in Winnipeg (see Blackman and Eastop

2006). However, intraspecific variation in many species of *Anoecia* is poorly documented, and we are unsure that this is indeed an undescribed species. Also, a single specimen of *Geoica* Hart found on *Hesperostipa curtiseta* (Hitchc.) Barkworth fell outside the documented variation within species of *Geoica* known to occur in North America. Finally, we collected *Pleotrichophorus pseudoglandulosus* (Palmer) and *Pseudoepameibaphis tridentatae* (Wilson). Both are known as above-ground feeders on sage (*Artemisia* L. (Asteraceae)) (Foottit and Richards 1993) but we collected them from unidentified graminoid roots and root crowns, respectively.

Four species of Pseudococcidae were collected. One specimen of *Heliococcus osborni* (Sanders), found on the soil surface and not associated with ants, represents a considerable northern extension of the distribution of this species and the first record for Canada (Kosztarab 1996). The other three species were ant-associated. *Chnaurococcus trifolii* (Forbes) is widespread in North America and has been previously reported from Alberta (Ben-Dov 2010a, citing Ben-Dov 1994, but no such record in Ben-Dov 1994). *Tridiscus sporoboli* (Cockerell) was previously known only from New Mexico and Nebraska (Ben-Dov 2010b). *Phenacoccus solenopsis* Tinsley is a widespread important pest of a variety of economically important plants (CAB International 2011); our collection is the first record of a population in Canada. *Phenacoccus solenopsis* was the only sternorrhynchan in this study found on non-graminoids (*Artemisia frigida* (Asteraceae) and *Rosa arkansana* (Rosaceae)). Graminoid host plants for the various pseudococcids were species of *Elymus*, *Festuca*, *Hesperostipa*, *Poa*, and *Carex*. There was no evidence that graminoid-feeding sternorrhynchan species were restricted to one host species.

None of the environmental data collected were significantly correlated with ants or subterranean sternorrhynchans ($p > 0.10$). Although we frequently found ants without sternorrhynchans (Figure 2.1), only four samples had root-feeding aphids (*Geoica utricularia* and *Anoecia* sp.) without tending ants, and all subterranean pseudococcids (Table 2.1) were found with ants.

2.4 Discussion

Although sampling intensity and study area size were limited, a large number of target species were collected including new records for Alberta or Canada. This demonstrates the current gap in knowledge of the diversity of subterranean arthropods in Canada. This may be due in part to a lack of taxonomists specializing in these taxa but the inherent difficulty of locating, sampling, and observing the behaviour of cryptic soil fauna also plays a role. For example, not all ant species collected with sternorrhynchans (notably *Myrmica latifrons* Starcke, *Tapinoma sessile*, both species of *Temnothorax* Mayr, and more surprisingly *Lasius coloradensis* Wheeler and *L. fallax* Wilson) were directly observed interacting with their associated sternorrhynchans (Table 2.1). To our knowledge, no published record exists of a species of *Temnothorax* tending sternorrhynchans above or below ground but species of *Lasius* are generally known to tend sternorrhynchans (Fisher and Cover 2007). *Lasius coloradenis* is particularly noted as being entirely subterranean and dependent on symbiotic relationships with root feeding sternorrhynchans (Hölldobler and Wilson 1990; Fisher and Cover 2007).

The lack of observed direct interaction may be a function of sample size or mis-categorization of some of the indirect associations. Breaking up of soil cores occasionally made it difficult to identify ant tunnels or nest chambers and the disturbance caused by sorting may have caused ants to abandon their sternorrhynchan associates. Almost all subterranean sternorrhynchans were found in the presence of ants and, for those species that were occasionally found alone, there were other samples in which they were tended by ants. Perhaps the pattern shown in Figure 2.1 is caused by a high density of ants in the area, resulting in almost all Sternorrhyncha co-occurring with ants. However, this seems unlikely as only 62% of all sampled quadrats contained ants above-ground or below. We suggest that the very small number of Sternorrhyncha found alone, limited to *Geoica utricularia* and *Anoecia* sp. in 3.4% of all quadrats, were either temporarily not tended by ants or may be the only two species in our study area to not always have an association with ants. This implies that although the

association may be facultative for ants, it might be obligatory for the other below-ground sternorrhynchans.

Although we had hoped to find environmental cues that would increase our likelihood of locating ants together with sternorrhynchans, there were no significant correlations with plant cover, soil moisture, slope, aspect, or presence of visible entrances to ant nests. This implies that either there are no environmental cues, we did not measure the relevant environmental factors, or our sample size was not adequate. Lastly, as previously noted for some taxa by Vogel and Kindler (1980), none of the sternorrhynchans in our study were found to be specific to a host plant species.

Biological surveys of below-ground ant and sternorrhynchan symbioses are rare and behavioural studies often limited to a few taxa (*e.g.*, Lapolla *et al*. 2002; Stuart and Polavarapu 2002; Kishimoto-Yamada *et al*. 2005) suggesting that such associations may be uncommon. However, our data suggest that they may be more widespread than previously thought. We feel that this is an overlooked relationship that merits more attention from taxonomists and ecologists.

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Table 2.1: Associations of ant species and Sternorrhyncha. Letter codes (a-z, aa-ii) represent individual quadrats. Letter codes shared between different ant-sternorrhynchan pairs indicate that observations came from the same quadrat: bolded and capitalized – direct association observed (either sternorrhynchans found in ant nest, or ants observed transporting sternorrhynchans); lower case – co-occurrence in same quadrat but no direct association observed. *E.g.*, *Anoecia* sp. is found in direct association with *L. pallitarsus* (**V**), but also in indirect association with *L. pallitarsus* and *T. rugalutus* in one quadrat (cc), along with *F. marginata* and *G. utricularia* (cc).

Formicidae / **Aphididae**	*Lasius coloradensis* Wheeler	*Lasius crypticus* Wilson	*Lasius fallax* Wilson	*Lasius flavus* (Fabricius)	*Lasius neoniger* Emery	*Lasius niger* (Linnaeus)	*Lasius pallitarsis* (Provancher)	*Myrmica fracticornis* Forel	*Myrmica latifrons* Starcke	*Tapinoma sessile* (Say)	*Temnothorax ambiguus* (Emery)	*Temnothorax rugatulus* (Emery)
Forda marginata Koch	j	-	-	**Q**, **Z**, **FF**	**B**	-	**N**, **S**, **U**, **X**, cc, **HH**	d, **J**	gg	-	q	cc
Anoecia sp.	-	-	-	-	-	-	**V**, cc	-	-	-	-	cc
Aphis middletonii Thomas	-	-	-	-	-	-	**X**	-	-	-	-	-
Geoica utricularia (Passerini) complex	j	**M**	-	**E**, **K**, **Z**, **AA**, dd, **EE**	-	-	**L**, o, **R**, **Y**, cc, dd, **HH, , II**	d, **J**	r	-	t	cc
Geoica sp.	-	-	-	**E**	-	-	-	-	-	-	-	-
Pleotrichophorus pseudoglandulosus (Palmer)	bb	-	-	-	-	-	-	-	-	bb	-	-
Pseudoepameibaphis tridentatae (Wilson)	-	-	-	-	-	-	**L**	-	-	-	-	-
Tetraneura sp.	-	-	-	-	-	-	-	**W**	-	-	-	-
Pseudococcidae												
Tridiscus sporoboli (Cockerell)	-	-	-	-	-	-	-	-	-	a	a	-
Chnaurococcus trifolii (Forbes)	j	-	-	k, q, **FF**	**C**	-	**L**, **R**	j	f, r	-	q	-
Phenacoccus solenopsis Tinsley	-	-	h	e, p	-	**N**	-	h	g	h, i	-	-

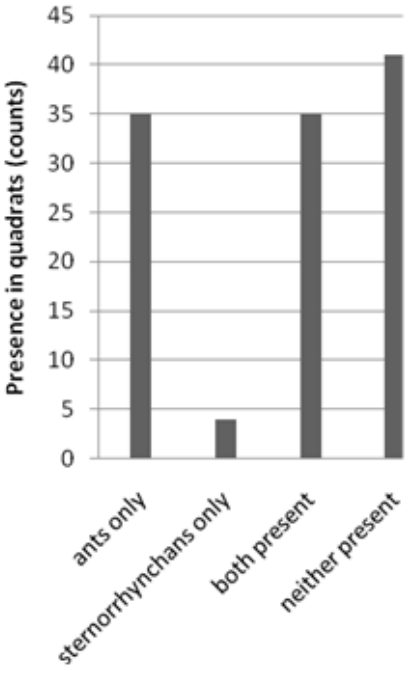

Figure 2.1: Frequency of occurrence and co-occurrence of ants and subterranean sternorrhynchans in 115 quadrats at Kinsella Ranch, Alberta, Canada.

Chapter 3: A fresh look at weight-estimation models for soil mites (Acari)[1]

3.1 Introduction

Quantification of organisms in a sample or an ecosystem is usually expressed either as abundance or as biomass. Biomass, the summation of individual body (dry or wet) weights per unit area (Bornebusch 1930; Petersen and Luxton 1982), is often a more ecologically relevant measure than abundance, particularly when abundance and biomass correlate poorly (Saint-Germain et al. 2007). When trying to understand whole-community dynamics, biomass acts as a common ecological currency for plants, animals and microbes (Hessen 1997).

In soil ecology, microarthropods such as mites and springtails are often counted rather than weighed (e.g. Huhta and Hanninen 2001; Belnap et al. 2005; St John et al. 2006; Ball et al. 2009; Kardol et al. 2009, and many others). Such abundance data are sometimes appropriate, for example, when applied to biodiversity assays or to population dynamics. At other times, this preference for counting rather than weighing is due to convenience or necessity stemming from the mensurative challenges caused by very small-bodied mites (Wallwork 1967). Small mites, which include juveniles and many adult Prostigmata and Endeostigmata, can make up the majority of the mites found in some soils (Kethley 1990). They are usually less than 250 μm in body length and weigh less than 3 μg. As such, weighing mites requires fine microbalances. Trying to establish dry weight instead of wet (fresh/live) weight, which is sometimes required for biomass, only exacerbates the difficulty.

These problems can be circumvented by determining biomass directly by weighing all collected individuals simultaneously (e.g. "total mite weight", "total springtail weight" and "total microarthropod weight"). However, these simplifications are only appropriate for coarse taxonomic groups, which, depending on the nature of the study, may not be sufficiently informative or

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biologically relevant. Ideally, to obtain biomass accurately for specific taxonomic groups, functional groups or feeding guilds, individual mites are first weighed separately and their body weights are summed. In addition to using individual body weights to calculate biomass, they can also be valuable biological measures on their own, e.g. in ecophysiological studies (Blackburn and Gaston 1999). A mite's body weight is highly correlated with metabolism (Berthet 1966; Luxton 1975) which directly affects soil respiration, and therefore other soil processes. Once published, species specific body weights can be used in other studies where only taxa and abundances are known, eliminating the need for weighing.

Collectively, weights of 140 species of soil mites have been published through weighing of individual mites, although the taxa weighed are almost solely Oribatida (Berthet 1963, 1964; Lebrun 1965; Block 1966; Elmes and Webb 1972; Wood and Lawton 1973; Luxton 1975; Mercer et al. 2001). Mercer et al. (2001) are the only authors to report non-oribatid weights (for nine taxa of Prostigmata and Mesostigmata), but these are not species specific. A caveat to the application of single weight values for all members of a given species is provided by Elmes and Webb (1972) and Luxton (1975), who found that mites' body weights can be highly variable within a species. The authors attribute this to weight differences between males, females and juveniles, gravid vs. non-gravid females, or from variation in gut contents at the time of weighing. It seems likely that intraspecific variation in body weight could also be due to natural variation within a population (e.g. seasonal) (Petersen and Luxton 1982) or between populations (e.g. local adaptation). Intraspecific ranges of mean adult body weight of over 25% have been reported (Luxton 1975). Such variation makes it potentially risky to use "species-specific" mites' body weights measured by other researchers for biomass estimation.

Given the above problems posed by weighing small mites, alternatives to direct weighing of individual mites have been established. The first method consists of weighing numerous individuals of the same species together and averaging their weight (Bornebusch 1930; Zinkler 1966; Chernova et al. 1971; Crossley et al. 1975; Douce 1976; Walter and Ikonen 1989), but this comes with

its own challenges. First, enough individuals of the same species are needed to meet the minimum detectable weight for the balance. Second, for many taxa, identification to species, or sometimes genus or family, can only be positively established by mounting mites on microscope slides. Through the slide mounting process, the specimen is fixed and cannot be returned to its original weight. In such circumstances, pure cultures are needed for absolute assurance that only one species is being weighed.

A second and often more broadly applicable method of establishing body weight employs one or more measures of body size such as body length, width and sometimes gnathosomal width, to estimate volume. A conversion factor is then applied to this volume to estimate body weight. Doing so involves the following assumption:

$$\Delta M = \Delta V * C$$

where M is the body weight (mass), V is the volume and C is a constant (Caruso and Migliorini 2009). This technique can also conveniently be applied to slide-mounted mites.

Table 3.1 shows the different body weight estimation models that have been developed for soil mites. In the oldest of these publications, Macfadyen (1952) briefly described using length and width measurements to estimate body weight and ultimately biomass for mites and Collembola, but regrettably, he did not report the conversion factor used, nor did he present any actual body weight data. Subsequently, several other authors developed similar models. Only three claim that their models can predict weight for all mite taxa, five report models useful for Mesostigmata, three for Prostigmata specifically, one for Astigmata, and twelve especially for Oribatida. The last group includes Lebrun's (1971) three shape-specific "oribatid form" equations. While most of these studies are specifically aimed at soil mites, some (Rogers et al. 1977; Hódar 1996) are more general and include both large and small arthropods. After somewhat of a temporal publication gap on the subject, Caruso and Migliorini (2009) published a

mathematically oriented paper that explains the biometrical and geometrical principles on which most of these formulae are founded and also contributed a novel model of their own.

No published studies (that the authors know of) have validated the strength of these size-based models by using new sets of mite specimens to test their predictive accuracy. Although Caruso and Migliorini (2009) did test their own size-based oribatid model and found it to work well, they used established weight measurement data reported by Lebrun (1971) to do so rather than collecting and weighing a new set of mites.

To date, the most comprehensive compilation of body weights of soil mites is that of Luxton (1975); however, while this includes 127 species of oribatids (no other types of mites), no body dimensions are reported. This lack of actual measurement data makes it difficult to assess the accuracy of the models, and consequently, it is currently not clear whether the weights of members of certain orders, suborders or finer taxa are systematically overestimated or underestimated. Most recently published studies using soil microarthropod biomass (e.g. Berg et al. 1998; De Deyn et al. 2003; Scheu et al. 2003; Holtkamp et al. 2008; Mulder et al. 2008; Bokhorst et al. 2012) rely on one or more of the weight prediction models in Table 3.1. It is therefore essential to determine how accurate and universally applicable these models are. In this article, we gather new length, width and weight measurements from a taxonomically and morphologically diverse array of soil mites collected in Alberta, Canada, and use them to test how well the published weight-estimation models perform.

3.2 Materials and methods

3.2.1 Collection, identification and measurement

We collected mites from two ecologically different areas in Alberta, Canada. Fifteen individuals were obtained from soil collected at a mixed deciduous-coniferous forest adjacent to the North Saskatchewan River in Edmonton (53º 31’ 46” N, 113º 31’ 24” W) (Table 3.3). The site’s overstory is dominated by aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.) with a

smaller proportion of white spruce (*Picea glauca* (Moench) Voss), and the understory has a high diversity of shrubs and herbs. The remainder of the mites were extracted from soil collected at the University of Alberta Research Ranch near Kinsella, Alberta (53º 1' 14" N, 111º 32' 21" W). The area consists of native fescue grassland with pockets of aspen woodland. We collected samples by coring and hand shovelling. Mites were extracted using a modified Tullgren funnel (Coleman et al. 2004) and collected live into containers with floors of moistened plaster of Paris mixed with activated carbon powder (~10:1).

With the aid of a Leica MZ6 (max 40x) (Leica Microsystems Ltd., Switzerland) dissecting stereomicroscope, we selected live mites (n = 78 individuals) from different taxonomic groups and a range of body sizes. This included 35 individual Oribatida (including 4 Astigmata), 21 Prostigmata (including 9 Heterostigmata), 4 Endeostigmata and 18 Mesostigmata (Table 3.2). This selection was made in order to maximize diversity of sizes and morphologies. For some taxa, we weighed more than one individual (separately) (e.g. four individuals of a single morphospecies of *Nanorchestes*), while others are represented by a single individual; however, each data point represents an individual rather than a taxon. After weighing and measuring (described below), we mounted each mite in polyvinyl alcohol medium (#6371A, BioQuip Products, Rancho Dominguez, California). Slides were placed on a 40° C slide warmer for a minimum of 4 days before we identified the mites. We identified the mites using compilations of keys, some published and others unpublished, from the Ohio State University Acarology Summer Program (http://www.biosci.ohio-state.edu/~acarolog/summerProgram/) and Walter et al. (2011), and with the help of Dr. David Walter (Royal Alberta Museum).

In order to prevent mites from running off of the tray of the microbalance, we killed them prior to weighing. A few mites were killed by freezing at –20°C for 24 hours, but as this was not always effective (i.e. some individuals became active after returning to room temperature) and we killed most mites by submerging them in 95% ethanol for ~5 minutes, then leaving them to air dry for 1 minute. We killed the mites immediately before weighing to avoid dehydration

while being stored in ethanol. This dehydration was observed to be a particular problem for Prostigmata (also by Huhta and Koskenniemi (1975)). All mites were individually weighed using a CAHN C-31 microbalance (CAHN Instruments Inc., Cerritos, California) sensitive to 0.1 μg. Due to this delicate sensitivity, each individual was weighed 3–7 times depending on the degree of variation in weight observed, and the measurements were averaged.

After weighing, we measured the length and width of each individual mite at 80× magnification using a Leica MZ16 (max 115×) dissecting microscope with a calibrated ocular micrometer (1 ocular unit = 12.5 μm). Length measurements for Oribatida, Prostigmata and Endeostigmata were taken from the anterior tip of the gnathosoma, excluding chelicerae, to the posterior margin of the idiosoma. Mesostigmata were measured from the anterior to the posterior margin of the idiosoma due to their variable tendency to extend or retract the gnathosoma. All mite widths were measured from the left to right margin of the idiosoma in dorsal view at the region of greatest body width. Maximum gnathosomal width was measured by slide mounting the mites and then using a Leica DM LB differential interference contrast (DIC) microscope at 400× magnification. Although we actually measured mass, we use the term "weight" throughout this article in order to be consistent with terminology in most other related publications including the recent mathematically oriented analysis by Caruso and Migliorini (2009).

3.2.2 Model testing

We tested the performance of 18 of the models shown in Table 3.1 (indicated by an asterisk). Because some models directly predict dry weight, we used 0.4 dry weight ratio (i.e. wet weight = 2.5 × dry weight) (Persson and Lohm 1977) to change their predictions to wet weights. We decided to use the most recent dry:wet ratio published for all mites, but acknowledge that this ratio differs between taxa (Table 3.3). We did not test the Uropodina model from Edwards (1967), Elmes and Webb's (1972) *Steganacarus magnusor* model, the "achipteriform, carabodiform and nothriform" oribatid models of Lebrun (1971), or the Astigmata model of Mercer et al. (2001) due to lack of, or insufficient numbers of, relevant specimens to test these very specific formulae. We excluded

the oribatid formula of Douce (1976) in part because we found the "maximum gnathosomal width" measurement needed for the model too difficult to measure consistently on these morphologically diverse and highly sclerotized mites. The nature of this character was also insufficiently described in Douce's paper for us to be confident of taking the measurements in the way intended by the author. Lastly, we did not test the Mercer et al.'s (2001) model for Mesostigmata because the authors measured the body length including the chelicerae, something we explicitly excluded.

The relative predictive power for each of the remaining 18 models was estimated by plotting actual (measured) wet weight against predicted wet weight and calculating the following: (1) R^2 value (Pearson product squared) of fitted linear relationships, (2) slope and (3) intercept. R^2 values were our primary method for comparing among models. After determining which produced the highest R^2 values, we evaluated the other model parameters (slope and intercept). In making the regression plots, we chose the *x*-axis for predicted weight and *y*-axis for measured weight as per the recommendations of Piñeiro et al. (2008). With these axes, slopes greater than 1 indicate that the formula underestimates measured body weight, and slopes less than 1 indicate overestimation. We performed these calculations for three groups of mite taxa separately: Oribatida, Mesostigmata and Prostigmata + Endeostigmata. The Prostigmata + Endeostigmata grouping was used because most members of these groups in our samples were soft-bodied and relatively ovoid in shape. We also tested Prostigmata without Endeostigmata and without both Endeostigmata and the prostigmatan group Heterostigmata, because heterostigmatans are generally much more dorsoventrally flattened compared to other Prostigmata. We then applied all prediction models to the entire mite assemblage to see which model (regardless of the intended target taxon) best predicted body weight for mites in general.

For all of these analyses, we initially plotted the relevant models' predictions in a scatter plot for visual inspection and here show best-fit linear regression lines for the best and worst-performing models for the taxon-specific analyses. For the all-mite analysis, we present the top five best-performing models

on normal and log10 transformed axes. The log10 presentation allows variation in weight in the smaller-bodied mites to be more readily seen. Statistical analyses were performed using Microsoft Excel 2007 for ease of use (direct analysis from spreadsheets), and spot checked in SPSS v17.0 (SPSS Inc., Chicago, Illinois) (all output proved identical). Figures were created either with Microsoft Excel 2007 or Sigma Plot v10.0 (Systat Software, Inc., San Jose, California).

3.3 Results

Our data set included 32 families of mites with body lengths ranging from 110 to 1020 μm (Eriophyidae sp. and *Dorycranosus* sp., respectively) (Table 3.3), distributed relatively evenly across the range (Figure 3.1A). Measured body weights ranged from 0.5 to 203.7 μg (Scutacaridae sp. and *Dorycranosus* sp., respectively), with most mites (61%) weighing less than 30 μg (Figure 3.1B).

When comparing taxon-specific models, oribatid body weight was best predicted by Lebrun (1971), Berthet (1963), Caruso and Migliorini (2009) and Engelmann (1961) by descending R^2 value (Table 3.4). While all models show R^2 values above 0.88 for oribatids, there is a large range in slopes (Figure 3.2A). All slopes were high (>1) showing that the actual weights of oribatids were consistently higher than the models' predictions (i.e. the models underestimated body weights). The model of Lebrun (1971) shows a slope closest to 1 (1.14), although not much different from those of Engelmann (1961) and Berthet (1963) (slopes = 1.16 and 1.17, respectively). Of the three weight prediction models specifically for Mesostigmata, that of Persson and Lohm (1977) had the highest R^2 (0.89); some of the oribatid models applied to our Mesostigmata data had higher R^2 and intercepts closer to 0 than the Persson and Lohm's (1977) model, but none had slopes closer to 1.0. Figure 3.2B shows how closely Persson and Lohm's model follows the 1:1 ratio. Prostigmata data, whether including Heterostigmata and Endeostigmata or not, showed little variation among the three models explicitly designed for Prostigmata. Douce's (1976) model produced the highest R^2 values (0.89–0.91), but it also resulted in the highest slopes (3.12–3.28). Figure 3.2C show the two most extreme slopes. Again, some of the oribatid

models show higher R^2 values and slopes closer to 1.0 when applied to the Prostigmata data. When applying all models to all Acari, the models of Lebrun (1971) and Berthet (1963) share the highest R^2 value (0.97), but Lebrun's slope is closest to one (1.09). Figure 3.2D shows the five best-performing models for all Acari based on R^2 and slope values.

As seen in Figure 3.3, where the log-scale axes place a higher emphasis on the mites in the lower weight range, smaller mites generally fall above the 1:1 line, indicating that their weight is being underestimated.

3.4 Discussion

3.4.1 Most models underestimated actual weight

According to our data, the majority of models underestimate mite weight to a varying degree, particularly for Oribatida. With a few exceptions, most models show a relatively high R^2 (>0.80). Intercepts are generally close to zero, but slopes vary greatly. Most slopes were greater than 1.0, although the few that were less than 1.0 were sometimes so by a large margin. Strong overestimation of weight occurred only when prostigmatid weight was predicted using general oribatid weight prediction models (Rogers et al. 1977; Hódar 1996).

This raises the question of why we found so many models to consistently underestimate actual mite's body weight. There are four possible explanations for this. The simplest is that our microbalance was not calibrated correctly; however, because this microbalance is in a diagnostic laboratory that holds a proficiency laboratory status with the Canadian Association for Laboratory Accreditation and is regularly calibrated, we consider this unlikely.

Secondly, as many of the models were made to predict dry weight, our dry weight to wet weight conversion factor of 2.5 (based on dry weight being on average 0.4 of wet weight, see Table 3.2) may have affected the observed performance of these models. However, a factor of 2.5 is actually *less* likely to produce underestimates of actual weight than most other published dry:wet ratios. These ratios are higher than 0.4 and would result in dry-to-wet factors of less than 2.5, and hence would produce an even lower wet-weight estimate.

Third, we deliberately strove to select a wide range of morphologies; however, it may be that the morphological composition of mites that other authors used to calculate their volume-to-weight conversion factors was markedly different from ours. If, for example, we had used mites of different proportions (e.g. all globular), we may have found a different "best-fit" line from which to derive the conversion factor.

Fourth, since it is not always clear how authors have measured body length and width, and particularly maximum gnathosomal width, it is possible that our measurements have consistently been smaller than those of other authors. Douce (1976, p. 326), for example, took measurements "under a compound microscope", which may have led to squashed mites under cover slips, causing a bias towards larger measurements. On the other hand, Hódar (1996) measured all arthropods using a stereomicroscope with a maximum magnification of 40×, equipped with an ocular micrometer of 50 μm precision. As mites were just a small portion of the regression models developed by Hódar (1996), with the other arthropods being at least an order of magnitude larger than mites, Hódar may have measured mites somewhat more crudely than we did. It is also not always clear what state specimen were in when weight was being determined. This is important because if specimens are initially stored in ethanol or formaldehyde prior to weighing, dry weight may be underestimated due to loss of lipids and other soluble materials that are leached from the tissues (Petersen and Luxton 1982), or quicker evaporation during the "wet-weighing" process.

Lastly, while we attempted to cover the range of body sizes as much as possible, the Oribatida from our samples showed an obvious "gap" between medium and large body sizes. This may have been due to our limited sample size; however, our own experience with the mite fauna of these two localities has shown this to be a real size gap, present also with larger sample sizes. Other habitats or geographic localities may not show this gap. However, Douce (1976) found a similar gap for Oribatida (Cryptostigmata) and Prostigmata, but not for Mesostigmata, which agrees with our oribatid and mesostigmatid distribution.

3.4.2 Oribatid models are best general predictors

Our most surprising result is that most well-performing oribatid weight predicting models did a better job of predicting prostigmatid weight than did the prostigmatid prediction models. Overall, Lebrun's (1971) model for Oribatida seems to work best for all mites that we measured. Lebrun's model not only most accurately predicts body weights when considering all mites at once (Figure 3.2D) but also outperforms almost all models specifically created for other orders and suborders, with the exception of Persson and Lohm's (1977) model for Mesostigmata (Table 3.4). Perhaps tellingly, Persson and Lohm's model is Lebrun's "Nothriform" oribatid model (Table 3.1) with an added correction factor. The models of Berthet (1963), Caruso and Migliorini (2009) and Engelmann (1961) are close seconds for estimating biomass of all our mites; that of Berthet (1963) was in fact the basis for Lebrun's model.

3.4.3 Does the observed variation in weight prediction matter at the community level?

It is clear that not all weight estimate models give comparable predicted weights, possibly meriting some caution when interpreting studies that have utilized some of the models that we observed to perform poorly. However, as mite body-weight is most often used to estimate the biomass contribution of higher taxa mites, or of mites as a whole, to a given soil community, it is important to ask whether variation in models greatly affects the estimated biomass. If authors are comparing biomasses among different groups of mites (most often Oribatida vs. Mesostigmata vs. Prostigmata), the risk is that the biomass of one taxon may be overestimated or underestimated compared to others. If the comparison is "mites" vs. other taxa of soil animals, the risk is of overestimating or underestimating the contribution of Acari to the biomass of all fauna. Based on soil mite abundance data from Clapperton et al. (2002), and using taxa and weights from this article as a crude hypothetical species composition, Figure 3.4 shows potential extremes for biomass estimation for higher taxa of mites. Using the best-predicting models, estimated weights for Oribatida, Mesostigmata and Prostigmata are 88 %, 93 %

and 93 % of "true weight", respectively. However, using the worst predictive models, percentages of "true weight" differed much more: 52 %, 82 % and 61 %. Our results also suggest that small-bodied mites may be particularly prone to underestimation of biomass (Figure 3.3).

If authors are attempting to estimate biomass of all soil arthropods, variation in model predictions will be most important when mites are the dominant organisms. Using data from Clapperton et al. (2002) again, for the average of Oribatida, Mesostigmata and Prostigmata predictions, the best weight prediction produces 91% of the "true" biomass, while the worst on average 69%. This seems like a large difference; however, the predicted biomass stays within the same order of magnitude. Compared to other groups of soil invertebrates (e.g. earthworms, whose biomass may naturally range from 10 to 100 g/m^2 (Coleman et al. 2004)), this difference may be within acceptable limits depending on the focus of the study. For example, data from De Deyn et al. (2003) show that while seemingly numerically insignificant, the biomass of larval Elateridae (click beetles) make them the dominant arthropod group by weight in some Dutch grassland soils. Using abundance and a generalized dry body weight provided by De Deyn et al. (2003), we can calculate dry biomass. If we consider this biomass to be "true", and then apply our best and worst case scenarios ("true" biomass × 0.91 and × 0.69, respectively, as calculated for the Clapperton et al. example above), we can clearly see that the difference in mite biomass estimation is almost negligible relative to some of the other soil invertebrate fauna like the Elateridae larvae (Figure 3.5).

3.4.4. Recommendations

Nonetheless, given that we do observe differences between model estimates, we recommend that authors should explicitly describe the formulae they use for biomass estimation and/or provide references to original literature that contain the formulae. Not doing so risks perpetuating errors or causing confusion. As an example, Streit et al. (1985) do provide formulae for body weight estimation, including references, but use the wrong formula for "Gamasina" because the secondary source of the formula (Persson and Lohm 1977) seems to have been

misinterpreted. In addition, some of the formulae were modified without explaining how or why.

In conclusion, our results show that some established weight-estimation models for mites are fairly robust and work well for the particular grassland and woodland mites included in this study, while other models performed more poorly. Although more research is needed to test how well the models will fare for mites from other habitats and geographic localities, based on our results we recommend using Lebrun's (1971) general Oribatida model for all mites except Mesostigmata, for which Persson and Lohm's (1977) model is most appropriate.

We have shown that even the best-performing models are not ideal; there is still room for improvement, particularly for non-oribatid mite groups. We hope to encourage future studies to use new data to develop novel models, or to improve the parameter estimates of Lebrun's (1971) models, particularly to adapt them for non-oribatid mite groups.

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Table 3.1: List of different models developed to predict mite body weight based on different combinations of length, width and maximum gnathosomal width.

Taxon	Dry weight (DW) or Wet weight (WW)	Formula (left in their original form)	Legend (units are in µg and µm unless otherwise specified)	Reference
Oribatida	WW (inferred, because not specifically noted)	M = L * W * D * C	M = weight, L = length, W = width, D = depth, and C = Conversion constant (not specified)	Macfadyen,1952
Oribatida	DW	Log M = 1.32 * (log L * log W) - 5.87	M = weight, L = length, and W = width	Engelmann 1961*
Oribatida (all, except ptychoid shaped)	WW (inferred, because not specifically noted)	$W = L^{1.58} * l^{1.45} * 10^{-6.61}$	W = weight, L = length, and l = width	Berthet 1963*
Trombidiformes	WW	Y= 3.87 * X	Y = length (mm), X = cubic root wet weight	Edwards 1967*
Oribatidae	WW	Y= 4.92 * X	Y = length (mm), X = cubic root wet weight	Edwards 1967*
Parasitidae	WW	Y= 3.95 * X	Y = length (mm), X = cubic root wet weight	Edwards 1967*
Uropodina	WW	Y= 3.53 * X	Y = length (mm), X = cubic root wet weight	Edwards 1967
Oribatida (all, except ptychoid shaped)	WW	log P = 1.53 * log L + 1.53 * log l - 6.67	P = weight, L = length, l = width	Lebrun 1971*
Oribatida "Achipteriform"	WW	log P = 2.09 * log L + 0.93 * log l - 6.67	P = weight, L = length, l = width	Lebrun 1971
Oribatida "Carabodiform"	WW	log P = 1.62 * log L + 1.40 * log l - 6.56	P = weight, L = length, l = width	Lebrun 1971
Oribatida "Nothriform"	WW	log P = 2.09 * log L + 0.84 * log l - 6.44	P = weight, L = length, l = width	Lebrun 1971
Steganacarus magnus (Oribatida)	WW	$W = 137L^3 - 15$	W = weight, L = length (mm)	Elmes and Webb 1972
Oribatida	DW	Y = 156.33 X - 1.31 (if Y < 0.72, than the alternative is suggested: $\log_e Y = 1.5 \log_e X + 6.11$)	Y = weight, X = the product of maximum gnathosomal width and maximum body width (mm2)	Douce 1976
Mesostigmata	DW	Y = 150.27 X - 2.32	Y = weight, X = maximum body length x maximum gnathosomal width (mm^2)	Douce 1976*

(*Continued*)

Table 3.1. (*Continued*).

Taxon	Dry weight (DW) or Wet weight (WW)	Formula (left in their original form)	Legend (units are in µg and µm unless otherwise specified)	Reference
Prostigmata	DW	Y = 19.26 X + 0.04	Y = weight, X = maximum body length x maximum body width (mm^2)	Douce 1976*
Mesostigmata (modified from Lebrun 1971's nothriform)	WW	log P = 0.85 * (2.09 * log L + 0.84 * log l - 6.44)	P = weight, L = length, l = width	Persson and Lohm 1977*
All mites > 300µm in length	DW	ln (Wt) = 3.682 + 2.761 ln (length)	Wt = weight, length in mm	Rogers et al. 1977*
Oribatida	DW	ln (Wt) = 3.944 + 2.790 ln (length)	Wt = weight, length in mm	Rogers et al. 1977*
Prostigmata, and Astigmata > 300µm in length	DW	ln (Wt) = 2.897 + 2.210 ln (length)	Wt = weight, length in mm	Rogers et al. 1977*
Mesostigmata	DW	Dry weight = 0.13029 + (42.9481 * $length^3$)	Length = length of dorsal shield	Walter and Ikonen 1989*
Acari	DW	$W = 0.053 * L^{2.494}$	W = weight, L = length	Hódar 1996*
Acari	WW	log Mµg = 2.117 + 2.711 * log x	Mµg = weight, x = length in mm	Mercer et al. 2001*
Oribatida	WW	log Mµg = 2.146 + 2.770 * log x	Mµg = weight, x = length in mm	Mercer et al. 2001*
Astigmata	WW	log Mµg = 2.143 + 2.550 * log x	Mµg = weight, x = length in mm	Mercer et al. 2001
Mesostigmata	WW	log Mµg = 2.064 + 2.857 * log x	Mµg = weight, x = length in mm	Mercer et al. 2001
Prostigmata	WW	log Mµg = 2.124 + 2.808 * log x	Mµg = weight, x = length in mm	Mercer et al. 2001*
Oribatida	WW	log M = 3 * log [L + W] - 17.17	M = weight, [L + W] is a function of length and width (see ref.)	Caruso and Migliorini 2009*

Models are in their original format, so abbreviations for the same parameters may vary. Models are listed in order of year of publication. Those tested in this paper are indicated by an asterisk after the reference.

Table 3.2: Average proportion dry weight for major mite taxa as reported by different authors, listed by year of publication.

Taxon	Proportion dry weight	Reference
Based on Oribatida and Mesostigmata	0.42	Block 1966
Prostigmata	0.48	Edwards 1967
Oribatida	0.41	Edwards 1967
Mesostigmata	0.40	Edwards 1967
Uropodina	0.43	Edwards 1967
Oribatida	0.47	Luxton 1975
All Acari	0.40	Persson and Lohm 1977
Mesostigmata	0.45	Walter and Ikonen 1989

Table 3.3: Identity and measurements of mites used in this study.

Order or Suborder	Family	Genus and species[1]	Life stage/sex	Length	Width	Wet weight	Gnathosomal width
Oribatida	Ceratozetidae	*Ceratozetes gracilis* (Michael, 1884)*	female	590	410	34.6	-
Oribatida	Damaeidae	*Epidamaeus* sp.	female	480	370	29.6	-
Oribatida	Eremaeidae	*Eueremaeus masinasin* Behan-Pelletier, 1993	female	490	260	12.7	-
Oribatida	Eremaeidae	*Eueremaeus masinasin* Behan-Pelletier, 1993	male	465	250	11.8	-
Oribatida	Eremaeidae	*Eueremaeus masinasin* Behan-Pelletier, 1993	male	460	250	12	-
Oribatida	Eremaeidae	*Eueremaeus masinasin* Behan-Pelletier, 1993	male	460	240	10.2	-
Oribatida	Galumnidae	*Pergalumna* sp.1 DEW	male	520	400	42	-
Oribatida	Gymnodamaeidae	*Gymnodamaeus ornatus* Hammer, 1952*	female	720	400	45.9	-
Oribatida	Gymnodamaeidae	*Gymnodamaeus* sp.*	female	600	380	36.8	-
Oribatida	Haplozetidae	*Peloribates* sp.4 DEW	male	400	250	9.8	-
Oribatida	Liacaridae	*Dorycranosus* sp.4 DEW*	female	790	570	105.7	-
Oribatida	Liacaridae	*Dorycranosus* sp.4 DEW*	female	1020	650	203.7	-
Oribatida	Liacaridae	*Dorycranosus* sp.4 DEW*	female	860	540	114.8	-
Oribatida	Nothridae	*Nothrus* sp.*	female	740	320	45	-
Oribatida	Nothridae	*Nothrus* sp.*	female	780	400	49.1	-
Oribatida	Nothridae	*Nothrus* sp.*	female	800	400	53.3	-
Oribatida	Nothridae	*Nothrus* sp.*	female	780	395	51.9	-
Oribatida	Oribatellidae	*Oribatella* sp.	male	390	230	10.4	-
Oribatida	Oribatulidae	*Oribatula* sp.1 DEW*	male	440	270	12.5	-
Oribatida	Oppiidae	not identified	-	250	130	2	-
Oribatida	Oppiidae	*Oppiella* sp.	female	250	120	1.6	-
Oribatida	Oppiidae	*Oppiella* sp.	female	240	150	2	-
Oribatida	Oppiidae	*Ramusella* sp.	female	245	125	2.6	-
Oribatida	Oppiidae	*Ramusella* sp.	female	230	120	1.9	-
Oribatida	Tectocepheidae	*Tectocepheus sarekensis* Trägårdh, 1910	female	270	170	3.9	-
Oribatida	Tectocepheidae	*Tectocepheus sarekensis* Trägårdh, 1910	female	290	180	2.2	-
Oribatida	Tectocepheidae	*Tectocepheus sarekensis* Trägårdh, 1910	female	290	165	3.8	-

(*Continued*)

Table 3.3. (*Continued*).

Order or Suborder	Family	Genus and species[1]	Life stage/sex	Length	Width	Wet weight	Gnathosomal width
Oribatida	Tectocepheidae	*Tectocepheus velatus* (Michael, 1880)	female	310	180	3.8	-
Oribatida	Trhypochthoniidae	*Trhypochthonius tectorum* (Berlese, 1896)	female	530	290	14.9	-
Oribatida	Enarthronota	not identified	-	180	90	0.7	-
Oribatida	not identified	not identified	nymph	290	200	2.2	-
Oribatida (Astigmata)	Acaridae	*Tyrophagus* sp.	female	210	100	2	-
Oribatida (Astigmata)	Acaridae	*Tyrophagus* sp.	female	380	200	8	-
Oribatida (Astigmata)	Acaridae	*Tyrophagus* sp.	female	390	210	8.8	-
Oribatida (Astigmata)	Acaridae	*Tyrophagus* sp.	female	420	200	8.1	-
Mesostigmata	Ascidae	not identified	male	260	160	2.9	62.5
Mesostigmata	Ascidae	*Arctoseius* sp.	female	340	110	4.5	72.5
Mesostigmata	Ascidae	*Asca* cf. *piloja* Hurlbutt, 1963	male	225	150	3.2	62.5
Mesostigmata	Eviphididae	*Copriphis* sp.	female	440	250	11.6	85
Mesostigmata	Eviphididae	*Copriphis* sp.	nymph	340	280	6.1	87.5
Mesostigmata	Eviphididae	*Copriphis* sp.	female	500	380	15.9	95
Mesostigmata	Eviphididae	*Copriphis* sp.	male	410	310	9.7	87.5
Mesostigmata	Laelapidae	not identified	nymph	560	340	31.7	112.5
Mesostigmata	Laelapidae	*Cosmolaelaps* sp. *claviger* group	female	460	240	12.8	95
Mesostigmata	Laelapidae	*Gaeolaelaps* sp.	female	470	170	8.2	112.5
Mesostigmata	Laelapidae	*Ololaelaps* sp.	female	710	450	47.3	145
Mesostigmata	Laelapidae	*Ololaelaps* sp.	female	680	470	61.1	142.5
Mesostigmata	Rhodacaridae	*Rhodacarellus* sp. nr. *subterraneus* Willman, 1935	female	260	110	1.3	67.5
Mesostigmata	Trachyuropodidae	*Trachyuropoda kinsella* Kontschán, 2010	female	750	430	53.4	-
Mesostigmata	Trachyuropodidae	*Trachyuropoda kinsella* Kontschán, 2010	male	740	430	40.4	-
Mesostigmata	Zerconidae	*Zercon* sp.	female	350	220	20.5	120
Mesostigmata	Zerconidae	*Zercon* sp.	female	530	370	22.5	125
Mesostigmata	Zerconidae	*Zercon* sp.	female	535	370	18.8	122.5
Prostigmata	Bdellidae	not identified	larva	250	110	1.3	-
Prostigmata	Bdellidae	*Bdella* sp.	-	560	280	22	-

(*Continued*)

Table 3.3 (*Continued*).

Order or Suborder	Family	Genus and species[1]	Life stage/sex	Length	Width	Wet weight	Gnathosomal width
Prostigmata	Bdellidae	*Bdella* sp.	-	640	310	32.9	-
Prostigmata	Eupodidae	*Eupodes* sp.	-	210	80	2.9	-
Prostigmata	Ereynetidae	not identified	nymph	260	130	2.2	-
Prostigmata	Erythraeidae	Abrolophis	larva	290	80	3.2	-
Prostigmata	Eriophyidae	not identified	female	110	50	1.4	-
Prostigmata	Rhagidiidae	not identified	female	550	180	8.9	-
Prostigmata	Rhagidiidae	*Coccorhagidia* sp.	-	530	170	7.1	-
Prostigmata/ Heterostigmata	Scutacaridae	not identified	-	160	120	1	-
Prostigmata/ Heterostigmata	Scutacaridae	not identified	-	190	130	1.3	-
Prostigmata/ Heterostigmata	Scutacaridae	not identified	-	180	140	1.3	-
Prostigmata/ Heterostigmata	Scutacaridae	not identified	-	160	110	0.5	-
Prostigmata/ Heterostigmata	Scutacaridae	not identified	-	213	143	1.2	-
Prostigmata/ Heterostigmata	Scutacaridae	not identified	-	190	115	2	-
Prostigmata/ Heterostigmata	Tarsonemidae	not identified	-	160	90	1.2	-
Prostigmata/ Heterostigmata	Tarsonemidae	not identified	-	150	80	1.2	-
Prostigmata/ Heterostigmata	Tarsonemidae	not identified	-	133	83	0.6	-
Prostigmata	Tetranychidae	*Bryobia* sp.	-	350	190	3.4	-
Prostigmata	Tetranychidae	*Bryobia* sp.	-	310	170	2.2	-
Prostigmata	Tydeidae	not identified	-	300	190	3.8	-
Endeostigmata	Nanorchestidae	*Nanorchestes* sp.*	-	470	330	18.7	-
Endeostigmata	Nanorchestidae	*Nanorchestes* sp.*	-	540	305	16.5	-
Endeostigmata	Nanorchestidae	*Nanorchestes* sp.*	-	560	380	34.2	-
Endeostigmata	Nanorchestidae	*Nanorchestes* sp.*	-	520	300	29.9	-

Notes: Life stage and sex are reported when known. All mites were adults unless noted otherwise. Length and width in µm, weight in µg. An asterisk (*) after a species name indicates that individuals were collected at a mixed deciduous-coniferous forest; other mite taxa were collected in native fescue grassland (see Materials and Methods).

[1]'DEW' indicates undescribed species included in the keys of Walter et al. (2011).

Table 3.4: Results of regressing observed values onto the predictions for various published models of mite biomass (slope, intercept, R2). Shaded cells indicate values for models not originally intended for that taxon. Boxes highlight the five highest R2 values per mite grouping. Abbreviations indicate what taxon the model was originally intended for: O = Oribatida (including Astigmata), M = Mesostigmata, P = Prostigmata, A= Astigmata.

	Oribatida			Mesostigmata			"Prostigmata" (including Heterostigmata and Endeostigmata)			Prostigmata (including Heterostigmata but not Endeostigmata)			Prostigmata (excluding Heterostigmata and Endeostigmata)			Acari (all)		
Model	Slope	Intercept	R^2	Slope	Intercept	R^2	Slope	Intercept	R^2	Slope	Intercept	R^2	Slope	Intercept	R^2	Slope	Intercept	R^2
Engelmann 1961 (O)	1.16	-5.51	**0.97**	*0.78*	*0.07*	***0.89***	*0.92*	*-0.71*	***0.94***	*0.92*	*-0.69*	***0.95***	*0.95*	*-1.19*	***0.95***	*1.07*	*-3.81*	***0.95***
Berthet 1963 (O)	1.17	-1.63	**0.99**	*0.86*	*1.99*	***0.90***	*1.14*	*-0.02*	***0.94***	*1.14*	*-0.04*	***0.97***	*1.15*	*-0.33*	***0.97***	*1.12*	*-0.98*	***0.97***
Edwards 1967 (O)	1.41	-2.58	0.91	*1.06*	*2.33*	*0.85*	*1.04*	*0.40*	*0.78*	*0.83*	*0.26*	*0.85*	*0.86*	*-0.21*	*0.82*	*1.34*	*-1.71*	*0.90*
Edwards 1967 (P)	*2.89*	*-2.58*	*0.91*	*2.17*	*2.33*	*0.85*	2.13	0.40	0.78	1.71	0.26	0.85	1.76	-0.21	0.82	*2.75*	*-1.71*	*0.90*
Edwards 1967 (M)	*2.72*	*-2.58*	*0.91*	2.50	0.09	0.87	*2.00*	*0.40*	*0.78*	*1.61*	*0.26*	*0.85*	*1.65*	*-0.21*	*0.82*	*2.59*	*-1.71*	*0.90*
Lebrun 1971 (O)	1.14	-1.28	**0.99**	*0.84*	*2.11*	***0.90***	*1.13*	*0.05*	***0.94***	*1.14*	*0.00*	***0.97***	*1.16*	*-0.24*	***0.97***	*1.09*	*-0.72*	***0.97***
Douce 1976 (M)	*n/a*	*n/a*	*n/a*	1.56	-1.33	0.86	*n/a*	*n/a*	*n/a*	*n/a*	*n/a*	*n/a*	*n/a*	*n/a*	*n/a*	*n/a*	*n/a*	*n/a*
Douce 1976 (P)	*5.55*	*-15.32*	*0.93*	*3.38*	*-4.97*	*0.87*	3.26	-2.90	0.91	3.12	-2.67	0.90	3.28	-3.60	0.89	*4.82*	*-10.63*	*0.88*
Persson and Lohm 1977 (M)	*1.37*	*-3.13*	***0.96***	0.99	1.62	**0.89**	*1.18*	*-0.29*	***0.91***	*1.06*	*-0.11*	***0.94***	*1.09*	*-0.63*	***0.93***	*1.30*	*-2.06*	***0.95***
Rogers et al. 1977 Acari	1.65	-4.69	0.90	1.20	1.00	0.86	1.10	0.03	0.78	0.88	0.00	0.83	0.92	-0.61	0.80	1.55	-3.33	0.88
Rogers et al. 1977 (O)	1.28	-4.42	0.90	*0.93*	*1.17*	*0.86*	*0.86*	*0.08*	*0.78*	*0.69*	*0.04*	*0.84*	*0.71*	*-0.55*	*0.81*	*1.20*	*-3.12*	*0.88*
Rogers et al. 1977 (P+A)	*3.47*	*-11.13*	*0.86*	*2.35*	*-3.13*	*0.86*	1.84	-1.16	0.77	1.47	-0.87	0.80	1.56	-1.89	0.77	*3.10*	*-8.02*	*0.84*
Hódar 1996 Acari	1.21	-7.48	0.88	0.85	-0.79	0.86	0.72	-0.47	0.77	0.58	-0.36	0.82	0.61	-1.15	0.79	1.11	-5.40	0.86
Walter and Ikonen 1989 (M)	*1.56*	*-3.09*	*0.91*	1.17	2.00	0.85	*1.50*	*0.03*	*0.78*	*0.92*	*-0.04*	*0.85*	*0.95*	*-0.52*	*0.81*	*1.49*	*-2.19*	*0.90*
Mercer et al. 2001 Acari	1.25	-5.17	0.89	0.90	0.69	0.86	0.82	-0.06	0.78	0.65	-0.06	0.83	0.68	-0.70	0.80	1.17	-3.69	0.88
Mercer et al. 2001 (O)	1.18	-4.60	0.90	*0.85*	*1.05*	*0.86*	*0.79*	*0.05*	*0.78*	*0.63*	*0.01*	*0.83*	*0.65*	*-0.59*	*0.81*	*1.10*	*-3.26*	*0.88*
Mercer et al. 2001 (P)	*1.24*	*-4.25*	*0.90*	*0.90*	*1.28*	*0.86*	0.84	0.11	0.78	0.68	0.06	0.84	0.70	-0.52	0.81	*1.17*	*-2.99*	*0.89*
Caruso and Migliorini 2009 (O)	1.18	-2.36	**0.98**	*0.87*	*1.73*	***0.89***	*1.08*	*-0.21*	***0.92***	*0.99*	*-0.07*	***0.94***	*1.02*	*-0.55*	***0.93***	*1.13*	*-1.55*	***0.96***

Notes: Italicized text indicates values for models not originally intended for that taxon. Bold values highlight the five highest R^2 values per mite grouping. Abbreviations indicate what taxon the model was originally intended for: O = Oribatida (including Astigmata), M = Mesostigmata, P = Prostigmata, A = Astigmata.

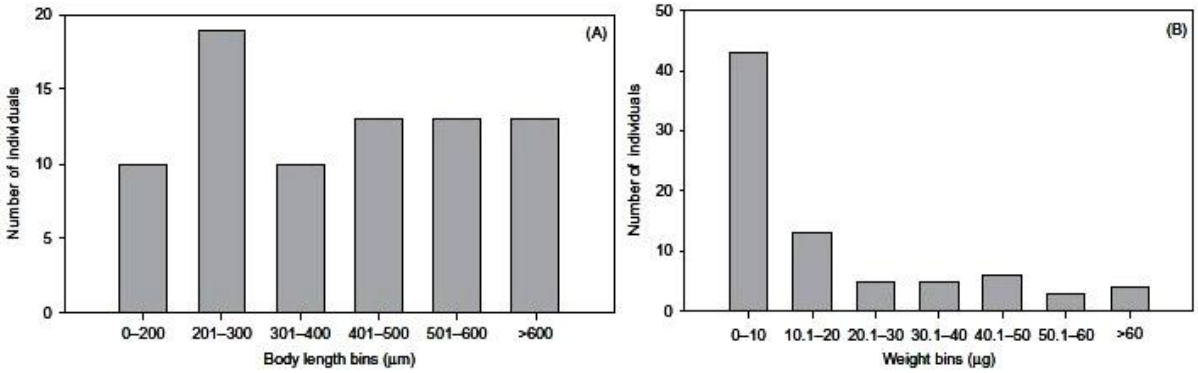
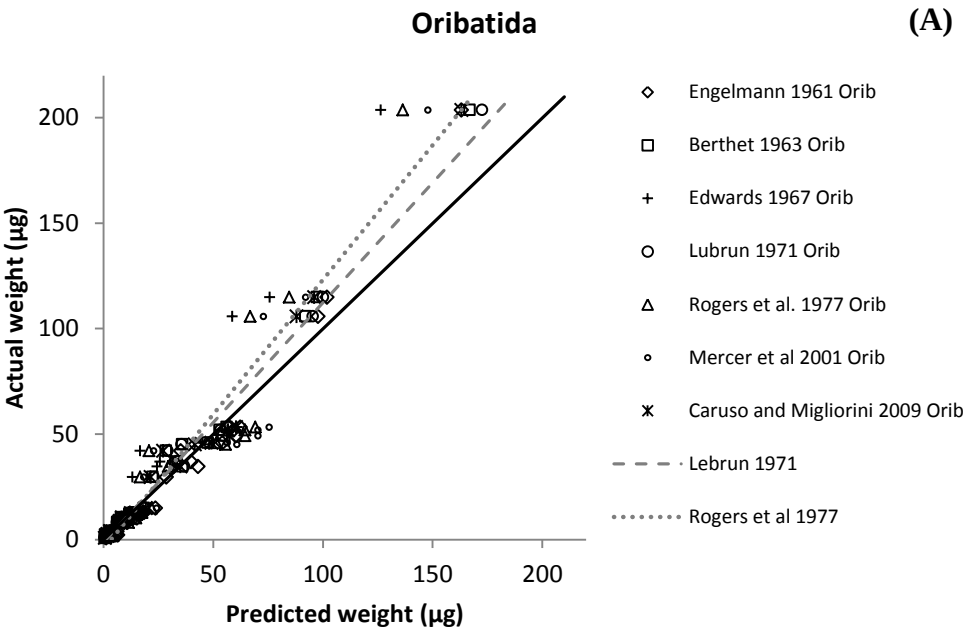
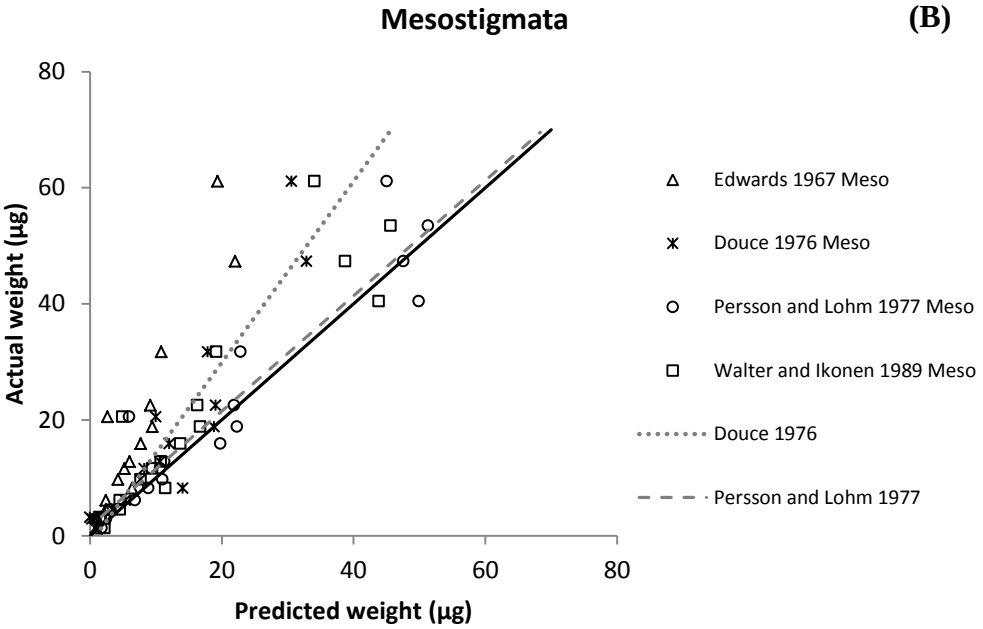
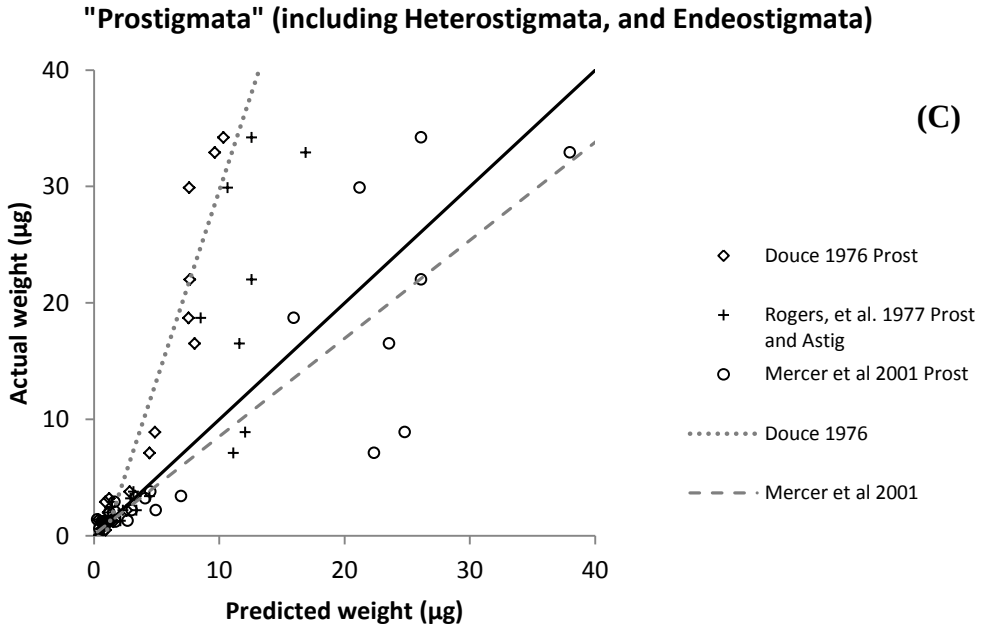


Figure 3.1: Histograms of (A) body lengths and (B) weights of mites used in the present study.


Oribatida
(A)
Actual weight (µg)
Predicted weight (µg)
0
50
100
150
200
Engelmann 1961 Orib
Berthet 1963 Orib
Edwards 1967 Orib
Lubrun 1971 Orib
Rogers et al. 1977 Orib
Mercer et al 2001 Orib
Caruso and Migliorini 2009 Orib
Lebrun 1971
Rogers et al 1977


Mesostigmata
(B)
Actual weight (µg)
Predicted weight (µg)
0
20
40
60
80
Edwards 1967 Meso
Douce 1976 Meso
Persson and Lohm 1977 Meso
Walter and Ikonen 1989 Meso
Douce 1976
Persson and Lohm 1977



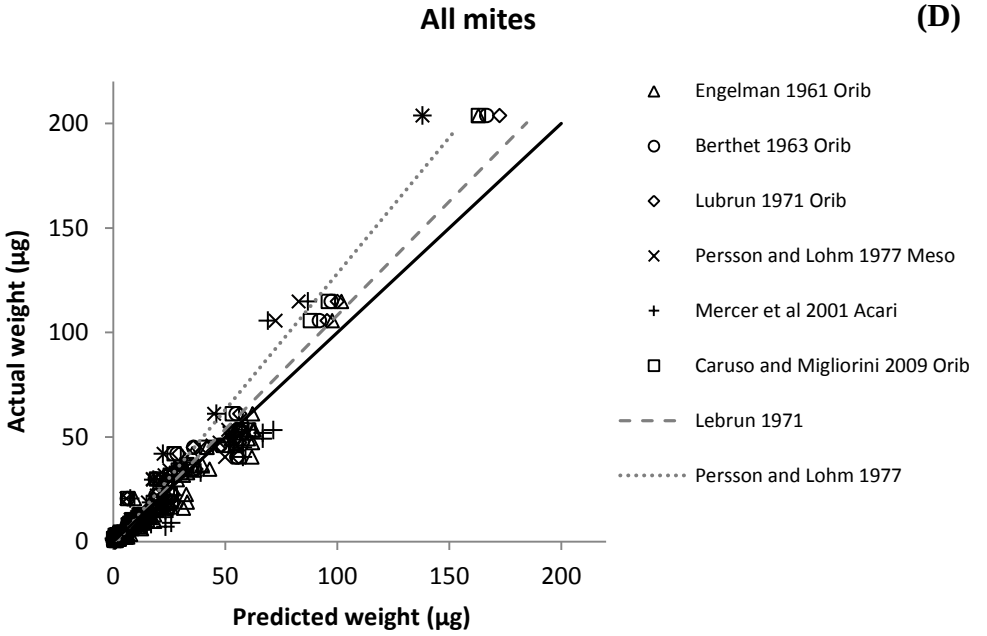


Figure 3.2: Scatter plot of predicted weight (based on length and width measurements – see Material and Methods section) versus actual weight (measured by us) for (A) Oribatida, (B) Mesostigmata, (C) "Prostigmata", including Heterostigmata and Endeostigmata (i.e. nonoribatid Acariformes), and

(D) all mites. (A–C) Regression lines for the best- and worst-performing models (see Materials and Methods). (D) Regression lines for the two best-performing models. Solid line is 1:1.

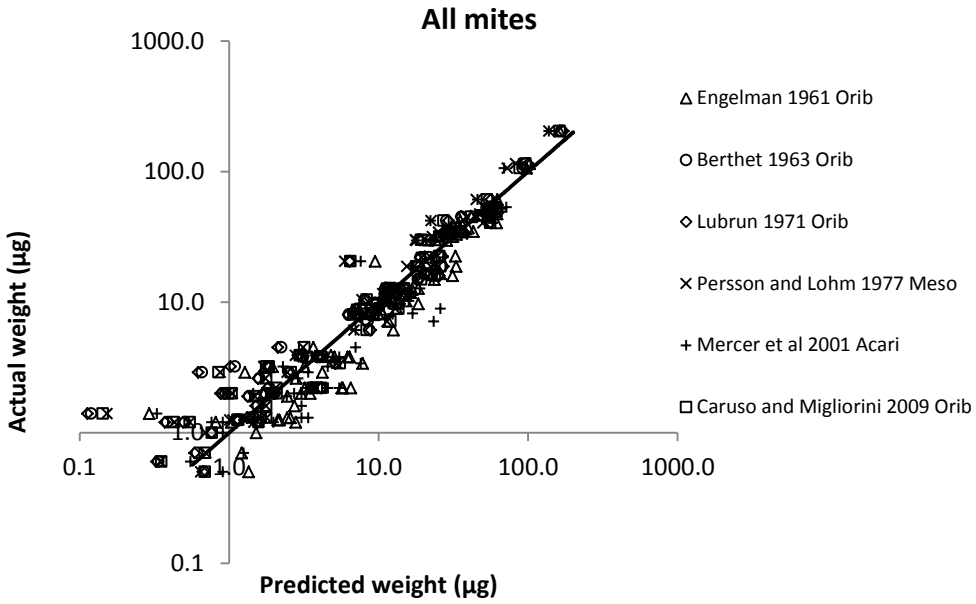


Figure 3.3: Scatter plot of predicted weight based on length and width measurements (see Materials and Methods) versus actual weight for all mites weighed in this study. Axes are logarithmically scaled. Lighter mites show a higher degree of weight underestimation. Solid line is 1:1.

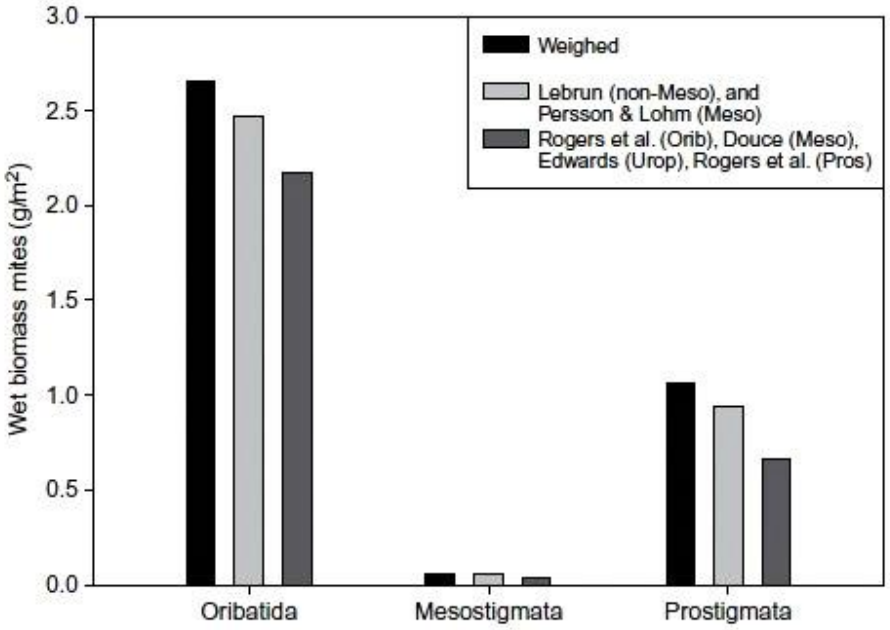


Figure 3.4: Biomass estimates using taxon-specific abundance data from Clapperton et al. (2002) of a fictional species composition (based on species we weighed) to show differences between biomass based on our wet weights (black bars), and biomass estimates from the best- (light grey) and worst-performing (dark grey) models for different mite taxa. Abbreviations of mite taxa in parentheses represent which model is used for which taxon, e.g. "Rogers et al. (Orib)" refers to the Rogers et al.'s (1977) model for Oribatida, applied to Oribatida. Only Lebrun's model is used for all taxa.

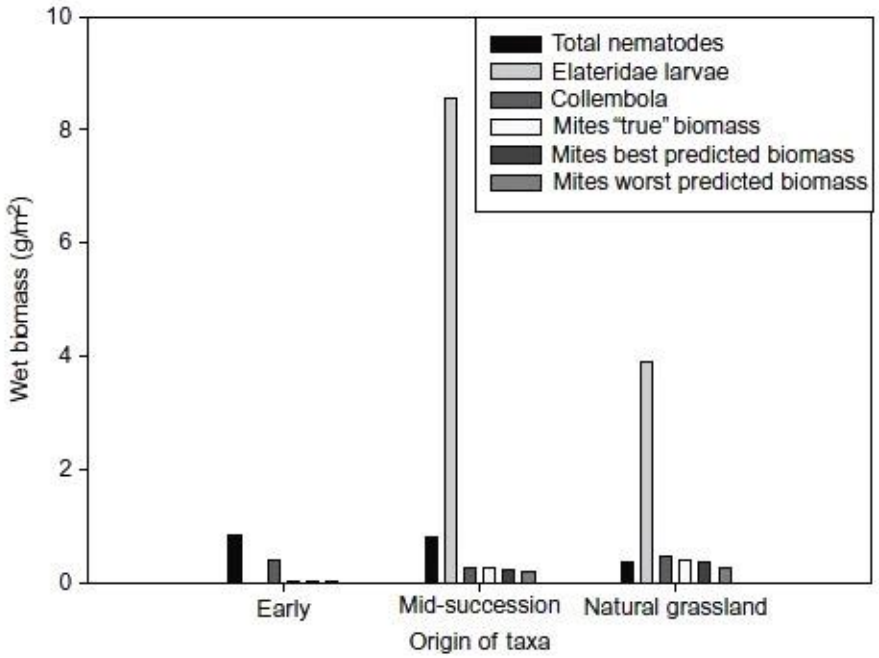


Figure 3.5: Biomass calculated using Dutch grassland successional data from De Deyn et al. (2003), and using our data as a hypothetical soil mite assemblage to predict biomass using the best and worst models as a comparison (see Discussion).

Chapter 4: Short-term drought disturbance stimulates abundance and biomass of mites (Arachnida: Acari)

4.1 Introduction

Mites can be found in almost all imaginable habitats and fill a wide range of ecological roles (Walter and Proctor, 1999). In soil, mites can be predatory, phytophagous, bacterivorous, fungivorous, saprophagous, and often omnivorous (Walter and Proctor, 1999; Krantz and Walter, 2009). They can function as modulating links in the belowground food web by suppressing particular fungi through feeding, distributing fungal spores, and fragmenting leaf litter to create more surface area for microbes, thereby stimulating decomposition (Coleman et al., 2004; Lilleskov and Bruns, 2005). However, while mites are very species rich and are the most abundant microarthropods in many soils, like other soil-dwelling biota, their diversity and abundance are susceptible to environmental stresses that affect the soil (Lindberg, 2003; Tsiafouli et al., 2005).

Grasslands regularly experience disturbance and stresses in the form of fire, grazing, drought, and flooding. In light of rapidly changing global climates, some grasslands are expected to experience longer and more intense periods of drought conditions, and more extreme high temperatures that could further exacerbate these stresses (Biello, 2007; IPCC, 2007). Mites can be the dominant microarthropod group in grassland soils (Seastedt, 1984; Bardgett, 2005, p. 35). Considering that grasslands cover a large part of the earth's surface (40% of dry land; World Resources Institute), and are an important economic resource, e.g. for cattle grazing, it is important to know how climate-related stresses influence soil mites that themselves affect ecological processes in grasslands.

The dominant stress on grassland soil fauna is low precipitation, which affects soil moisture content. Previous research has shown that drought generally reduces mite abundances and species richness (Ford, 1938; Wauthy and Vannier, 1988; Berg et al., 1998; Lindberg et al., 2002; Taylor and Wolters, 2005; Gergocs and Hufnagel, 2009), although it has been found that for drought-adapted

grassland mites, addition of water through irrigation may reduce abundances (O'Lear and Blair, 1999). It can be difficult to determine from the literature what mite taxa are driving responses to changes in soil moisture availability, because mites are often only identified to the very coarse category of "suborder", i.e., Mesostigmata, Oribatida, Prostigmata. Experimental warming of soil has had mixed effects on mite abundance, with some studies showing a positive response, some a negative one, but most no significant response at all (Sjursen et al., 2005; Bokhorst et al., 2008; Briones et al., 2009). Prolonged extreme heat (in combination with lowered soil water content) will cause most mites to migrate; this behaviour is the operational basis of Tullgren/Berlese extractors (Edwards, 1991). Grazing by livestock can decrease mite abundance (Kay et al., 1999; Battigelli et al., 2003), but this can vary according to the dominant mite taxon (Clapperton et al., 2002). Grazing probably influences mite abundances indirectly through altering soil bulk-density and moisture, and possibly the physiology and composition of the vegetation (Bardgett et al., 1998; Clapperton et al., 2002).

To date, the majority of studies on soil microarthropod fauna discussed above have utilized Tullgren or high gradient extractors to extract animals from soil samples. It has long been known that these extraction methods, which rely on desiccation to drive microarthropods out of the soil, can vary greatly in extraction efficiency and in taxon bias (McSorley and Walter, 1991). Samples from semi-arid to arid soil from grasslands may be particularly susceptible to this bias, because some resident taxa may be specifically adapted to heat and drought and will not respond behaviourally to drying soil in funnels. As an alternative, flotation extraction, although more labour intensive, may be more appropriate for getting a complete picture of soil fauna from dry grasslands (Walter et al., 1987).

Alberta (Canada) is one of the few places that still harbour native fescue grasslands. As discussed by Desserud et al. (2010), the area of this threatened community type has been reduced by 83% by human activities since European settlement of the area. In light of climate change, which predicts more extreme weather conditions (Shen et al., 2005; CCCma, 2012), we wanted to test what type of effect short term disturbance in the form of summer drought, summer

warming, and defoliation (to emulate grazing pressure, albeit minus soil compaction) would have on mite assemblages in this increasingly shrinking grassland community. We hypothesized that short-term drought would alter assemblage structure of the mites in favour of drought-adapted taxa. Based on previous studies, we did not expect a significant effect of warming alone on mite abundance, biomass, or taxon richness, but considered an interaction between warming and the other treatments to be likely. Lastly, we expected that defoliation might have a positive effect on mite abundance and biomass, due to increased output of root exudates (Bertin et al., 2003). Because our study site was relatively arid locally, we used kerosene extraction to ensure that even those mites that do not respond behaviourally to drying soil would be adequately sampled.

In some cases, abundance data can be insufficient to completely understand soil faunal responses in an ecological context (Saint-Germain et al., 2007). Therefore, to more fully interpret mite population responses, we also tested whether mite biomass was affected by the treatments, and whether those results correlate with abundance data.

4.2 Materials and Methods

4.2.1 Field site

Research was conducted at the University of Alberta Research Ranch in Kinsella, Alberta, Canada (53º01.20N, 111º32.35W). The area consists of native fescue grassland, within aspen parkland, which is geographically positioned between grasslands to the southeast and boreal forest to the northwest. A description of the area's soil and vegetation is provided by Attaeian (2010) and Newton *et al.* (2011). The study site was situated on a gently sloping hilltop facing east. The soil has never been tilled and the grassland has only been lightly grazed.

4.2.2 Treatments

Our treatments started in the first week of May 2007 ending in the second week of August 2007, effectively lasting a little over 3 months. The short field season is

characteristic for this climate, and is contingent on time of snowmelt in spring and the cooling temperatures in fall.

Treatments included two levels of defoliation, one level of warming, one level of drought, and controls. The original experimental design was fully factorial with five replicates (blocked) for a total of 60 plots. However, for this study only two blocks were used, resulting in 24 plots. With this limited sample size, we did not apply the full factorial model, and instead analysed the three treatment categories (temperature, defoliation, and precipitation) separately. For the defoliation treatments we used a lawn mower and shears to cut vegetation to the height of 3 and 7 cm to simulate low- and high-intensity grazing, respectively. The warming treatment was applied using open-top chambers (Figure 4.1A), which increased the ambient air temperature by 2-4 degrees during the day (Bork et al., 2008). Drought treatment plots were covered by rainout shelters. Control plots were covered by sham shelters that allowed all precipitation to fall through. Shelters were constructed of lumber anchored down using rebar, and topped by plastic sheeting (Dura-Film Super 4™ 6-mil polyethylene film; AT Plastics, Edmonton, Alberta, Canada) with different sized slits (Figure 4.1B). The slits allowed either 100% rain through or approximately 50% for drought treatments. Soil moisture was highly variable, but drought-treatment plots had an average of approximately 8-13% volumetric water content, while controls had 21-26% (Bork et al., 2008).

4.2.3 Sampling and mite extraction

Soil mite sampling was done on the 7 August 2007. Soil cores were all taken on the same day using a rubber mallet to pound PVC pipes measuring 10 cm long and 5 cm across (47 mm bore diameter) into the soil. Following the coring, the samples were transferred to jars containing 80% ethanol for preservation. A single core was taken per plot.

Soil microarthropods were extracted using kerosene flotation. This extraction method was a modified version of the hexane flotation method (Walter et al., 1987; Proctor, 2001), and relies on the physical affinity between arthropod

cuticle and hydrocarbons. Soil cores were first broken up manually and rinsed over a 150 μm sieve. Samples were transferred to a 500 mL Erlenmeyer flask and submerged in 70% ethanol with a small amount of kerosene added. The Erlenmeyer was then stoppered and gently rolled and shaken for 1 minute in order to coat suspended microarthropods with kerosene. The sample was uncorked and put in a vacuum chamber for 15 min. The vacuum removed much of the air bubbles locked in the vegetation, thereby reducing the amount of plant debris in the final extraction. After 15 minutes, the Erlenmeyer was gently tapped by hand to dislodge the air bubbles that had formed in the solution. The sample was again placed in the vacuum chamber for another 15 minutes. Material accumulated at the ethanol-kerosene interface was then siphoned off, rinsed with 95% ethanol (to remove kerosene residues), and then stored in 80% ethanol. Each soil sample was run through this procedure three times to produce a yield of > 80% of all soil microarthropods contained within the original soil core (unpublished data). If floated samples still contained a lot of non-arthropod debris, a consecutive float was done on the refined sample using 80% ethanol. This higher concentration of ethanol causes less non- microarthropod organic matter to float up and thus produces a cleaner sample.

While more labour intensive, the flotation method produces very high yields of microarthropods and shows less taxonomic bias than traditional Berlese/Tullgren extractors for sandy (not richly organic) soil (Walter et al., 1987). Kerosene flotation also made it possible to store samples for long periods of time, removing constraints of time and the number of extractors available.

4.3.4 Identification and body size estimation

Mites were identified using Krantz and Walter (2009), the Almanac of Alberta Oribatida (Walter et al., 2011), unpublished keys from the Ohio State University's summer acarology course, and an unpublished key to Astigmata by B.M. OConnor (University of Michigan). For identification, mites were cleared in 85% lactic acid (when needed) and mounted in polyvinyl alcohol medium (6371A, BioQuip Products, Rancho Dominguez, California). Slides were placed

on a 40ºC slide warmer for a minimum of 4 days. Once cured, each slide was examined using a Leica DMLB compound microscope with differential interference contrast at 200-400x magnification. For data analysis most taxa are identified to genus or species level except for Prostigmata, which are identified to family. Some prostigmatid mite families were sub sampled and identified to genus for biological interpretation of the results. For analysis at the traditional "suborder" level for mites (Oribatida, Prostigmata, Mesostigmata), we separated Astigmata from Oribatida and Heterostigmata from the Prostigmata (except in the taxon richness analysis). This was done because Astigmata and Heterostigmata are functionally distinct from most of the rest of their respective suborders in having dispersal stages associated with larger-bodied arthropods, and therefore may show different sensitivities to the treatments. Endeostigmata, while included in the analysis of "all Acari", are mostly excluded from further analyses because of their extremely low abundance in our samples.

Mites were counted using Leica MZ6 (max 40x) and MZ16 (max 115x) dissecting stereomicroscopes. Very small mites (<200µm) (juvenile Prostigmata, Tydeidae, Brachychthoniidae, juvenile Astigmata, Heterostigmata, and Endeostigmata), which were very numerous were exhaustively counted but were sub-sampled for identification. Sub-sampling was done for counts of > 40 very small mites by mounting and identifying approximately one quarter of the total number of mites in a sample. Mite selection for sub-sampling was by drawing an "x" on the Petri dish containing the haphazardly scattered sample, and counting and identifying the mites in one of the four quarters of the dish created by the "x". Counting started from the center, until the desired number of mites was collected.

Biomass for all acariform mites (non-Mesostigmata) was calculated using Lebrun's (1971) formula intended for oribatid mites, which works well for most other mite groups (Newton and Proctor, 2013). Mesostigmatan biomass was calculated using Person and Lohm's (1977) formula. Average length and width were determined from slide mounts using a Leica DMLB differential interference contrast (DIC) microscope at 400x magnification which produces an effective maximum resolution of 2.5 µm. When enough specimens were available, 5 to 10

haphazardly selected individuals were measured per taxon (occasionally this included a male or juvenile). Length measurements of mites were taken as described by Newton and Proctor (2013). Average mite body weight per sample was calculated by dividing biomass per sample by the abundance of mites in that sample.

4.3.5 Other data collected from field site

A total of 26 environmental factors were measured or calculated for correlation with mite assemblage structure: 10 factors related to plants, 2 to soil nutrients, and 14 to soil microbial measures. Biomass of shrubs, forbs, graminoids, and litter was determined by harvesting from a 10 x 100 cm quadrat in each plot on 16-22 July 2007 (methods in White, 2013). Root biomass was sampled from 0-5 and 5-20 cm soil cores. Vegetation diversity indices (richness, evenness, Shannon, and Simpson) were calculated from 50 x 50 cm permanent quadrats within treatment plots, on July 17-19 (White, 2013). NH_4 and NO_3 content of the soil were determined using PRS^{TM} probes (Western Ag Innovations, Saskatoon, SK). These probes were installed on 22 July and collected on 22 August 2007. Using chloroform fumigation-extraction method, dissolved organic carbon (DOC) and nitrogen (DON), and microbial carbon (MBC) and nitrogen (MBN) were determined from soil cores collected 0-5 and 5-20 cm deep on 20 July 2007 (methods in Attaeian, 2010). Lastly, 0-10 cm soil cores were collected on 29 July 2007, from which phospholipid fatty acid (PLFA) profiles were constructed to estimate relative abundance (mol % of the total PLFAs) of total bacteria, total fungi, actinomycete, gram-positive bacteria, gram-negative bacteria, and arbuscular mycorrhizal fungi (Attaeian, 2010).

4.3.6 Analysis

We analyzed the relationship between mite abundance and biomass using Pearson correlation, and the R^2 of the best fit (linear) line. In order to explore general patterns in higher taxonomic categories (all Acari, Prostigmata, Oribatida, and Mesostigmata), individual treatment responses were tested using one-way ANOVA. We did not formally test for interactions because of the loss of

normality, and statistical power, due to the low number of replicates. However, during preliminary data exploration, we did not find any indications of interactions, further justifying our decision not to include them in our formal analysis. To compare more finely resolved taxa (families and genera) we used non-parametric Mann-Whitney U-tests and Kruskal-Wallis tests because data were not normally distributed even after applying various transformations. Because body weight was calculated per family or genus, and these were the same taxonomic units used for the non-parametric tests (which rely on ranking data), only abundance data were used as we found that they produced almost identical results to biomass. Finally, Pearson correlations between abundance and richness of mites and environmental factors were determined. Even though we performed multiple correlation analyses, we did not use Bonferroni adjustments in an attempt to reduce committing type II errors and possibly missing informative environmental factors (Moran, 2003). Thus it is possible that our analyses returned some spurious significant correlations. All analyses were performed in SPSS (release 17.0.0, 2008, Chicago, Illinois).

4.4 Results

4.4.1 Abundance-biomass relationships

A total of 8418 mites were collected and identified. Mite abundance and biomass were highly correlated ($r = 0.65$, $p = 0.001$, $R^2 = 0.42$) (Figure 4.2). This relationship also showed in the rest of the analyses, where abundance and biomass showed very similar or identical responses to treatments.

4.4.2 Treatment effects

Considering richness, abundance, and biomass, mites responded only to drought, but to no other treatments (Table 4.1). Taxon richness was not significantly affected by the treatments (precipitation, $F_{(1,22)} = 1.93$, $p = 0.18$; warming, $F_{(1,22)} = 0.03$, $p = 0.89$; defoliation, $F_{(2,21)} = 0.19$, $p = 0.83$) but showed a slight trend to increase under drought conditions. We identified a total of 70 mite taxa from our samples (Appendix I, Table II.1 and II.2). This included 20 families of Oribatida

(including 1 family of Astigmata), 15 families of Prostigmata (including 4 Heterostigmata), 8 families of Mesostigmata, and 2 families of Endeostigmata. Because Prostigmata (including Heterostigmata) and Endeostigmata were only identified to family, total number of species is expected to be considerably higher than 70. For example, through sub-sampling of prostigmatan families that showed some response to drought, we identified 10 additional genera (see below).

Abundance of all mites together showed a very weak increase ($F_{(1,22)}$ = 3.09, p = 0.09) due to the drought treatment, while biomass increased more markedly ($F_{(1,22)}$ = 7.40, p = 0.01). When dividing mites into "suborders", Prostigmata showed increases in both abundance and biomass in response to drought, while Oribatida only showed this for biomass (Table 4.1). However, abundance of Oribatida did show a significant increase when Astigmata were excluded from the group (Figure 4.3).

Particular families, genera, and life stages of Prostigmata and Oribatida responded to the drought treatment ($p < 0.1$), driving the effects seen in the higher taxa. The strongest drought treatment responses are seen in Tydeidae, juvenile Oribatida, Cunaxidae, Stigmaeidae, and adult Astigmata (Acaridae: *Tyrophagus* sp.), in ascending order of p-values (Table 4.2). The following genera were found to make up the majority of the above families of Prostigmata: Tydeidae - *Tydeus, Coccotydaeolus*, and *Paratydaeolus*; Cunaxidae - *Cunaxa, Pulaeus, Pseudobonzia,* and *Scutopalus*; Stigmaeidae - *Stigmaeus, Eustigmaeus,* and *Ledermuelleriopsis*.

Some mite group abundances correlated with our measured environmental factors. Stigmaeidae and Tydeidae showed the greatest number of significant correlations, with four each. Stigmaeid abundance was most strongly positively correlated with actinomycete content of the soil (R^2 = 0.30, p = 0.006), gram negative bacterial biomass (R^2 = 0.24, p = 0.016), litter biomass (R^2 = 0.24, p = 0.017), and gram positive bacterial biomass (R^2 = 0.18, p = 0.039). Tydeids were most strongly linked to litter biomass on the soil surface (R^2 = 0.36, p = 0.002), gram negative bacterial biomass (R^2 = 0.22, p = 0.022), dissolved organic carbon

at 1-5cm soil depth ($R^2 = 0.18$, $p = 0.042$), and actinomycete content ($R^2 = 0.17$, $p = 0.043$). Adult Astigmata most strongly correlated, albeit negatively, with volumetric root biomass at 5-20 cm ($R^2 = 0.30$, $p = 0.005$), but positively with dissolved organic carbon at 1-5 cm and 5-20 cm soil depth ($R^2 = 0.42$, $p = 0.015$, and $R^2 = 0.24$, $p = 0.016$, respectively). Cunaxidae only correlated with total forb biomass ($R^2 = 0.18$, $p = 0.039$). Juvenile-oribatid abundance did not correlate significantly with any of the tested measures. In total we performed 105 (5 taxa x 26 environmental variables) correlation analyses.

Lastly, when testing for treatment effects on average mite body weight per sample we found no significant relationships (precipitation, $F_{(1,22)} = 0.45$, $p = 0.51$; temperature, $F_{(1,22)} = 1.15$, $p = 0.30$; defoliation, $F_{(2,21)} = 0.43$, $p = 0.66$); however, when comparing average mite body weight per sample to abundance of mites, we did observe a significant negative correlation ($R^2 = 0.32$, $p = 0.004$) indicating that samples with large numbers of mites tended to have smaller-bodied individuals (Figure 4.4).

4.5 Discussion

4.5.1 Treatment effects

Neither warming nor defoliation treatments showed any effect on mite measures, partially supporting our hypotheses. While we predicted that warming would not have a significant effect, we hypothesized that defoliation would increase mite numbers and biomass. However, as predicted, drought did change the mite assemblage structure by increasing the abundance and/or biomass of particular taxa. Even though it has been hypothesized that mites from arid and semi-arid soils may be adapted to drought (Walter et al., 1987), observations of stimulatory effects of reduced soil moisture have not previously been reported. As potential indirect support of our observations, O'Lear and Blair (1999) found that low soil moisture need not have negative effects on mite abundance. In contrast, through an irrigation experiment and transplanting soil cores, their study showed that added precipitation can reduce mite numbers, indirectly supporting the idea of

drought-adapted taxa. As in this experiment, Tydeidae showed the strongest response to changes in soil moisture content.

Although highly speculative, we suggest that the increases in mite numbers we observed may be linked to effects of short-term drought disturbance on nutrient availability. The drought treatment may have induced a sudden influx of organic matter into the system due both to increased mortality of organisms unable to withstand drought, and to plant roots producing exudates as a stress response. These exudates have been shown to be able to increase microbial biomass (Bertin et al., 2003), which in turn provide an extra direct or indirect food source for mites able to withstand the drought stress. However, we did not find any robust evidence for elevated carbon or nitrogen levels, whether in dissolved organic or microbial form, caused by any of the treatments in the 2 blocks used to observe mite responses. In addition, using all 5 blocks of this experiment, Attaeian (2010) observed that microbial carbon (MBC) decreased with lowered precipitation and high intensity defoliation, in (5-20cm) deep soil. However, she found that warming increased MBC in shallow soil (1-5cm). Because of these varied responses, it is difficult to generalize about any type of causation with regard to effects of the climate change treatments on the MBC, and in turn on the soil mite community.

While average body size of mites was not affected by any of the treatments, it did show a significant decrease in relation to mite abundance per sample. This implies that relatively large mites do not coexist together in large numbers. Although outside the scope of this paper, this pattern may be indicative of some broader ecological mechanism. Many authors have identified similar patterns for other non-mite taxa, i.e. many small organisms and few large ones coexisting in a particular area (Brown, 1995; Loder et al., 1997; Blackburn and Gaston, 1999; White et al., 2007), and so this size-abundance pattern in mites may be interesting to pursue in the future.

4.5.2 Finer taxa of mites

Induced drought was associated with an increase in abundance and biomass of Tydeidae, juvenile Oribatida (excluding Astigmata), Cunaxidae, Stigmaeidae, and adult *Tyrophagus* (Astigmata). It is challenging to pinpoint the cause(s) of these taxon-specific responses, particularly because these groups appear to have relatively little in common. Tydeids are known for being resistant to desiccation, but their feeding habits are diverse (Krantz and Walter, 2009). Tydeidae in this study consists of at least 3 genera, the most common being *Tydeus*. While this genus contains fairly common species, there have been conflicting reports of what resources these mites make use of (Krantz and Walter, 2009). Tydeidae are considered to fungivorous, phytophagous, predatory, or omnivorous. It is not clear why tydeid abundance in this study would correlate to litter cover on the soil surface, but the gram negative bacterial biomass, dissolved organic carbon, and actinomycete content of the soil may all be direct or indirect resources for these mites.

All genera of Cunaxidae are predators of other arthropods. *Cunaxa* are ambush predators, while *Pulaeus* are cruise predators that may sometimes also consume nematodes (Krantz and Walter, 2009). Although very speculative, we suggest that forb cover, which was the only significant correlate for cunaxids, may hint at prey being associated with one or multiple forb species. However, without a more focussed study, it is impossible to determine exactly what prey is being consumed in this particular situation.

Stigmaeus and *Eustigmaeus* are the two most species-rich genera within the family Stigmaeidae. These mites have been found to feed on mosses, but may also be predators of other invertebrates, or omnivorous (Krantz and Walter, 2009). Why stigmaeids were found to positively correlate with actinomycete biomass, bacterial biomass, and litter cover is unclear. It may be that these measures correlate with another, unmeasured, causative factor. For example, increased bacterial and fungal biomass may increase prey abundance/quality. On the other hand, actinomycete correlation may be due to fungal feeding by this group. While

never before reported, it is not outside of the realm of possibilities considering how little is known about specific feeding habits of specific soil inhabiting taxa.

Tyrophagus (Astigmata) is a cosmopolitan acarid genus whose members are saprophages and fungivores (Krantz and Walter, 2009). Because of this diet, and their ability to phoretically disperse as deutonymphs, they are able to exploit labile resources. *Tyrophagus* abundance correlated negatively with volumetric root biomass in deeper soil, but positively with dissolved organic carbon in shallow and deeper soil depths. Lower root biomass may be due to root mortality from the induced drought conditions. The dead root matter could function as an additional resource for these saprophagous mites. In turn, the higher levels of dissolved carbon may possibly be partly the result of *Tyrophagus*' feeding activities. The macerating action of their 'chewing' would increase surface area and allow microbial decomposition to produce more dissolved organic matter, including carbon.

A number of correlations are left unexplained. We preformed multiple correlations in an attempt to explore possible relationships between these mites and various environmental variables, to ultimately explain the increases in abundance and biomass that we have observed. However, we did not apply a Bonferroni adjustment to avoid type II errors; as a result we must be cautious of the possibility of spurious results.

Lastly, the unidentified oribatid juveniles may be detritivores, fungivores, and/or predators of nematodes. This group did not significantly correlate with any of our environmental measures, which may be due to the diversity of taxa contained within this group. These taxa presumably have different feeding habits and environmental tolerances.

4.5.3 Current understanding and future direction

While we cannot give a definitive explanation for why drought unexpectedly caused increases in mite abundance and biomass, we have shown that different mite taxa may be associated with different environmental changes caused by the drought. Decreases in mite abundance or biomass through drought, either via

mortality or via stimulating migration, has been well documented. Causal factors for this decline are usually considered to include physical limitations of the mites (lack of mobility to escape lethal environmental extremes or poor cuticular moisture barrier) or differences in life history traits (mode of reproduction and feeding preferences) (Wauthy and Vannier, 1988; Siepel, 1996). However, understanding stimulating effects on abundance and biomass, such as what we observed, is more difficult. These increases could be due to a higher amount of available resources as we have suggested here, but may also be related to effects of predator- and/or competitor-release (Paine, 1966). If predators and/or competitors are not drought-resistant, their effects on populations of more drought-resistant mites will decrease as soil moisture declines. However, this is purely speculative as there currently is no supporting empirical evidence of this mechanism in relation to soil mites.

To understand the mechanisms behind these stimulatory effects of drought-treatment on particular mite taxa, we propose future research to focus on microcosm experiments. In these more controlled settings, drought-tolerant species may be used in combination with non-tolerant species, either as competitors or as predators. Although soil biologists increasingly aspire to study big-picture processes (e.g. Kardol et al., 2011), to avoid a black-box approach to soil ecology it is imperative to understand the fundamental species-interaction mechanisms that may govern soil microarthropod populations, and in turn, soil processes.

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Table 4.1: Treatment analysis of abundance (AB) and biomass (BM) of all mites and mite "suborders" using ANOVA. 'Excl.' = excluding. Asterisks indicate statistically significant treatment effects (*p < 0.05, **p < 0.01). N = 24.

Treatment	Abundance/Biomass (AB / BM)	Taxon	Explained variation (adjusted R^2)	F-value	p-value
Drought	AB	All Acari	0.08	3.09	0.093
Drought	BM	All Acari	0.22	7.40	**0.013***
Defoliation	AB	All Acari	0.07	0.22	0.807
Defoliation	BM	All Acari	0.07	0.22	0.804
Warming	AB	All Acari	0.04	0.09	0.774
Warming	BM	All Acari	0.04	0.03	0.858
Drought	AB	Oribatida	0.001	1.03	0.321
Drought	BM	Oribatida	0.14	4.80	**0.039***
Drought	AB	Oribatida excl. Astigmata	0.22	7.42	**0.012***
Drought	BM	Oribatida excl. Astigmata	0.08	2.88	0.104
Drought	AB	Mesostigmata	0.03	1.72	0.204
Drought	BM	Mesostigmata	0.03	0.31	0.583
Drought	AB	Prostigmata	0.12	4.02	0.057
Drought	BM	Prostigmata	0.29	10.33	**0.004****
Drought	AB	Prostigmata excl. Heterostigmata	0.12	4.02	0.058
Drought	BM	Prostigmata excl. Heterostigmata	0.30	10.68	**0.004****
Drought	AB	Heterostigmata	0.02	0.44	0.513
Drought	BM	Heterostigmata	0.02	0.40	0.532

Table 4.2: Drought treatment effects on abundances of mite families. N = 24.

Treatment	Taxon	Z-Stat	p-value
Drought	Oribatida juv.	2.46	**0.012***
Drought	Tyrophagus adults	1.83	0.068
Drought	Cunaxidae	2.21	**0.028***
Drought	Stigmaeidae	1.94	0.06
Drought	Tydeidae	2.54	**0.01***

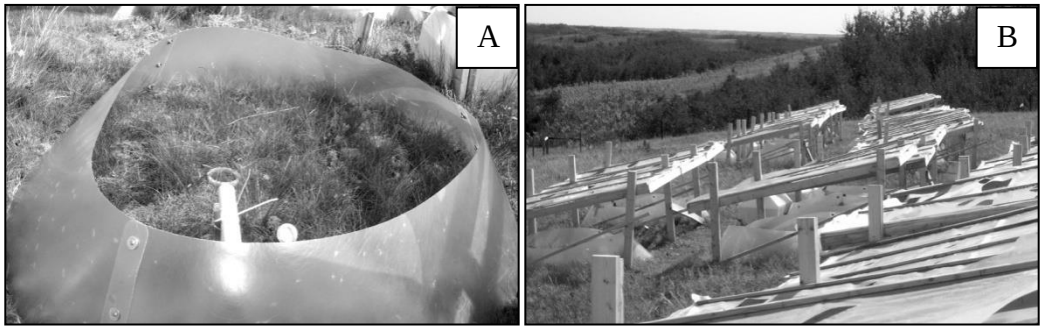

Figure 4.1: Warming treatments were applied using open top chambers (A), while drought treatments were applied using rainout shelters (B). The controls were fitted with large slits allowing 100% precipitation to enter the plot, while the drought treatment (shelters with narrow slits) reduced precipitation to approximately 50% (Bork et al., 2008).

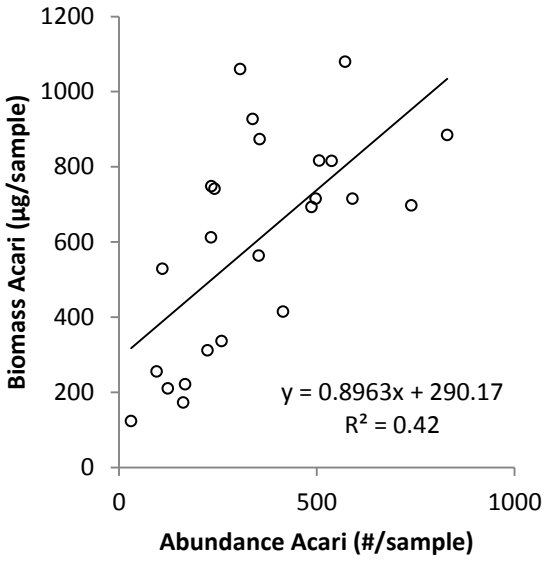

Figure 4.2: Scatter plot of mite abundance and biomass. The best fit line shows a significant positive correlation (N = 24, Pearson Correlation = 0.65, p = 0.001).

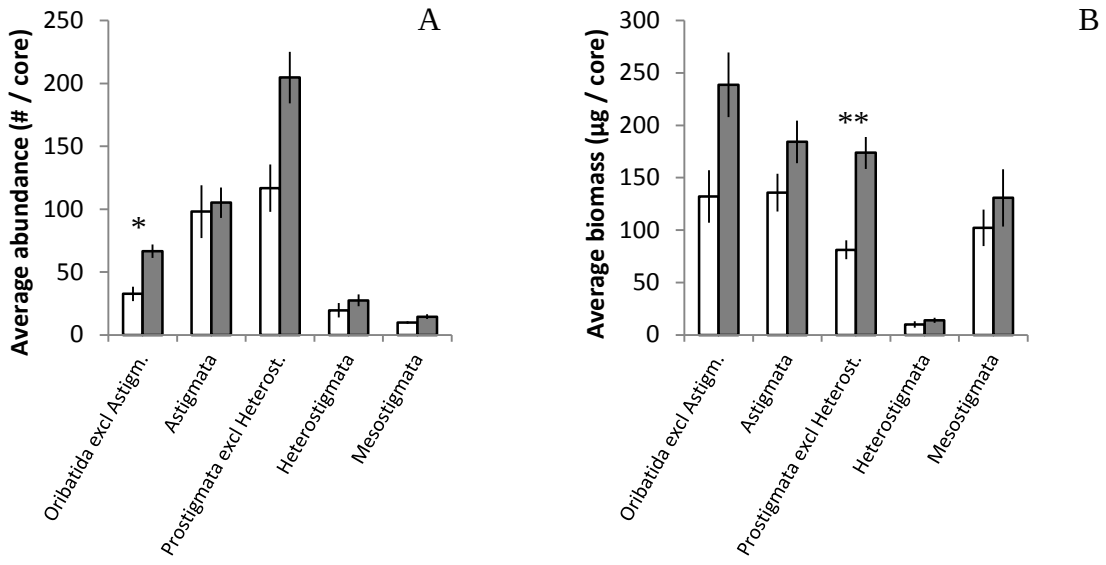

Figure 4.3: Drought treatment effects on average abundance (A) and biomass (B) of soil mites collected per sample. White and shaded bars represent control and drought treatments, respectively. 'Excl.' = excluding, 'Heterost.' = Heterostigmata. Error bars are ± 1 S.E.

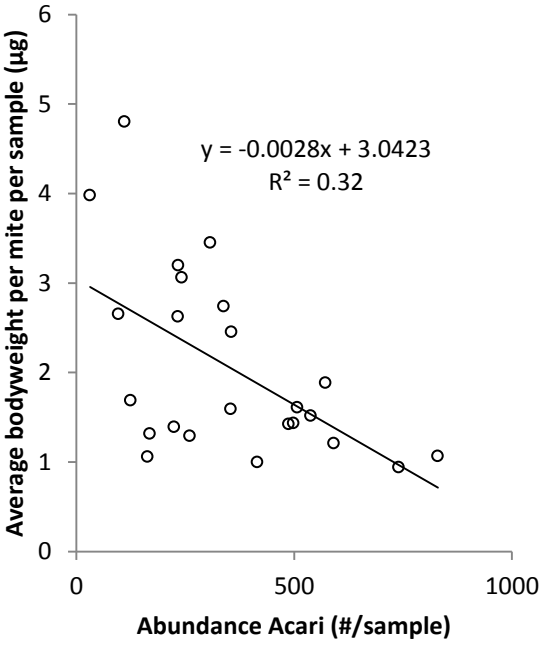

Figure 4.4: Scatter plot of mite abundance and average mite body weight per sample. The best fit line shows a significant negative correlation (N = 24, Pearson Correlation = 0.57, p = 0.004).

Chapter 5: Climate change treatment effects on soil microarthropods in a temperate grassland.

5.1 Introduction

Grasslands cover a large proportion of the North American continent, of which a minor part remains as native grassland. Much of this native grassland has been lost due to urbanization, grazing, and agricultural practices. In light of the current rapid pace of climate change (IPCC, 2007; CCCma, 2012), it is important to understand how environmental stresses like warming and altered precipitation patterns affect this endangered ecosystem. Much research has focussed on the effects of climate change on grassland vegetation (e.g. Vittoz et al., 2009). In turn, the soil component supporting these grassland ecosystems has also received much attention, particularly with regard to changes in decomposition rates and microbial responses (Anderson, 1991; Couteaux et al., 1995; Aerts, 2006; Liu et al., 2009; Castro et al., 2010; Sheik et al., 2011). However, relatively little is known about the effects of climate change on the grassland-inhabiting soil biota.

After microbes, protists, and nematodes, microarthropods are the most numerous organisms in the soil, and consist of many functional groups. The most abundant microarthropods are mites (Acari) and springtails (Collembola) (Seastedt, 1984; Bardgett, 2005, p. 35); the relative dominance of these two major taxa depends on vegegation and soil types. Soil microarthropods may affect both the below- and above-ground ecosystems in a variety of ways. Soil mites, particularly Oribatida, are known for promoting primary decomposition and nutrient cycling (Behan-Pelletier and Kanashiro, 2010). However, many mites and springtails are also fungal feeders and can either stimulate fungal productivity, or selectively suppress the fungal species they prefer to feed on (Coleman, 2008). This can alter fungal community composition and, particularly if mycorrhizal fungi are affected, can have consequences for plant communities. Soil microarthropods may also aid in dispersing microbial propagules (Renker et al.,

2005). Finally, the predatory mites may control populations of prey taxa like nematodes (Krantz and Walter, 2009).

To date, mite and springtail abundance, biomass, and richness is known to be most significantly influenced by soil moisture, with drought reducing numbers for all of these measures (Ford, 1938; Wauthy and Vannier, 1988; Harte et al., 1996; Berg et al., 1998; Lindberg et al., 2002; Taylor and Wolters, 2005; Gergocs and Hufnagel, 2009). However, increased precipitation may not necessarily result in an increase in abundance, and instead can induce decreases in soil microarthropod abundance (O'Lear and Blair, 1999). Though temporal distribution of precipitation has been suggest to affect soil microarthropods (Holland et al., 2013), this is currently an understudied area. Warming treatments produce a much more muted and variable mite and springtail response than drought treatments, with some studies reporting increases in abundances, some reporting decreases, but most showing minimal affects (Sjursen et al., 2005; Bokhorst et al., 2008; Briones et al., 2009).

In North America, grazing is essential for maintaining grasslands, and preventing forestation. Grazing has been shown to decrease mite abundance (Kay et al., 1999; Battigelli et al., 2003), but this can vary depending on the locally dominant mite taxon (Clapperton et al., 2002). Grazing probably influences mite abundances indirectly through altering soil bulk-density, litter layer, soil moisture and possibly the physiology and composition of the vegetation (Bardgett et al., 1998; Clapperton et al., 2002). It can be difficult to determine from the literature what mite taxa are accounting for all of the above mentioned responses, because soil mites are often only identified to the very coarse "subordinal" categories of Mesostigmata, Oribatida, Astigmata and Prostigmata.

We are unaware of any studies that have looked at these different climate stresses in combination with grazing, on soil microarthropod communities in native Northern Fescue grasslands. Here we present the results of a climate

change experiment carried out in the Parklands ecoregion in Alberta, Canada, which contains this endangered type of grassland. We simulated climate change via warming and reduced and increased precipitation treatments. We also imposed defoliation treatments to simulate grazing and assessed how all of these factors affected soil microarthropod diversity, abundance, biomass, and assemblage structure. We hypothesized that drought would lower soil microarthropod taxon richness, abundance and biomass. Based on previous studies, we did not expect a significant effect of warming or defoliation alone. However, we did hypothesize significant interactions; in particular, we expected that warming and defoliation might exacerbate the effects of drought. Finally, we hypothesized that the soil micro-arthropod assemblage would change due to the precipitation treatment.

5.2 Materials and Methods

5.2.1 *Field site*

Research was conducted at the University of Alberta Research Ranch in Kinsella, Alberta, Canada (53º01.20N, 111º32.35W). The area consists of native fescue grassland, within aspen parkland (which is geographically positioned between grasslands to the southeast and boreal forest to the northwest), experiencing an average annual temperature of 2.6 °C and precipitation of 431.3 mm (Env. Can., 2013). A detailed description of the area's soil and vegetation is provided by Attaeian (2010), Newton *et al.* (2011), and White (2013). The study site was situated on a gently sloping hilltop facing east. The soil has never been tilled and the grassland has only been lightly grazed.

5.2.2 *Treatments*

Our treatments ran for 3 field seasons for ~2.25 consecutive years from May 2007 to August 2009. Field seasons lasted from the first week of May to the second week of August, effectively encompassing a little over 3 months. The short field

season is characteristic for this climate, and is contingent on time of snowmelt in spring and the cooling temperatures in fall.

Treatments included warming, reduced and added precipitation, two defoliation intensities, and controls. The full factorial experimental design has 5 replicates (blocked) for a total of 90 plots, measuring 2 m x 2 m. Warming treatment was applied using open top chambers made of fibreglass (Sunlite-HP, Solar Components Corporation/Kalwall Corporation, Manchester, NH, USA), which increased the ambient air temperature by 2-4 ºC during the day (Bork et al., 2008).

Drought treatment plots were covered in rainout shelters (Dura-Film Super 4™ 6-mil polyethylene film; AT Plastics, Edmonton, Alberta, Canada); the precipitation from these shelters was collected in holding tanks and then added to the plots with increased precipitation treatment. The precipitation-added treatment was applied only in the second and third field seasons due to logistical constraints in 2007. We did not control the absolute amount of water received by the plots, and instead relied upon natural rainfall patterns. Shelters were constructed of lumber anchored down using rebar, and topped by plastic sheeting with different sized slits. The slits allowed either 100% of the rain through for control treatments, or approximately 50% for drought treatments. Though soil moisture was variable, drought-treatment plots had an average of 8-13% volumetric water content, while controls had 21-26% (Bork et al., 2008). For the defoliation treatments we used a mower and shears to cut vegetation to a height of 3 and 7 cm in midsummer (June 15-30) to simulate low- and high-intensity grazing.

5.2.3 *Environmental measures*

While the breadth of this collaborative experiment also included analyses of vegetation composition, root demography, decomposition, soil microbial community, and soil respiration, the findings we present in this paper are focused

on the effects of the treatments on soil microarthropods; however, we do include several of the variables we felt were most likely to be correlated with microarthropod assemblages. The main environmental measures we considered were soil moisture and soil and air temperature. Other measures included as extrinsic variables for ordinations are microbial C and N, dissolved organic C and N (Y. Lin, University of California, unpublished data used with permission), vegetation richness, evenness, Shannon indices, Simpson indices (methods and data in White, 2013), and the percent of precipitation removed or added to specific plots. As soil moisture loggers were set up in only 2 of the 5 replicated blocks in order to validate our treatments, we used an alternative measure applicable to all plots. Controls were presumed to receive 100% of ambient precipitation, while precipitation on drought plots were calculated by the difference between the ambient precipitation and the amount of run-off water collected in the holding tanks. This water was then added to another plot. Precipitation received in the experimental area was measured using two Davis Rain Collector II buckets (Davis Instruments, Hayward, CA, USA).

5.2.4 Sampling, microarthropod extraction and identification

Soil mite sampling was done on 10 Aug 2009. Soil cores were all taken on the same day using a rubber mallet to pound PVC pipes measuring 10 cm deep by 5 cm wide (47 mm bore diameter) into the soil. Samples were then transferred to Tullgren/Berlese funnels at the Royal Alberta Museum, where they were left to extract under 20 W halogen lights for five days.

Mites were identified using Krantz and Walter (2009), the Almanac of Alberta Oribatida (Walter et al., 2011), unpublished keys from the Ohio State University's summer acarology course, and an unpublished key to Astigmata by B.M. OConnor (University of Michigan). For data analysis most taxa are identified to genus or species level except for prostigmatid mites and Collembola, which are identified to family. When analysing "suborders" of mites (Oribatida,

Prostigmata, Mesostigmata), Astigmata are separated from Oribatida, as are the Heterostigmata from the Prostigmata (except in the taxon richness analysis). This was done because the cohorts Astigmata and Heterostigmata are functionally distinct from most other members of their respective sub-orders in having life-stages modified for dispersal on larger-bodied arthropods, and therefore may show different sensitivities to the treatments.

Mites were counted using a Leica MZ6 (max 40x) and MZ16 (max115x) dissecting stereomicroscope. Very small (<200 µm) (juvenile Prostigmata, Tydeidae, Brachychthoniidae, juvenile Astigmata, Heterostigmata, and Endeostigmata), which were very numerous, were sub-sampled for identification. These tiny but numerous mites can be easily overlooked by non-acarologists, but may play an important role in these grasslands (Walter, 1988). Sub-sampling was done by identifying on average a quarter of the total number of tiny mites in a sample, if numbering over 40 individuals. Mite selection for sub-sampling was by drawing an "x" on the Petri dish containing the haphazardly scattered sample, and counting and identifying the mites in one of the four quarters of the dish created by the "x". Counting started from the center, until the desired number of mites was collected.

Biomass for all acariform mites (non-Mesostigmata) was calculated using Lebrun's (1971) formula intended for oribatid mites, which works well for other mite groups (Newton and Proctor, 2013). Mesostigmatan biomass was calculated using Person and Lohm's (1977) formula. Average length and width were determined from slide mounts using a Leica DMLB differential interference contrast (DIC) microscope at 400x magnification, which produces an effective maximum resolution of 2.5 µm. When enough specimens were available, 5 to 10 haphazardly selected individuals were measured per taxon (occasionally this included a male or juvenile). Length measurements of mites were taken as described by Newton and Proctor (2013). Average mite body weight per sample

was calculated by dividing biomass per sample by the abundance of mites in that sample.

5.2.5 *Data analysis*

Statistical data was analyzed using SPSS (release 17.0.0, 2008, Chicago, Illinois). For count data, models (Normal, Poisson, or Negative binomial distribution) for analyses of variance (ANOVA) were selected based on best fit, i.e. Deviance/df, never exceeding an overdispersion of 1.6. When normally distributed, continuous data were analysed using general linear models (GLM), or otherwise using generalized linear models (GLZ) gamma distribution. Non-parametric Kruskal-Wallis (KW) and Mann-Whitney U (MW-U) tests were used when overdisperion was above 1.7. Bar graphs and scatterplots were produced using Microsoft Excel 2007. Non-metric Multidimensional Scaling (NMS) ordinations were constructed using raw data in PC-Ord (release 5.0, 2008, MjM software, Gleneden Beach, Oregon). Clustering of sample plots was analyzed using Multi-Response Permutation Procedure (MRPP). Single counts (singletons) of taxa were excluded, as well as two outlier plots due to being devoid of any microarthropods.

5.3 Results

5.3.1 *Richness*

A total of 15,472 arthropods were extracted from the 90 soil cores, of which the majority were microarthropods. The microarthropods collected consisted of 14,492 mites, and 253 springtails. Mites were found at an average density of ~88,990/m^2 in control plots, which equates to ~0.248g/ m^2. Springtails were numerically insignificant, and equate to ~230/m^2. We identified 18 families (25 genus- or species-level taxa) of Oribatida, 19 families of Prostigmata, 12 families (25 genera, or 33 species) of Mesostigmata, 2 families (3 genera) of Endeostigmata, and 4 families of Collembola (Appendix II, Table II.3). Because of this strong difference between mite and springtail abundances, we have not

included springtails for richness, abundance, and biomass analysis, but did include them in the ordination.

Overall mite taxon richness showed a response only to drought ($p < 0.001$), while the other treatments and interactions did not produce any significant effects (lowest $p > 0.18$). Taxon richness of all three main mite "suborders" were affected by drought and showed a similar pattern (Figure 5.1); Oribatida, Prostigmata, and Mesostigmata each showed a significant reduction in taxon richness (Orib: $p < 0.001$; Pros: $p < 0.01$; Meso: $p < 0.001$). However, Mesostigmata also showed a reduction in taxon richness due to defoliation ($p = 0.019$), and warming ($p = 0.014$) (Figure 5.2).

5.3.2 *Abundance and biomass*

Abundance and biomass correlate strongly when split into Oribatida (excluding Astigmata), Astigmata, Prostigmata (excluding Heterostigmata), Heterostigmata, and Mesostigmata (Figure 5.3). Because of this, treatment responses for biomass were very similar to those for abundance (Appendix II, Table II.2), and therefore we elaborate only on results of the latter.

Total mite abundance was less, but not significantly so, under the influence of lowered precipitation ($p = 0.08$) (Appendix II, Table II.2), and showed a significant interaction between temperature and defoliation treatment (Figure 5.4). This interaction demonstrates that while warming increased mean abundance of mites under no- or low-intensity defoliation conditions, under heavy defoliation this effect was negated. When considering separate mite taxa, the precipitation treatment significantly affected abundances, except for Prostigmata (excluding Heterostigmata) and Astigmata (Figure 5.5), but even these taxa show the same overall pattern, i.e. decreased abundance under drought treatment. Abundance responses to warming varied (Figure 5.6). While abundance of Prostigmata (excluding Heterostigmata) was positively correlated with warming

($p = 0.04$), endeostigmatan abundance showed the opposite ($p = 0.03$). Other taxa were not as strongly affected by temperature increase. Defoliation lowered heterostigmatan abundance, but did not significantly affect abundance of other taxa (Figure 5.7). Prostigmatan abundance showed an interaction between the temperature and defoliation treatment ($p = 0.01$) producing an almost identical pattern to Figure 5.3 (all mites). Significant temperature x defoliation and precipitation x defoliation interaction effects (both $p < 0.01$) were found for heterostigmatan abundance (Figure 5.8).

5.3.3 *Mite assemblages*

3-D NMS ordination using the finest taxonomic level shows that only precipitation was strongly correlated with the pattern of samples created by the mite taxa (MRPP: $p < 0.0001$) (Axis 1 and 2: Figure 5.9A). Pair-wise comparisons show that drought-plot clustering is significantly stronger compared than that of control ($p = 0.001$) and added-precipitation plots ($p < 0.000001$). Control and added-precipitation plots did not differ significantly ($p = 0.15$). Warming also displayed significant, but less pronounced clustering (MRPP: $p = 0.03$) (Figure 5.9B), while defoliation did not produce any clustering of samples (MRPP: $p = 0.45$). The ordination depicts vectors for the extrinsic factors percent precipitation ($r = 0.34$), small mites ($r = 0.48$), total mites ($r = 0.56$), and taxon richness ($r = 0.6$) pointing away from the drought plots. All other extrinsic variables had an $r < 0.1$.

5.4 Discussion

5.4.1 *Abundances and biomass*

Springtails were found at such low numbers that they were excluded from the analyses. However, the seemingly low abundance may be misleading, as previous years of sampling using a kerosene flotation method (see Chapter 3) for extraction

rather than Tullgren funnels have shown springtail abundances to be higher, although still much less than that of mites (see Chapter 4).

While biomass results were not entirely identical to abundance results, with very few exceptions the patterns were very similar for both metrics (Appendix II, Table II.2). Few studies calculate both soil mite abundance and biomass, and as a result it can be challenging to compare between studies. Our results show that, at least at our geographic location, both measures are fairly interchangeable when testing for treatment effects. However, we did observe that while Prostigmata are indisputably the most abundant mite group in these grasslands, Oribatida were the most dominant with regard to biomass.

5.4.2 Main treatment effects

As hypothesized, drought treatment had the strongest effect on taxon richness, abundance, and biomass of mites. Almost all measures were negatively correlated with drought, whereas the added-precipitation treatment had either no significant effect, or a positive trend. The latter may be in part because the added precipitation treatment was active for a shorter period of time than the other treatments (two rather than three field seasons). Declines in abundance and richness with low soil moisture content have been consistently reported in the literature (Harte et al., 1996; Tsiafouli et al., 2005). We found that total mite abundance was not significantly reduced, but this was mainly because the most abundant group (Prostigmata excluding Heterostigmata) was not significantly affected by the drought treatment. However, total mite biomass was significantly reduced ($p < 0.01$). Like Prostigmata, neither Astigmata nor Endeostigmata experienced a significant reduction in abundance due to drought. Prostigmata did show a reduction in richness, indicating that while fewer taxa are able to survive extreme drought, those that do can still thrive. At a glance, it becomes clear that the dominant prostigmatid family –Tydeidae, experiences the strongest temperature driven increases in abundance and is driving this pattern (Figure

5.10). This is indicative of certain taxa, in this case Tydeidae, being better adapted to low soil moisture.

The only significant effect of the warming treatment was a reduction of taxon richness of Mesostigmata, although it is difficult to compare richness results of Mesostigmata and Oribatida to Prostigmata because the first two taxa were identified to genus or species, and Prostigmata were identified only to family. This for the most part supports our hypothesis as we did not expect any effects of warming alone. However, Briones et al. (2009) tested the effects of combined warming and defoliation on grassland microarthropods -identified to family- and found that the treatment did not affect the richness of mites, including that of Prostigmata. Briones et al. (2009) also found that warming increased the abundance of Prostigmata and Endeostigmata. Warming increases microarthropod metabolism, possibly causing the increase in abundance. However, warming can also decrease soil moisture content due to increased evaporation. Since Prostigmata are not being negatively affected by drought, it may be that only Prostigmata can exploit the biological benefits from warming by being more resistant to desiccation.

High intensity defoliation significantly reduced mesostigmatan taxon richness, but left other mites unaffected; the reason for this remains unclear. Mite abundances were relatively unaffected by defoliation mostly supporting our hypothesis, with the exception of Heterostigmata, which showed a significant reduction. This lack of response is somewhat contrary to what other research has documented. Clapperton et al. (2002) found that grazing by cattle reduces both abundance and richness of most mites, particularly Prostigmata. However, as Clapperton et al. note, this is probably driven by secondary effects of grazing like changes in the litter layer, of which there was a pronounced reduction in their system due to grazing. This would have been an effect of cattle disturbing the top soil layers, something lacking in our experimental manipulations. However, some

cattle-associated disturbances may be reproduced by mowing alone, as Schon et al. (2012) report that oribatid assemblages are more similar between grazed and mown samples, compared to those taken under fence lines that were defoliated but not trampled by cattle.

5.4.3 *Interactive effects of precipitation, warming, and defoliation treatments*

In our full-factorial design we also identified several significant interactions, supporting our hypothesis. While drought did not reduce prostigmatid (excluding Heterostigmata) abundance, there was a significant interaction of defoliation and warming. This interaction revealed that warming generally increased prostigmatid mite numbers, except under high defoliation conditions. This implies a non-linear response where the stimulatory effects of warming are negated and possibly reversed when defoliation is too intense. Abundance of Heterostigmata displayed a very similar warming and defoliation interaction, in addition to a complex interaction between precipitation and defoliation. Although we did not have actual grazing in our experiment, this finding does tentatively warn against intense grazing regimes. Clapperton et al. (2002) found that grazing intensity was correlated with higher soil temperature and lower soil moisture content, but since we did not see negative effects on Prostigmata due to drought, the cumulative temperature increase caused by warming plus intense defoliation may be the cause.

5.4.4 *Microarthropod assemblages*

MRPP analysis showed that mite assemblages in drought plots were significantly distinct from those in the control and added-precipitation plots. The warming treatment had a less pronounced effect. However, the ordination showed considerable overlap of treatment plots, indicating a general lack of distinct assemblages based on treatments. These results partially support our hypotheses as we predicted only the precipitation treatment to show a significant effect. This variation may have been caused by environmental variables not accounted for in

our study. The large spread of plots perpendicular to the precipitation vector supports this. Certainly warming accounts for part of this spread, as it can be seen that warming and control plots cluster perpendicular to drought and control + added precipitation plots. As we have already identified interactions between our treatments, it is to be expected that these will also be reflected in the ordination. Some important possible indirect effects, which we did not include in this analysis, may be variation in structure and microclimates in the soil influenced by bulk density or thickness of the litter layer, or differences in associated plant assemblages, particularly plant identities and variation in root demography.

It is currently not clear how or whether changes to soil microarthropod assemblages might functionally affect this grassland. One of the difficulties in predicting this is due to uncertainty about feeding habits of the mites most strongly affected by our treatments. While many soil ecology studies attempt to analyze shifts in feeding guilds or trophic groups, trophic classifications can be over-generalized, particularly as most soil mites are much more opportunistic and omnivorous than traditionally presumed (Walter et al., 1986; Walter, 1987; Walter and Ikonen, 1989). In addition, many species identified in this study are undescribed, increasing the risk of making erroneous assumptions of feeding behaviour.

5.4.5 Conclusion

Large-scale climate change experiments such as this rarely consider soil microarthropods, and when they do, it has been to a very coarse taxonomic level (Xu et al., 2012). We have shown that several taxa of soil mites are negatively affected by drought, and that interactions between warming and grazing may also cause declines in mite abundance and/or diversity, giving us reason to be cautious of intensive grazing regimes if climates cause reduced rainfall in the future. Further research is necessary to ascertain how these changes will functionally affect grasslands.

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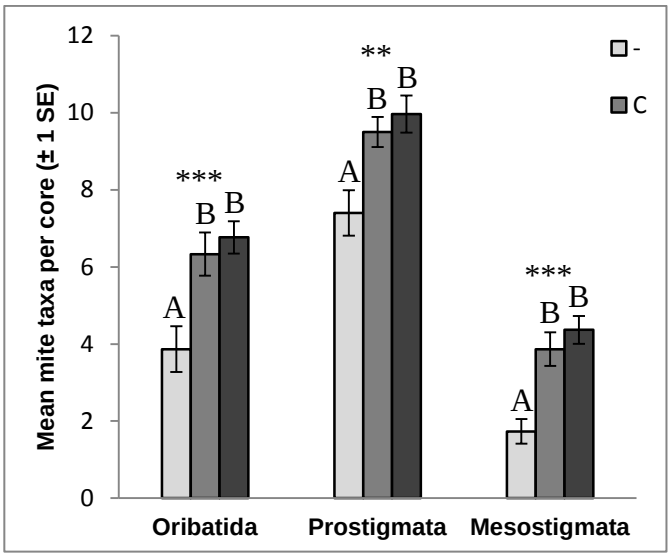

Figure 5.1: Mean taxon richness under precipitation treatments for mite "suborders". Light, medium and dark bars indicate drought (-), control (C), and added (+) precipitation, respectively. **p < 0.01, ***p < 0.001 - ANOVA.

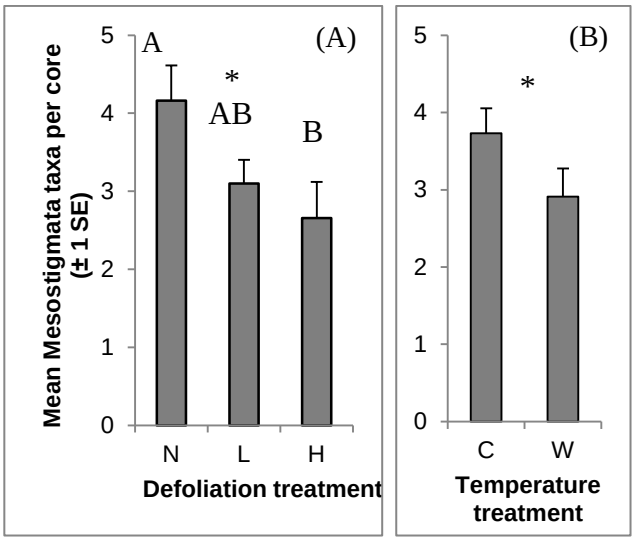

Figure 5.2: Mean taxon richness for Mesostigmata under (A) defoliation and (B) temperature treatments. X-axes show no (N), low (L), high (H) intensity defoliation, and the control (C) and warming (W) treatment. ANOVA indicated significant differences in taxon number for both defoliation and temperature. *$p < 0.05$.

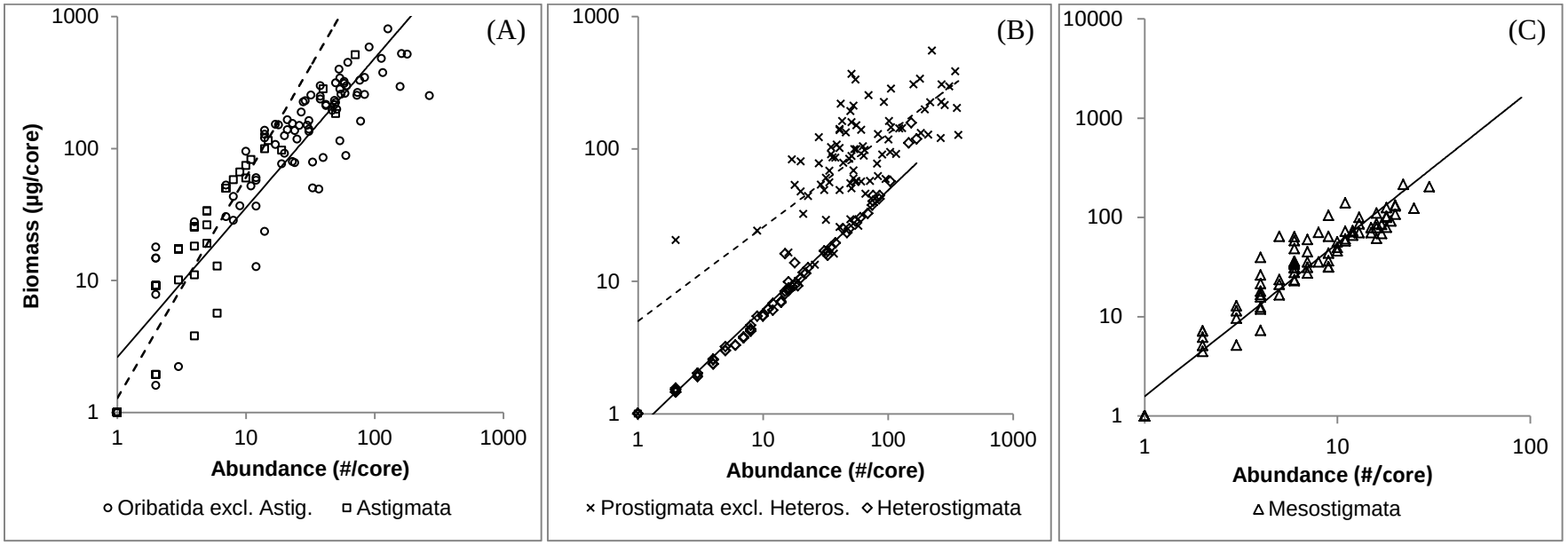

Figure 5.3: Correlations of abundance and biomass of (A) Oribatida (excluding Astigmata), Astigmata, (B) Prostigmata (excluding Heterostigmata), Heterostigmata, and (C) Mesostigmata. Best fit lines were used to calculate R^2 values. Oribatida (excluding Astigmata): solid line, $R^2 = 0.85$; Astigmata: dashed line, $R^2 = 0.90$; Prostigmata (excluding Heterostigmata): dashed line, $R^2 = 0.54$; Heterostigmata: solid line, $R^2 = 0.98$; Mesostigmata: solid line, $R^2 = 0.92$.

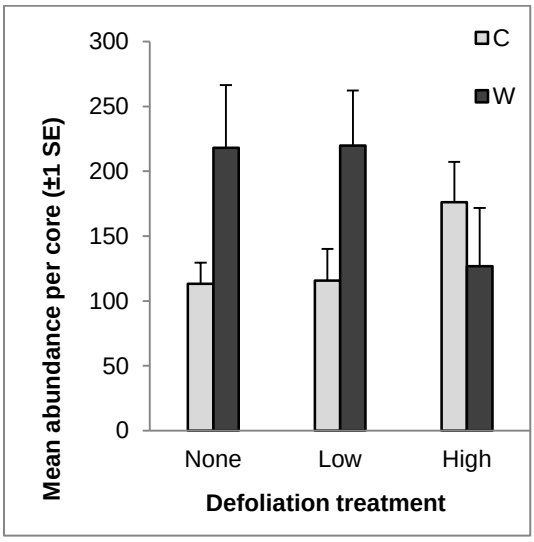

Figure 5.4: Interaction of temperature x defoliation treatment on total mite abundance (p = 0.012). Legend shows temperature treatments: control (C) and warming (W).

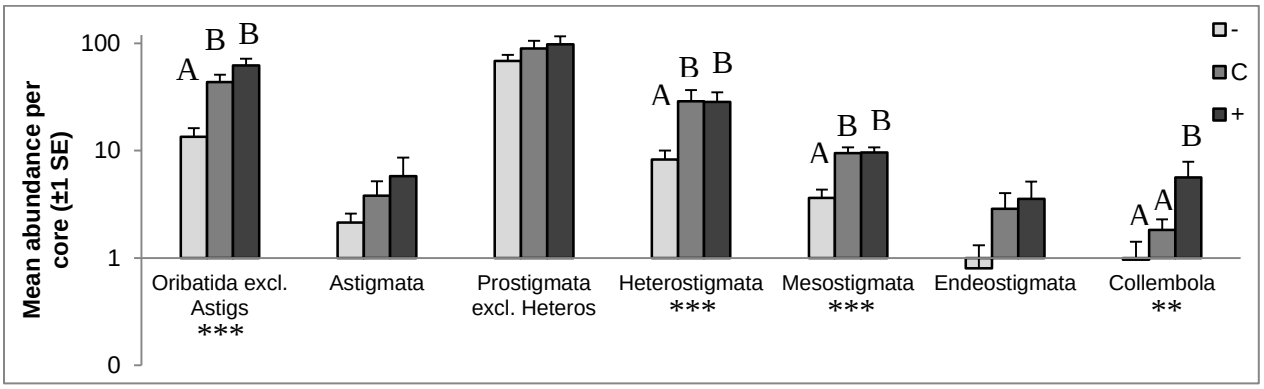

Figure 5.5: Mean abundances per mite taxon under precipitation treatments. Light, medium and dark bars indicate drought (-), control (C), and added (+) precipitation, respectively. The y-axis is logarithmically scaled. Results of ANOVA or KW tests are reported as **p < 0.01 and ***p < 0.001.

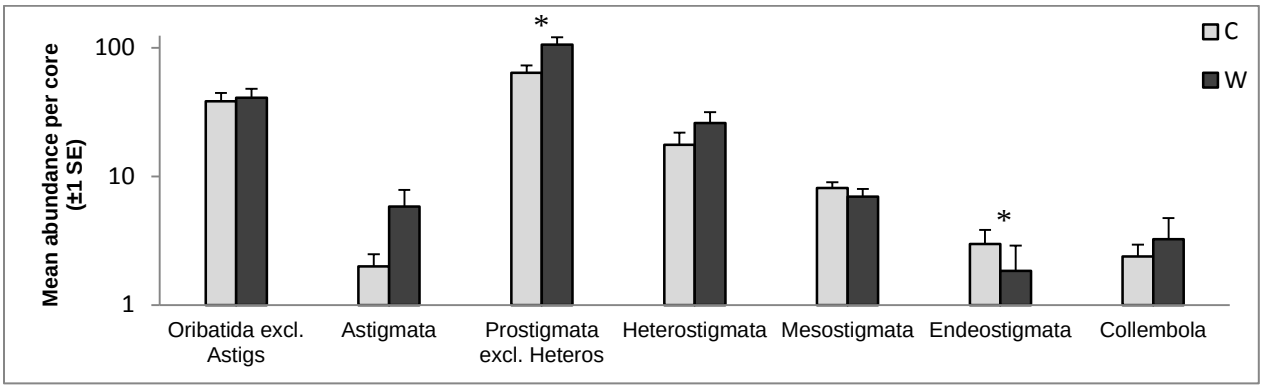

Figure 5.6: Mean abundances per mite taxon under temperature treatments. Light and dark bars indicate control (C) and warming (W), respectively. The y-axis is logarithmically scaled. Results of ANOVA or MW-U tests are reported as *$p < 0.05$.

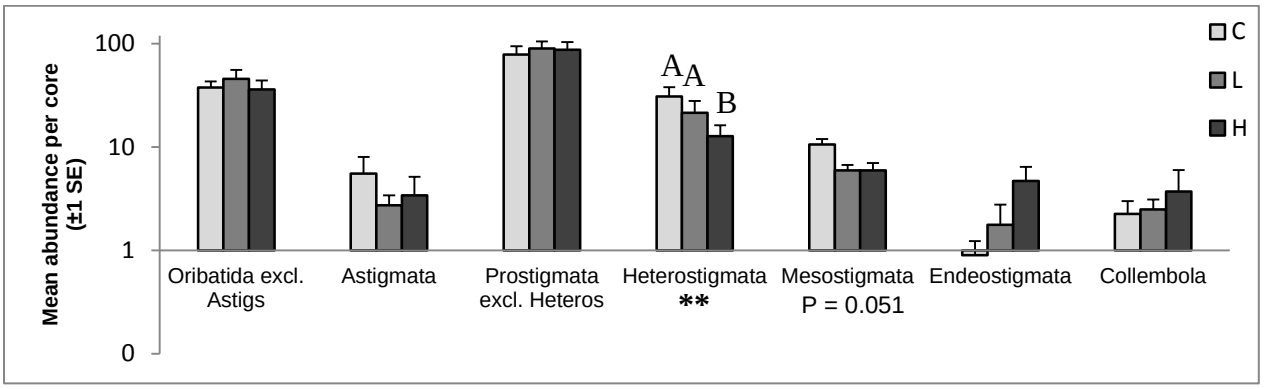

Figure 5.7: Mean abundances per mite taxon under defoliation treatments. Light, medium and dark bars indicate control (C), low intensity (L), and high (H) intensity defoliation, respectively. The y-axis is logarithmically scaled. Results of ANOVA or KW tests are reported as **$p < 0.01$.

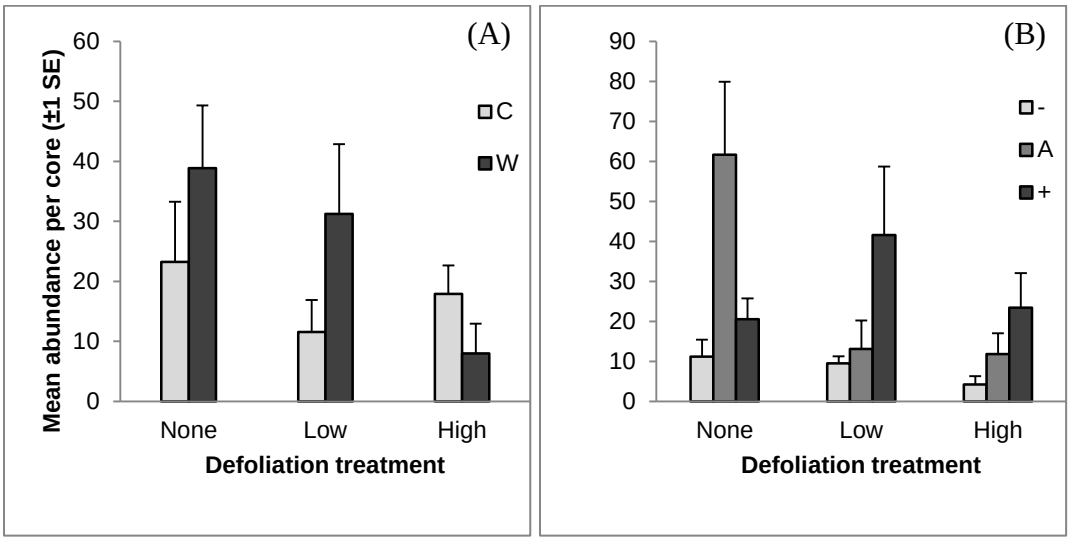

Figure 5.8: Interaction of (A) defoliation x warming, and (B) defoliation x precipitation treatments on mean heterostigmatan abundance ($p < 0.001$ and $p = 0.002$, respectively). Legend shows temperature and precipitation treatments: control (C), warming (W), drought (-), ambient rainfall (A), and added precipitation (+).

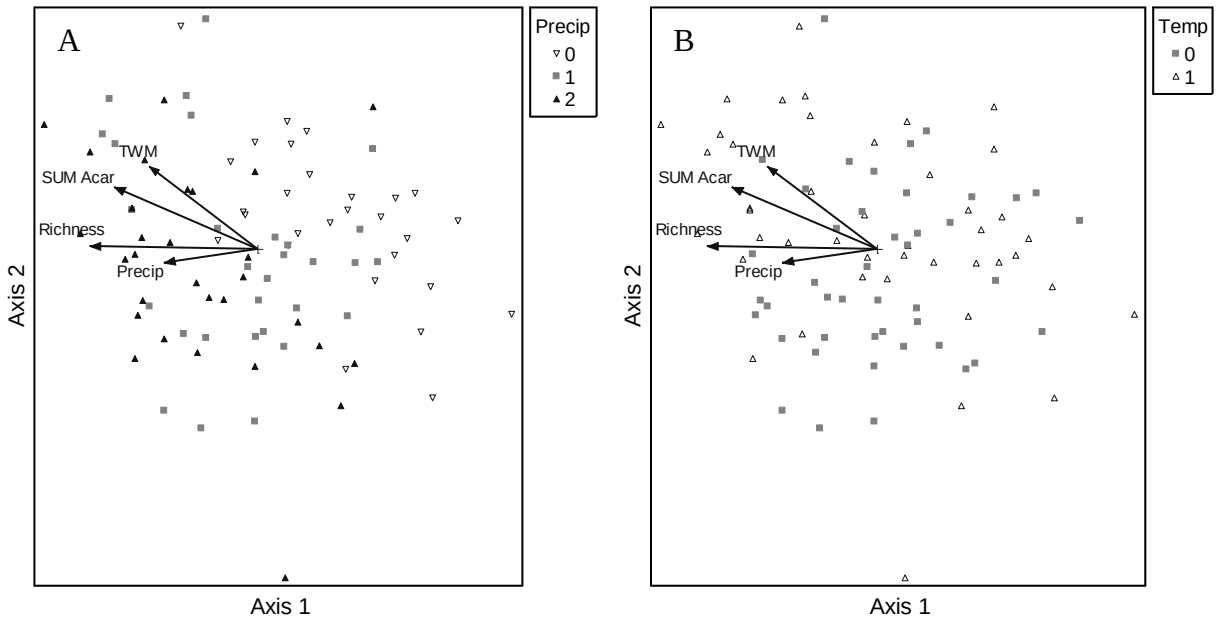

Figure 5.9: Axes 1 and 2 of a 3-D NMS ordination based on soil mite assemblages (stress: 14.3; instability: 0.0034). In Fig. 9A, symbols represent drought (0), control (1), and added precipitation (2) plots. In Figure 9B, symbols represent control (0) and warmed (1) plots. Vectors for extrinsic variables show that percent ambient precipitation (Precip) is negatively correlated to drought plots. The very abundant tiny white mites (TWM), consisting mostly of prostigmatid juveniles, are not significantly affected by the drought treatments but are positively related to the warming plots. The vector for total mite abundance (SUM Acar) is drawn between added precipitation and warming plots. Soil microarthropod richness (Richness) is positively related to percent precipitation.

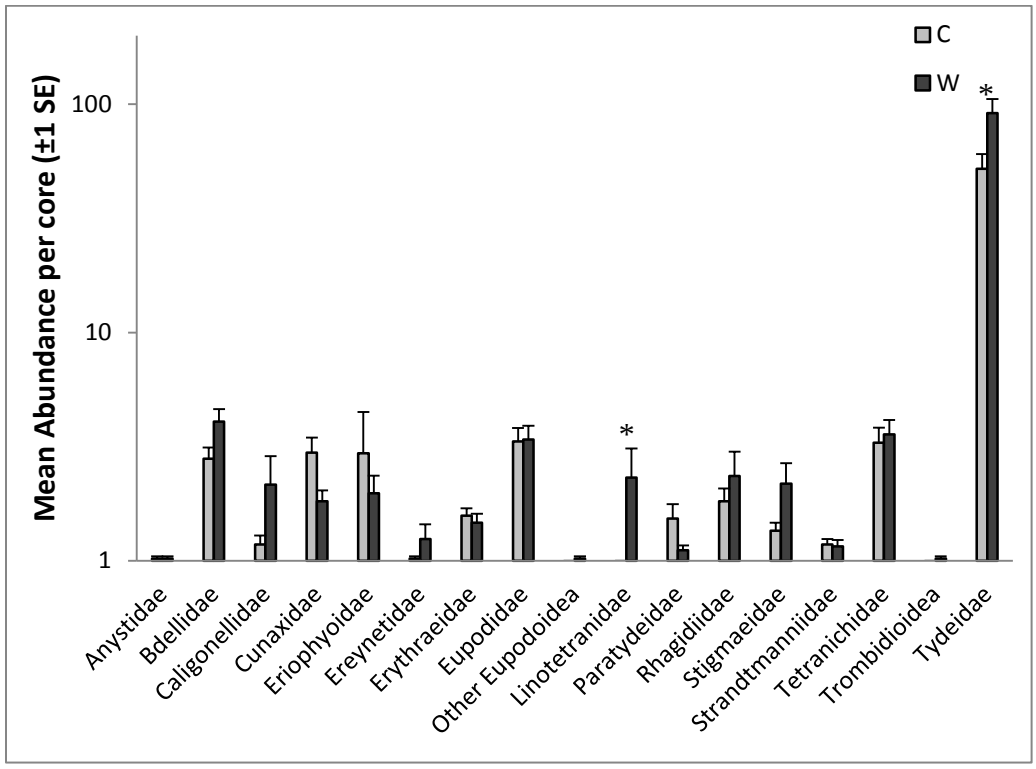

Figure 5.10: Mean abundances (+1) per prostigmatid family under temperature treatments. Light and dark bars indicate control and warming, respectively. The y-axis is logarithmically scaled. Results of ANOVA or KW tests are reported as *$p < 0.05$.

Chapter 6: Summary and synthesis

6.1 Summary

Here I present a summary of Chapters 2-5, addressing my research questions and objectives. Following that is a synthesis of my thesis together with recommendations for future research.

Chapter 2 research question/objectives

1. What subterranean ant taxa and their sternorrhynchan associates can be found at the University of Alberta Research Ranch in Kinsella?
2. Are there any clues, in the shape of particular soil and/or landscape features to determining the presence of subterranean ants that tend root-feeding sternorrhynchans?
3. Are there any specific plant-insect or ant-sternorrhynchan associations, and if so, how exclusive are these associations?

Throughout my thesis research it became apparent that much baseline data on soil biota in Alberta are lacking. In Chapter 2 I and my colleagues identified over a quarter of the province's recorded ant species in a relatively small geographical area. I found that it is exceedingly difficult to observe any above-ground signs of subterranean ants or their sternorrhynchan symbionts, and that they show no plant-host species specificity. However, almost all were collected from graminoids. It also became clear that most ant species in my study area can establish symbiotic relationships with multiple species of aphids or mealybugs. With the exception of a very few aphids that I found in the absence of ants, all Sternorrhyncha were found with an ant host, and while I did not find Sternorrhyncha in all individual ant nests, they were found with all "subterranean" ant species at least once. This suggests that this phenomenon is much more wide spread than initially thought, particularly in grasslands, keeping in mind that the Sternorrhyncha were almost exclusively collected from graminoid roots and root crowns. It also suggests a diffuse rather than species-specific type of mutualism. None the less, while not quantified, I observed ants picking up aphids and carrying them to safety upon breaching the ant

nests; sometimes ant larvae were present but were forgone for the Sternorrhyncha indicating some form of adaptation to protect this resource for the ants.

The paucity of research literature on the subject is surprising considering the possibly significant impacts of this below-ground herbivory caused by the Sternorrhyncha (but see LaPolla et al., 2002; Stuart and Polavarapu, 2002; Kishimoto-Yamada et al., 2005); I have even observed ants tending aphids on dandelion root crowns in my own back yard in Edmonton, making me suspect that ants, whether mutualistically beneficial or not, are exploiting root feeding sternorrhynchans in Alberta far beyond the confines of a single native fescue grassland. Besides pursuing this research in grasslands, I recommend future research to also consider whether this interaction can also be found in ecoregions other than grasslands.

Chapter 3 research question/objectives

1. Gather new length, width and weight measurements from a taxonomically and morphologically diverse array of Albertan soil mites.
2. Review all published body weight estimation formulae
3. How well do published weight-estimation models perform when tested with the new data from Albertan mites?

In contrast to the very limited volume of published literature on subterranean ants, mite biomass estimation has a much richer history. Many authors over the past 40 years have attempted to estimate mite body weights in order to calculate their biomass in soil communities (e.g. Lebrun, 1971; Rogers et al., 1977; Hódar, 1996; Caruso and Migliorini, 2009). However, very few have attempted to validate their equations with independently gathered data. Comparing all of these equations to newly collected bodyweight data, I have shown that some equations, in particular that of Lebrun (1971), work remarkably well. However, it also became clear that biomass of oribatids mites is the most accurately estimated, while that of the Prostigmata is relatively poorly predicted by the few equations specifically built for them. While there is some work to be done, overall this is good news for much ecological research (e.g. Berg et al., 1998; De Deyn et al., 2003; Scheu et al., 2003; Holtkamp et al., 2008; Mulder et al., 2008; Bokhorst et al., 2012) that has been performed in the past relying on these relatively untested estimation methods.

Chapter 4

1. Do short-term drought, warming, and defoliation alter abundance, biomass, taxon richness, and assemblage structure of temperate grassland soil mites in favour of drought-adapted taxa?

While short-term warming and defoliation failed to produce any significant changes to mite richness, abundance, or biomass, drought caused mite abundance and biomass to increase. This increase, which has not previously been reported in the literature, was mostly driven by particular prostigmatid taxa, and by oribatid juveniles. The reason for this increase still eludes me, as the environmental measures correlating with the increase of these mite taxa do not sufficiently explain the observed pattern. While the mechanism is obscure, there may be clues in the duration of treatment. I looked at soil microarthropods after the drought treatment ran for a relatively short period of time (a little over 3 months), whereas other studies are analyzed after a much longer treatment period (6 years; Lindberg and Bengtsson, 2006; 3 field seasons, Chapter 5 of this thesis). This short summer drought is possibly a time span that the some grassland soil mites are adapted to, and as a result can exploit a temporary resource not measured in my analysis. Two published short term drought experiments showed a reduction in mite abundance, although only oribatids were observed. However, one of these studies was performed in a spruce and beech forest (Taylor and Wolters, 2005) and the other in a Mediterranean pine forest (Tsiafouli et al., 2005), suggesting that the responses I observed may be unique to (semi-arid) grasslands. Finally, mite populations are known to fluctuate throughout the year (Block, 1966), possibly causing differences in sampling dates to skew observations; using only a single time point during the year to sample mite assemblages demand caution when comparing results between studies.

Chapter 5

1. What effects do treatments simulating climate change and variation in grazing management (reduced and increased precipitation, warming, and defoliation) over three consecutive summers, have on microarthropod assemblages in a temperate grassland

community? Specifically, how do these factors, and their possible interactions, affect soil mite diversity, abundance, biomass, and assemblage structure?

All climate change treatments elicited responses from soil mites, although the response differed between taxa. As expected, drought was the strongest driver, reducing overall mite taxon richness, abundance, and biomass. However, prostigmatid abundance and biomass were not negatively affected. Instead, an interaction between grazing and warming showed that while grazing negatively affected mites, and warming did so positively, when combined the effect of warming was negated by high intensity defoliation. Prostigmata and occasionally Endeostigmata are traditionally considered the numerically dominant taxon in grasslands; however, when comparing community dominance by biomass it becomes clear that oribatid mites outweigh the Prostigmata (Appendix II, Table II.1). While it is still difficult to determine what influence these changes to the mite community will have on the rest of the ecosystem, we can tentatively say that drought is a concern because it does negatively affect mite abundance and diversity. In addition, while our intensity of warming does not pose a threat by itself it may interact with grazing, if too much of the vegetation is removed.

6.2 Discussion and synthesis

6.2.1 Diversity

This thesis touches on a variety of topics, and together they make it clear that there is still much work to be done in the field of soil ecology, and particularly on soil biota. Many ecologists are doing excellent work modelling soil food webs, or doing larger community style analyses on soil biota (e.g. Holtkamp et al., 2008; Malmstrom et al., 2009; Schon et al., 2012), however, much basic and fundamental data is missing.

Of the 12 species of Sternorrhyncha found to be tended by ants at Kinsella (Chapter 2), three mealybug species were new records for Canada, and one was an undescribed species of aphid. Of the estimated 500,000-1,000,000 mite species worldwide (of which the majority is edaphic) (Krantz and Walter, 2009), only about 55,000 have been described to date (Walter and Proctor, 1999). Not only is there a shortage of taxonomic experts (Guerra-García et al., 2008), the diversity is also overwhelming. In my field site I identified at least 115 taxa of mites, despite

no Prostigmata having been identified to species, and most not to genus. Of these species many were not yet reported for Alberta, or only recently so (Walter et al., 2011). Some of those collected mites were undescribed species; one of those mite species belongs to the Strandtmanniidae, a new family record for Canada. The diversity that I observed at Kinsella is similar to what has been reported for rough fescue prairie at Porcupine Hills near Stavely, Alberta, by Clapperton et al. (2002), and is generally in agreement with taxa found in other Canadian grassland types (Behan-Pelletier and Kanashiro, 2010).

Developments in molecular biology have made soil biota more accessible to scientific study; however, most of this research is focussed on microbial life in the soil (e.g. Zhang et al., 2005). DNA barcoding of mites and other soil invertebrates may alleviate some of the problems (Young et al., 2012), but with just an identity code, one cannot do much more than diversity research, missing out on morphological clues to the organism's life history.

6.2.2 Natural history

Dealing with this overwhelming diversity is a challenge by itself, but adding to ecological complexity is the increasing evidence that many soil arthropod taxa are opportunistic and omnivorous (Moore et al., 1988; Walter, 1988), and may change their feeding preference based on what resources are available. Some work has been done on carbohydrase activities in mites, and stable isotope analysis (Siepel and De Ruiter-Dijkman, 1993; Schneider et al., 2004), to try to establish functional groups or feeding guilds. However, these studies cannot confirm whether the results are broadly applicable to communities outside of the limited study area.

My study on somewhat mundane ants and their root-feeding sternorrhynchan symbionts also identifies a gap in our basic knowledge on interspecific relationships of soil animals. As another example, my collections revealed a previously undescribed uropodine mite, *Trachyuropoda kinsella*, that may be associated with ant nests (Kontschán et al., 2010). Some closely related species of *Trachyuropoda* are indeed ant-associates, but without direct observation, we can only speculate. This lack of relatively basic observational data further complicates our attempts to predict how changes in mite assemblages will affect the rest of the

ecosystem, and forces “big picture” ecologists to sometimes make precarious assumptions to fit their models.

6.2.3 Methods

If extreme diversity and a lack of basic life history and interspecific behavioural data are not challenging enough, soil ecologists have an additional impediment; due to the opaque nature of soil, and the small size of most of its invertebrate inhabitants, it is not possible to observe the biota directly. Instead, we rely on extracting the organisms through various techniques, depending on the targeted taxa. However, all of these techniques are known to be biased, or inefficient depending on the soil type, particularly for microinvertebrates (McSorley and Walter, 1991). For one of my studies, I chose to use kerosene floatation as an extraction method (Appendix III). This method is an adaptation of the hexane flotation method (Walter et al., 1987), which I modified to make more practical for samples from Kinsella. The extractions were labour intensive, but had a very high extraction efficiency, and samples did not need to be rushed to be extracted while microarthropods were still alive, as samples can be stored in ethanol for long periods before extraction. Researchers have been aware of Tullgren, Berlese, and high gradient extractor biases for a long period of time (Andre et al., 2002), but the ease of use of these live-extraction methods has kept them as preferred approach. I suggest that future studies use kerosene extraction to determine which taxa are poorly represented by the traditional live-extraction techniques. More importantly, the current practice confirms that we knowingly harbour a skewed view of what organisms constitute the soil community.

When microarthropods are extracted, they are usually counted to establish abundance. When biomass data is required, it is often obtained by estimating body weights. However, as I show in Chapter 3, blind faith in the reliability of all estimation formulae for mites is not always warranted. Many formulae have rarely or never been reassessed for accuracy, and if they have been, it is not with newly acquired mite data, but rather with measures from previous, sometimes relatively old, publications. While a few formulae work well for some groups like Oribatida and Mesostigmata, others show strong over- or under-estimations, particularly for Prostigmata. I hope that future researchers are careful in choosing an appropriate estimation formula, weigh

more mites from different habitats and of different body forms, and improve on existing body weight estimation formulae.

6.2.4 Climate change

The induced environmental changes in my experiments have shown that mite assemblages are susceptible to change, particularly by drought, but also by warming and defoliation to some extent. The consequences for the rest of the grassland community at Kinsella are difficult to predict without more focused and controlled mesocosm experiments to tease out specific mechanisms. However, we can make some predictions. Natural grasslands this far north in Alberta are devoid of earthworms due to historical glaciation, implying that oribatid mites may be one of the few groups of organisms that fragment organic detritus here, increasing its accessibility for primary decomposers. A decrease in the abundance of these mites may reduce decomposition rates. In addition, drought also influences primary decomposers directly (Jensen et al., 2003; Liu et al., 2009), which would only exacerbate the effects. As more results are forthcoming from other large scale climate change experiments, we will be able to piece together how generalizable my results are.

6.2.5 Future direction

Large scale experiments such as the one described in this thesis (Chapter 4 and 5) give us a unique opportunity to observe the net outcome for a particular set of environmental alterations in a natural setting, and allow for interactions between treatments. These types of experiments are in great need of replication in different regions, and I encourage other researchers to do so.

However, maybe more importantly, there is an even greater need for basic natural-history and observational studies on soil organisms. Currently, soil microbial diversity is a hot topic, mostly due to the advent of molecular techniques (Hirsch et al., 2010). This is a great development, but in our rush to do a multitude of diversity analyses, we should not lose sight of one of the most important end goals: understanding what actually happens in soil. To do this, we need to know what lives in the soil, and what those inhabitants do. While my research has focussed on mites, there is a multitude of other small organisms like protozoa, nematodes, springtails, proturans, pauropods, and tardigrades, which are in need of a closer look. It is this

diversity and the interconnectedness that makes soil ecology so challenging. Soil has been referred to as “the planet’s most complex biomaterial” (Young and Crawford, 2004) for good reason.

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Appendix I

Table I.1: Table of all identified taxa at fine taxonomic levels, including their total abundance (# individuals per core), biomass (µg per core), and a count of how many samples (cores) the taxon was found in.

		Abundance			Biomass (µg)			
(Sub) order/ cohort	Family, genus, species	Total	Mean	Range	Total	Mean	Range	Present in # of samples (out of 24)
Oribatida	Unidentified juvenile	**419**	17.5	0-63	**882.8**	36.8	0-132.7	**23**
Oribatida	Brachychthoniidae sp.1	**74**	3.1	0-20	**45.7**	1.9	0-12.4	**14**
Oribatida	Brachychthoniidae sp.2	**25**	1.0	0-10	**15.3**	0.6	0-6.1	**7**
Oribatida	Brachychthoniidae sp.3	**9**	0.4	0-4	**5.2**	0.2	0-2.3	**5**
Oribatida	Brachychthoniidae sp.4	**7**	0.3	0-3	**7.4**	0.3	0-3.2	**4**
Oribatida	Brachychthoniidae sp.5	**1**	0.0	0-1	**0.2**	0.0	0-0.2	**1**
Oribatida	Enarthronota sp.1	**193**	8.0	0-27	**60.0**	2.5	0-8.4	**18**
Oribatida	Enarthronota sp.2	**3**	0.1	0-3	**0.8**	0.0	0-0.8	**1**
Oribatida	Eremaeidae, *Eueremaeus masinasin* Behan-Pelletier, 1993	**14**	0.6	0-4	**236.1**	9.8	0-67.4	**8**
Oribatida	Galumnidae sp.1	**23**	1.0	0-9	**540.7**	22.5	0-211.6	**6**
Oribatida	Galumnidae sp.2	**3**	0.1	0-3	**114.6**	4.8	0-114.6	**1**
Oribatida	Gehypochtoniidae, *Gehypochthonius*	**23**	1.0	0-9	**31.8**	1.3	0-12.5	**6**
Oribatida	Gymnodamaeidae, *Joshuella*	**8**	0.3	0-3	**40.0**	1.7	0-15.0	**5**
Oribatida	Haplozetidae, *Peloribates*	**23**	1.0	0-9	**315.7**	13.2	0-123.5	**8**
Oribatida	Hypochthoniidae, *Hypochthonius rufulus* Koch, 1835	**1**	0.0	0-1	**24.7**	1.0	0-24.7	**1**
Oribatida	Licnodamaeidae, *Licnodamaeus*	**3**	0.1	0-1	**7.6**	0.3	0-2.6	**3**
Oribatida	Oppiidae, *Discoppia*	**23**	1.0	0-6	**13.1**	0.5	0-3.4	**7**
Oribatida	Oppiidae, *Oppiella*	**2**	0.1	0-1	**5.0**	0.2	0-2.5	**2**
Oribatida	Oppiidae, *Ramusella*	**98**	4.1	0-64	**148.4**	6.2	0-96.9	**11**
Oribatida	Oribatelidae, *Oribatella*	**8**	0.3	0-4	**72.1**	3.0	0-36.0	**3**
Oribatida	Oribatellidae, *Tectoribates*	**2**	0.1	0-2	**9.0**	0.4	0-9.0	**1**
Oribatida	Oribatulidae, *Zygoribatula*	**2**	0.1	0-1	**22.0**	0.9	0-11.0	**2**

		Abundance			Biomass (µg)			
(Sub) order/ cohort	Family, genus, species	Total	Mean	Range	Total	Mean	Range	Present in # of samples (out of 24)
Oribatida	Oribatulidae, *Zygoribatula*	**9**	0.4	0-4	**149.9**	6.2	0-66.6	**5**
Oribatida	Parakalummidae, *Neoribates*	**1**	0.0	0-1	**20.1**	0.8	0-20.1	**1**
Oribatida	Passalozetidae, *Bipassalozetes*	**7**	0.3	0-7	**28.9**	1.2	0-28.9	**1**
Oribatida	Phenopelopidae, *Peloptulus*	**6**	0.3	0-2	**91.3**	3.8	0-30.5	**4**
Oribatida	Scheloribatidae, *Hemileius*	**1**	0.0	0-1	**3.2**	0.1	0-3.2	**1**
Oribatida	Scheloribatidae, *Scheloribates pallidulus* (Koch, 1841)	**1**	0.0	0-1	**12.6**	0.5	0-12.6	**1**
Oribatida	Tectocepheidae, *Tectocepheus sarekensis* Trägårdh, 1910	**141**	5.9	0-30	**961.0**	40.0	0-204.5	**20**
Oribatida	Tectocepheidae, *Tectocepheus velatus*(Michael, 1880)	**14**	0.6	0-6	**67.3**	2.8	0-28.9	**8**
Oribatida	Thyrisomidae, *Banksinoma spinifera* (Hammer, 1952)	**1**	0.0	0-1	**9.4**	0.4	0-9.4	**1**
Oribatida	Trhypochthoniidae, *Trhypochthonius tectorum* (Berlese, 1896)	**48**	1.0	0-16	**508.6**	10.6	0-119.7	**12**
Astigmata	Acaridae, *Tyrophagus*	**2439**	50.8	1-443	**3840.3**	80.0	4.6-267.5	**24**
Prostigmata	Unidentified juvenile	**7**	0.3	0-3	**0.8**	0.0	0-0.4	**5**
Prostigmata	Bdellidae	**29**	1.2	0-7	**563.6**	23.5	0-136.1	**11**
Prostigmata	Cunaxidae	**134**	5.6	0-30	**553.9**	23.1	0-124.0	**20**
Prostigmata	Eriphyoidae	**30**	1.3	0-12	**7.3**	0.3	0-2.9	**7**
Prostigmata	Erythraeidae	**14**	0.3	0-4	**85.0**	1.8	0-11.3	**9**
Prostigmata	Eupodidae	**36**	1.5	0-6	**62.8**	2.6	0-10.5	**13**
Prostigmata	Unidentified Eupodoidea	**20**	0.8	0-20	**3.3**	0.1	0-3.3	**1**
Prostigmata	Linotetranidae sp.1	**14**	0.6	0-6	**71.5**	3.0	0-30.7	**6**
Prostigmata	Linotetranidae sp.2	**1**	0.0	0-1	**5.1**	0.2	0-5.1	**1**
Prostigmata	Paratydeidae	**9**	0.4	0-3	**15.8**	0.7	0-5.3	**6**
Prostigmata	Rhagidiidae	**7**	0.3	0-1	**9.3**	0.4	0-1.3	**7**
Prostigmata	Stigmaeidae sp.1	**68**	2.8	0-13	**263.9**	11.0	0-50.5	**19**
Prostigmata	Stigmaeidae sp.2	**12**	0.5	0-4	**49.7**	2.1	0-16.6	**6**
Prostigmata	Tetranychidae (non-Bryobiinae)	**14**	0.6	0-2	**84.0**	3.5	0-12.0	**9**
Prostigmata	Tetranychidae, Bryobiinae	**21**	0.9	0-9	**248.6**	10.4	0-106.6	**8**
Prostigmata	Tydeidae sp.1	**1551**	64.6	1-162	**816.4**	34.0	0.5-85.3	**24**
Prostigmata	Tydeidae sp.2	**1890**	78.8	3-254	**220.4**	9.2	0.4-29.6	**24**
Heterostigmata	Pygmephoridae/Microdispidae	**48**	2.0	0-24	**27.5**	1.1	0-13.8	**5**
Heterostigmata	Microdispidae	**35**	1.5	0-8	**19.8**	0.8	0-4.5	**6**

		Abundance			Biomass (µg)			
(Sub) order/ cohort	Family, genus, species	Total	Mean	Range	Total	Mean	Range	Present in # of samples (out of 24)
Heterostigmata	Pygmephoridae	**38**	1.6	0-18	**21.7**	0.9	0-10.3	**8**
Heterostigmata	Scutacaridae	**258**	10.8	0-73	**132.3**	5.5	0-37.4	**17**
Heterostigmata	Tarsonemidae	**187**	7.8	0-28	**85.5**	3.6	0-12.8	**20**
Mesostigmata	Unidentified juvenile	**50**	2.1	0-9	**187.4**	7.8	0-33.7	**17**
Mesostigmata	Unidentified male	**4**	0.2	0-2	**18.0**	0.8	0-9.0	**3**
Mesostigmata	Ascidae, *Arctoseius*	**17**	0.7	0-4	**51.8**	2.2	0-12.2	**8**
Mesostigmata	Ascidae, *Asca*	**27**	1.1	0-6	**126.9**	5.3	0-28.2	**12**
Mesostigmata	Ascidae, *Gamasellodes*	**1**	0.0	0-1	**2.0**	0.1	0-2.1	**1**
Mesostigmata	Laelapidae, *Cosmolaelaps* sp.1	**8**	0.3	0-4	**47.8**	2.0	0-23.9	**4**
Mesostigmata	Laelapidae, *Cosmolaelaps* sp.2	**7**	0.3	0-2	**55.2**	2.3	0-15.8	**6**
Mesostigmata	Laelapidae, *Euandrolaelaps*	**7**	0.3	0-2	**82.0**	3.4	0-23.4	**6**
Mesostigmata	Laelapidae, *Geolaelaps*	**5**	0.2	0-2	**38.8**	1.6	0-15.5	**3**
Mesostigmata	Laelapidae, *Ololaelaps*	**5**	0.2	0-3	**206.0**	8.6	0-123.6	**2**
Mesostigmata	Laelapidae, *Pseudoparasitus*	**7**	0.3	0-5	**148.2**	6.2	0-105.9	**2**
Mesostigmata	Macrochelidae, *Macrocheles schaeferi* Walter, 1988	**2**	0.1	0-1	**50.5**	2.1	0-25.2	**2**
Mesostigmata	Phytoseiidae, *Amblyseius*	**57**	2.4	0-12	**534.6**	22.3	0-112.5	**14**
Mesostigmata	Phytoseiidae, *Neoseiulus*	**19**	0.8	0-5	**122.9**	5.1	0-32.3	**10**
Mesostigmata	Rhodacaridae, *Rhodacarellus*	**29**	1.2	0-12	**47.6**	2.0	0-19.7	**10**
Mesostigmata	Uropodina (non-*Trachyuropoda*)	**23**	1.0	0-9	**389.5**	16.2	0-152.4	**6**
Mesostigmata	Uropodina, *Trachyuropoda Kinsella* Kontschán, 2011	**22**	0.5	0-12	**667.0**	13.9	0-170.1	**4**
Mesostigmata	Zerconidae	**4**	0.2	0-2	**20.5**	0.9	0-10.3	**3**
Endeostigmata	Alicorhagiidae, *Alicorhagia* or *Stigmalycus*	**42**	1.8	0-11	**64.1**	2.7	0-16.8	**9**
Endeostigmata	Nanorchestidae, *Nanorchestes*	**16**	0.7	0-4	**3.4**	0.1	0-0.9	**8**
Endeostigmata	Nanorchestidae, *Speleorchestes*	**11**	0.5	0-10	**5.7**	0.2	0-5.2	**2**

Table I.2: Summary table of identified taxa at coarse taxonomic levels, including their total abundance (# individuals per core), biomass (µg per core), and a count of how many samples (cores) the taxon was found in.

	Abundance			Biomass (µg)			
Summary of higher taxa	Total	Mean	Range	Total	Mean	Range	Present in # of samples (out of 24)
Total Acari	**8418**	350.8	31-830	**14509.0**	463.4	123.4-1078.9	**24**
Acariformes	**8124**	338.5	26-816	**11712.1**	361.1	63.7-934.5	**24**
Parasitiformes (Mesostigmata)	**294**	12.3	0-33	**2796.8**	102.3	0-539.3	**23**
Oribatida	**3632**	151.3	13-467	**8290.7**	268.0	45.1-692.2	**24**
Oribatida excl. Astigmata	**1193**	49.7	5-121	**4450.3**	132.2	6.7-497.9	**24**
Astigmata	**2439**	101.6	8-444	**3840.3**	135.8	29.0-437.1	**24**
Prostigmata	**4423**	184.3	12-442	**3348.2**	91.3	18.4-352.6	**24**
Prostigmata excl. Heterostigmata	**3857**	160.7	10-432	**3061.4**	81.3	17.2-332.8	**24**
Heterostigmata	**566**	23.6	0-110	**286.8**	10.0	0.9-45.8	**23**
Endeostigmata	**69**	2.9	0-22	**73.2**	1.8	0-20.9	**15**

Appendix II

Table II.1: All identified taxa, including their total abundance (# individuals per core), biomass (µg per core), and a count of how many samples (cores) the taxon was found in.

		Abundance			Biomass (µg)			
(Sub) order/ cohort	Family, genus, species	Total	Mean	Range	Total	Mean	Range	Present in # of samples (out of 90)
Oribatida	Unidentified juveniles	**767**	8.522	0 - 57	**460.2**	5.1	0 - 34.2	**76**
Oribatida	Brachychthoniidae sp.1	**21**	0.233	0 - 10	**13.0**	0.1	0 - 6.2	**5**
Oribatida	Brachychthoniidae sp.2	**62**	0.689	0 - 22	**37.9**	0.4	0 - 13.4	**14**
Oribatida	Brachychthoniidae sp.3	**15**	0.167	0 - 8	**8.7**	0.1	0 - 4.6	**4**
Oribatida	Brachychthoniidae sp.4	**95**	1.056	0 - 45	**101.1**	1.1	0 - 47.9	**14**
Oribatida	Ceratozetidae, *Ceratozetes* sp.	**1**	0.011	0 - 1	**13.1**	0.1	0 - 13.1	**1**
Oribatida	Enarthronota sp.2	**591**	6.567	0 - 221	**183.6**	2.0	0 - 68.6	**35**
Oribatida	Enarthronota sp.3	**165**	1.833	0 - 71	**82.5**	0.9	0 - 35.5	**9**
Oribatida	Enarthronota sp.4	**1**	0.011	0 - 1	**0.0**	0.0	0 - 0.0	**0**
Oribatida	Eremaeidae, *Eueremaeus masinasin* Behan-Pelletier, 1993	**135**	1.5	0 - 13	**2,276.3**	25.3	0 - 219.2	**40**
Oribatida	Galumnidae sp.1	**8**	0.089	0 - 2	**188.1**	2.1	0 - 47.0	**6**
Oribatida	Galumnidae sp.2	**2**	0.022	0 - 2	**76.4**	0.8	0 - 76.4	**1**
Oribatida	Gehypochthoniidae, *Gehypochthonius*	**21**	0.233	0 - 6	**29.1**	0.3	0 - 8.3	**9**
Oribatida	Gymnodamaeidae, *Gymnodamaeus*	**10**	0.111	0 - 2	**461.0**	5.1	0 - 92.2	**7**
Oribatida	Gymnodamaeidae, *Joshuella* sp.	**25**	0.278	0 - 10	**125.1**	1.4	0 - 50.0	**6**
Oribatida	Haplozetidae, *Peloribates* sp. 4 DEW	**147**	1.633	0 - 18	**2,017.4**	22.4	0 - 247.0	**41**
Oribatida	Haplozetidae, *Pilobates* sp.	**2**	0.022	0 - 2	**26.6**	0.3	0 - 26.6	**1**
Oribatida	Haplozetidae, *Xylobetes* sp.	**2**	0.022	0 - 1	**35.5**	0.4	0 - 17.8	**2**
Oribatida	Licnodamaeidae, *Licnodamaeus* sp.	**1**	0.011	0 - 1	**2.5**	0.0	0 - 2.5	**1**
Oribatida	Licnodamaeidae, *Licnodamaeus* sp. 1 DEW	**4**	0.044	0 - 4	**10.2**	0.1	0 - 10.2	**1**
Oribatida	Oppiidae, *Discoppia* sp.	**61**	0.678	0 - 14	**34.8**	0.4	0 - 8.0	**23**

Oribatida	Oppiidae, *Oppiella* sp.	**40**	0.444	0 -	28	**100.4**	1.1	0 -	70.3	**9**
Oribatida	Oppiidae (unidentified)	**253**	2.811	0 -	29	**383.2**	4.3	0 -	43.9	**47**
Oribatida	Oppioidae	**5**	0.056	0 -	1	**5.4**	0.1	0 -	1.1	**5**
Oribatida	Oribatellidae, *Oribatella* sp.	**271**	3.011	0 -	37	**2,441.0**	27.1	0 -	333.3	**43**
Oribatida	Oribatellidae/ Achipteriidae, *Tectoribates* sp.	**6**	0.067	0 -	3	**26.9**	0.3	0 -	13.4	**4**
Oribatida	Oribatulidae, *Oribatula* sp. 1 DEW	**2**	0.022	0 -	1	**16.9**	0.2	0 -	8.5	**2**
Oribatida	Oribatulidae, *Zygoribatula* sp. 1 DEW	**4**	0.044	0 -	1	**43.9**	0.5	0 -	11.0	**4**
Oribatida	Oribatulidae, *Zygoribatula* sp.2	**3**	0.034	0 -	1	**56.2**	0.6	0 -	18.7	**3**
Oribatida	Passalozetidae, *Bipassalozetes* sp.	**2**	0.022	0 -	1	**6.2**	0.1	0 -	3.1	**2**
Oribatida	Passalozetidae, *Bipassalozetes* cf. *intermedius* (Mihelĉič, 1954)	**4**	0.044	0 -	4	**19.3**	0.2	0 -	19.3	**1**
Oribatida	Phenopelopidae, *Peloptulus* sp.	**51**	0.567	0 -	8	**776.4**	8.6	0 -	121.8	**21**
Oribatida	Scheloribatidae, *Scheloribates* sp.	**1**	0.011	0 -	1	**12.6**	0.1	0 -	12.6	**1**
Oribatida	Tectocepheidae, *Tectocepheus sarekensis* Trägårdh, 1910	**733**	8.144	0 -	44	**4,995.7**	55.5	0 -	299.9	**74**
Oribatida	Tectocepheidae, *Tectocepheus velatus* (Michael, 1880)	**66**	0.733	0 -	16	**317.4**	3.5	0 -	76.9	**20**
Oribatida	Thyrisomidae, *Banksinoma* sp.	**1**	0.011	0 -	1	**9.4**	0.1	0 -	9.4	**1**
Oribatida	Trhypochthoniidae, *Trhypochthonius tectorum* Berlese, 1880 (adult)	**2**	0.022	0 -	2	**59.8**	0.7	0 -	59.8	**1**
Oribatida	Trhypochthoniidae, *Trhypochthonius tectorum* Berlese, 1880 (juvenile)	**3**	0.033	0 -	3	**22.1**	0.2	0 -	22.1	**1**
Prostigmata	Anystidae	**2**	0.022	0 -	1	**27.2**	0.3	0 -	13.6	**2**
Prostigmata	Bdellidae	**219**	2.433	0 -	16	**4,256.4**	47.3	0 -	311.0	**58**
Prostigmata	Caligonellidae, *Molothrognathus* sp.1	**60**	0.667	0 -	26	**156.3**	1.7	0 -	67.7	**8**
Prostigmata	Cunaxidae	**126**	1.4	0 -	14	**520.8**	5.8	0 -	57.9	**41**
Prostigmata	Eriophyoidae	**132**	1.467	0 -	69	**32.1**	0.4	0 -	16.8	**22**
Prostigmata	Ereynetidae	**12**	0.133	0 -	9	**21.7**	0.2	0 -	16.3	**4**
Prostigmata	Erythraeidae	**47**	0.522	0 -	4	**489.3**	5.4	0 -	41.6	**32**
Prostigmata	Eupodidae	**213**	2.367	0 -	15	**371.8**	4.1	0 -	26.2	**55**
Prostigmata	Unidentified Eupodoidea	**1**	0.011	0 -	1	**0.0**	0.0	0 -	0.0	**0**
Prostigmata	Linotetranidae	**59**	0.656	0 -	32	**301.4**	3.3	0 -	163.4	**6**
Prostigmata	Paratydeidae	**29**	0.322	0 -	9	**50.9**	0.6	0 -	15.8	**14**
Prostigmata	Rhagidiidae	**98**	1.089	0 -	28	**130.3**	1.4	0 -	37.2	**29**
Prostigmata	Stigmaeidae sp.1	**65**	0.722	0 -	16	**252.2**	2.8	0 -	62.1	**22**
Prostigmata	Stigmaeidae sp. 2	**4**	0.044	0 -	2	**16.6**	0.2	0 -	8.3	**3**
Prostigmata	Strandtmanniidae	**15**	0.167	0 -	2	**39.2**	0.4	0 -	5.2	**11**
Prostigmata	Tetranychidae	**91**	1.011	0 -	13	**545.8**	6.1	0 -	78.0	**31**
Prostigmata	Tetranychidae, Bryobiinae msp. 1	**126**	1.4	0 -	21	**1,491.8**	16.6	0 -	248.6	**33**
Prostigmata	Tetranychidae, Bryobiinae msp. 2	**2**	0.022	0 -	1	**0.0**	0.0	0 -	0.0	**0**
Prostigmata	Trombidioidea	**1**	0.011	0 -	1	**1.5**	0.0	0 -	1.5	**1**

Prostigmata	Tydeidae sp. 1	**1,964**	21.82	0 -	204	**229.0**	2.5	0 -	23.8	**84**
Prostigmata	Tydeidae sp. 2	**1,412**	15.69	0 -	170	**348.0**	3.9	0 -	41.9	**78**
Prostigmata	Tydeidae sp. 3	**68**	0.756	0 -	61	**146.2**	1.6	0 -	131.1	**4**
Prostigmata	Tydeidae sp. 4	**18**	0.2	0 -	5	**28.4**	0.3	0 -	7.9	**7**
Prostigmata	Unidentified Tydeidae	**2,914**	32.38	0 -	158	**1,533.9**	17.0	0 -	83.2	**87**
Mesostigmata	Unidentified juveniles	**49**	0.544	0 -	7	**201.3**	2.2	0 -	28.8	**24**
Mesostigmata	Unidentified males	**2**	0.022	0 -	1	**12.3**	0.1	0 -	6.2	**2**
Mesostigmata	Ascidae (unidentified)	**28**	0.311	0 -	9	**80.3**	0.9	0 -	25.8	**14**
Mesostigmata	Ascidae, *Antennoseius* (*Antennoseius*) sp.	**1**	0.011	0 -	1	**9.8**	0.1	0 -	9.8	**1**
Mesostigmata	Ascidae, *Arctoseius* sp.	**6**	0.067	0 -	1	**21.8**	0.2	0 -	3.6	**6**
Mesostigmata	Ascidae, *Asca* sp.	**28**	0.311	0 -	8	**112.5**	1.2	0 -	32.1	**11**
Mesostigmata	Ascidae, *Asca nesoica* (Athias-Henriot, 1961)	**20**	0.222	0 -	3	**88.0**	1.0	0 -	13.2	**16**
Mesostigmata	Ascidae, Asca cf *piloja* (Hurlbutt, 1963)	**34**	0.378	0 -	5	**124.4**	1.4	0 -	18.3	**18**
Mesostigmata	Ascidae, *Gamasellodes* cf. *claudiae* Walter (or nr *claudiae*)	**2**	0.022	0 -	2	**6.4**	0.1	0 -	6.4	**1**
Mesostigmata	Digamasellidae, *Dendrolaelaps* sp.	**2**	0.022	0 -	2	**10.3**	0.1	0 -	10.3	**1**
Mesostigmata	Eviphididae (unidentified)	**8**	0.09	0 -	7	**5.1**	0.1	0 -	5.1	**1**
Mesostigmata	Eviphididae, *Alliphis* sp.	**3**	0.033	0 -	3	**21.0**	0.2	0 -	21.0	**1**
Mesostigmata	Eviphididae, *Copriphis* sp.	**33**	0.367	0 -	5	**494.2**	5.5	0 -	86.5	**19**
Mesostigmata	Laelapidae (unidentified)	**58**	0.644	0 -	5	**302.2**	3.4	0 -	26.1	**28**
Mesostigmata	Laelapidae, *Cosmolaelaps* sp. *claviger* group	**30**	0.333	0 -	4	**185.4**	2.1	0 -	24.7	**18**
Mesostigmata	Laelapidae, *Cosmolaelaps* n. sp. *cuneifer* group	**2**	0.022	0 -	1	**9.7**	0.1	0 -	4.8	**2**
Mesostigmata	Laelapidae, *Cosmolaelaps* sp. ss *vacua* group	**9**	0.1	0 -	5	**42.8**	0.5	0 -	23.8	**2**
Mesostigmata	Laelapidae, *Euandrolaelaps*, cf *karawaiewi* (Berlese, 1904)	**18**	0.2	0 -	5	**231.0**	2.6	0 -	64.2	**11**
Mesostigmata	Laelapidae, *Gaeolaelaps* sp. W	**26**	0.292	0 -	4	**170.9**	1.9	0 -	26.3	**15**
Mesostigmata	Laelapidae, *Hypoaspis* sp. B	**19**	0.211	0 -	6	**281.0**	3.1	0 -	88.7	**9**
Mesostigmata	Laelapidae, *Ololaelaps veneta* (Berlese, 1903)	**3**	0.033	0 -	1	**70.6**	0.8	0 -	23.5	**3**
Mesostigmata	Laelapidae, *Pseudoparasitus* sp.	**14**	0.156	0 -	3	**198.6**	2.2	0 -	42.6	**9**
Mesostigmata	Laelapidae, *Stratiolaelaps* sp.	**1**	0.011	0 -	1	**23.0**	0.3	0 -	23.0	**1**
Mesostigmata	Macrochelidae, *Macrocheles schaeferi* (Walter, 1988)	**5**	0.056	0 -	2	**80.9**	0.9	0 -	32.3	**4**
Mesostigmata	Melicharidae, *Proctolaelaps* sp.	**1**	0.011	0 -	1	**7.0**	0.1	0 -	7.0	**1**
Mesostigmata	Phytoseiidae (unidentified)	**31**	0.344	0 -	4	**106.8**	1.2	0 -	13.8	**22**
Mesostigmata	Phytoseiidae, *Amblyseius* sp. nr. *chilicotti* (Chant & Hansell, 1971)	**7**	0.078	0 -	5	**46.9**	0.5	0 -	33.5	**3**
Mesostigmata	Phytoseiidae, *Amblyseius* sp. *nicola* group	**3**	0.033	0 -	1	**19.4**	0.2	0 -	6.5	**3**
Mesostigmata	Phytoseiidae, *Amblyseius isuki* (Chant & Hansel, 1971)	**8**	0.089	0 -	2	**57.2**	0.6	0 -	14.3	**7**
Mesostigmata	Phytoseiidae, *Chelaseius tundra* (Chant & Hansell, 1971)	**3**	0.033	0 -	2	**13.6**	0.2	0 -	9.1	**2**
Mesostigmata	Phytoseiidae, *Neoseiulus iroquois* (Chant & Hansell, 1971)	**27**	0.3	0 -	12	**186.0**	2.1	0 -	82.7	**13**

Mesostigmata	Phytoseiidae, *Neoseiulus salish* (Chant & Hansell, 1971)	**27**	0.3	0 -	4	**134.8**	1.5	0 -	20.0	**18**
Mesostigmata	Phytoseiidae, *Neoseiulus* sp nr *shanksi* (Congdon, 2002)	**1**	0.011	0 -	1	**0.0**	0.0	0 -	0.0	**0**
Mesostigmata	Phytoseiidae, *Neoseiulus vallis* (Schuster & Pritchard, 1963)	**2**	0.022	0 -	1	**9.1**	0.1	0 -	4.6	**2**
Mesostigmata	Rhodacaridae, *Rhodacarellus* sp. nr. *Subterraneus* Willmann, 1934	**89**	0.989	0 -	7	**185.5**	2.1	0 -	14.6	**34**
Mesostigmata	Uropodina sp.	**7**	0.078	0 -	2	**68.6**	0.8	0 -	19.6	**6**
Mesostigmata	Uropodina, *Trachyuropoda kinsella* Kontschán, 2010	**12**	0.133	0 -	2	**387.1**	4.3	0 -	64.5	**10**
Mesostigmata	Zerconidae (unidentified)	**5**	0.056	0 -	2	**21.1**	0.2	0 -	8.5	**4**
Mesostigmata	Zerconidae, *Mixozercon*	**46**	0.511	0 -	6	**260.4**	2.9	0 -	34.0	**23**
Mesostigmata	Zerconidae, *Zercon* sp. nr. *Alaskensis* Sellnick, 1957	**11**	0.122	0 -	7	**54.4**	0.6	0 -	34.6	**4**
Prostigmata (Heterostigmata)	Microdispidae	**486**	5.4	0 -	148	**434.6**	4.8	0 -	154.6	**37**
Prostigmata (Heterostigmata)	Pygmephoridae	**41**	0.456	0 -	10	**23.4**	0.3	0 -	5.7	**12**
Prostigmata (Heterostigmata)	Scutacaridae	**639**	7.1	0 -	81	**327.6**	3.6	0 -	41.5	**48**
Prostigmata (Heterostigmata)	Tarsonemidae	**802**	8.911	0 -	89	**366.9**	4.1	0 -	40.7	**74**
Oribatida	Astigmata	**353**	3.922	0 -	70	**2,315.6**	25.7	0 -	509.9	**51**
Endeostigmata	Alicorhagidae, *Alicorhagia* sp.	**10**	0.111	0 -	4	**15.3**	0.2	0 -	6.1	**6**
Endeostigmata	Nanorchestidae, *Nanorchestes* spp.	**188**	2.089	0 -	43	**48.1**	0.4	0 -	9.3	**22**
Endeostigmata	Nanorchestidae, *Speleorchestes* sp.	**19**	0.211	0 -	6	**9.8**	0.1	0 -	3.1	**9**
Collembola	Unidentified	**3**	0.033	0 -	1	-	-		-	**-**
Collembola	Entomobryidae	**1**	0.011	0 -	1	-	-		-	**-**
Collembola	Hypogastruridae	**138**	1.533	0 -	65	-	-		-	**-**
Collembola	Onychiuridae	**94**	1.044	0 -	16	-	-		-	**-**
Collembola	Sminthuridae	**17**	0.189	0 -	6	-	-		-	**-**
Acari	Total	**14,480**	160.9	0 -	599	**34349.6**	381.7	0 -	1557.3	**89**
Collembola	Total	**253**	2.811	0 -	65	-	-		-	**-**
Oribatida incl. Astigmata	Total	**3,936**	43.73	0 -	273	**17,791.5**	197.7	0 -	1079.2	**86**
Oribatida excl. Astigmata	Total	**3,583**	39.81	0 -	266	**15,475.9**	172.0	0 -	799.0	**84**
Astigmata	Total	**353**	3.922	0 -	70	**2,315.6**	25.7	0 -	509.9	**51**
Prostigmata incl. Heterostigmata	Total	**9,644**	107.2	0 -	533	**11,708.8**	130.1	0 -	567.3	**89**
Prostigmata excl. Heterostigmata	Total	**7,676**	85.29	0 -	365	**10,990.9**	122.1	0 -	548.9	**89**
Heterostigmata	Total	**1,968**	21.87	0 -	168	**717.9**	8.0	0 -	53.8	**78**
Mesostigmata	Total	**681**	7.567	0 -	29	**4,341.6**	48.2	0 -	213.2	**79**
Endeostigmata	Total	**217**	2.411	0 -	43	**73.2**	0.8	0 -	9.3	**33**

Table II.2: Statistical results of mite abundance and biomass analysis.

Abundance			Biomass		
Taxon	**Treatment***	**p-value**	**Taxon**	**Treatment***	**p-value**
Acari[1]	T	0.15	Acari[2]	T	0.09
	D	0.98		D	0.08
	P	0.08		P	**0.00**
	T x D	**0.01**		T x D	0.08
	T x P	0.37		T x P	0.16
	D x P	0.13		D x P	0.41
	T x D x P	0.71		T x D x P	0.65
Oribatida w/out Astigs[1]	T	0.63	Oribatida w/out Astigs[4]	T	0.89
	D	0.45		D	0.32
	P	**0.00**		P	**0.00**
	T x D	0.55		-	-
	T x P	0.33		-	-
	D x P	0.73		-	-
	T x D x P	0.85		-	-
Astigmata[4]	T	0.30	Astigmata[3]	T	0.21
	D	0.86		D	0.40
	P	0.69		P	0.07
	-	-		T x D	0.10
	-	-		T x P	**0.03**
	-	-		D x P	0.41
	-	-		T x D x P	0.30
Prostigmata w/out Heteros[1]	T	**0.04**	Prostigmata w/out Heteros[3]	T	**0.03**
	D	0.74		D	0.10
	P	0.50		P	0.94
	T x D	**0.01**		T x D	**0.03**
	T x P	0.19		T x P	0.18
	D x P	0.21		D x P	0.12
	T x D x P	0.51		T x D x P	0.09
Heterostigmata[1]	T	0.56	Heterostigmata[3]	T	0.30
	D	**0.00**		D	**0.01**
	P	**0.00**		P	**0.00**
	T x D	**0.00**		T x D	**0.00**
	T x P	0.51		T x P	0.48
	D x P	**0.00**		D x P	**0.00**
	T x D x P	0.70		T x D x P	0.53
Mesostigmata[1]	T	0.20	Mesostigmata[2]	T	0.42
	D	**0.05**		D	**0.00**
	P	**0.00**		P	**0.00**
	T x D	0.18		T x D	0.28
	T x P	0.30		T x P	0.68
	D x P	0.86		D x P	0.45
	T x D x P	0.30		T x D x P	0.19
Endeostigmata[4]	T	**0.03**	Endeostigmata[4]	T	0.06
	D	0.08		D	0.08
	P	0.06		P	0.06

Note: *T: temperature, D: defoliation, P: precipitation; [1]Negative binomial distribution, [2]Normal distribution, [3]Gamma distribution, [4]Non-parametric

Statistically significant p-values ($\alpha = 0.05$) are in bold font. N = 90.

Appendix III

Kerosene floatation extraction protocol*

By: Jeffrey Newton 5th December 2007 [Latest edits: 2 June 2013]

Email: jsnewton@ualberta.ca

1. Check if sample is still **fully submerged in 80% ETOH** ensuring it is totally soaked and not partially dried up. This is to avoid using a rotten sample and to keep from having bits floating that are not supposed to float. (Samples used are cores of 5 cm diameter, 10 cm deep, grassland soil from Canadian parklands/fescue prairie.)

2. **Write down** the sample number, dates and separate planned floats. Make sure to leave space for comments. E.g. float was really dirty or soil was clumpy or lots or roots.

3. **Sieve soil** in the (minimum of) 150 μm sieve, making sure to break up the soil and root clumps. Do this in the sink under running water. Make sure not to spill any soil! And rinse fingers, hose, etc. above sieve! (You can use a finer sieve, but I have good results with this. You may lose a few tiny Prostigs but compared to a Tullgren you will have more Prostigs than you have ever extracted, given that they are present in your soilcore.)

4. **Wash the soil out of sieve** using 70% ETOH onto the 500 mL Erlenmeyer using a funnel with large enough bore. Make sure all rinsing is done using 70% ETOH as to not change the ETOH % for the float. Again, rinse ALL soil into the Erlenmeyer (also that of your funnel and spatula).

5. **Add 70% ETOH** up to about 0.5 cm below the neck of the Erlenmeyer and add an extra 0.5-1.0 cm of **kerosene** so the liquid just reaches the neck.(Or start a little higher, it's easier to siphon a smaller surface area, so if your Erlenmeyer neck is long enough, put the ETOH higher. Also, make sure you leave a small air-bubble to mix.)

6. Close Erlenmeyer with a black rubber stopper. Make sure this is tight; you don't want kerosene all over you, or worse, lose your sample! Gently **roll the bottle with its contents** back and forth in your hands making sure the kerosene gets evenly distributed. (**Do not shake**; this will cause your sample to take forever to float.) The less kerosene you see after the mixing the better it has been distributed. You should see finer and finer spheres of kerosene. I mix for around 1-2 minutes.

7. Remove the rubber stopper. Place Erlenmeyer in **vacuum chamber**** at full vacuum for 15 minutes, release vacuum and tap glass to remove air bubbles (see Figure 1). Vacuum for another 15 minutes. (Total vacuum time is 30 minutes.) Be warned, sometimes you sample might bubble violently, so raise the vacuum **slowly** as to not have your sample overflow.

8. GENTLY remove Erlenmeyer from the vacuum chamber and **siphon off the residue layer between the ETOH and the kero†**. Be as thorough as possible. Anything that looks like dirt floating below the kerosene layer should be removed. It's best to siphon until all kero is gone. Deposit this residue into a small 45μm sieve (you really don't want to lose anything at this point). Use 95-97% ETOH to rinse out the kerosene. The high concentration of ETOH should dissolve the kero. This step is critical, otherwise your critters will float in your Petri dish when you are ID-ing and slide mounting. Not to mention that they will decompose.

9. Once the residue is free of kerosene, **transfer to a vial that has a label inside** (!). Do the transfer using 80% ETOH and fill the vial with the same.

10. I have added a "**Mini-float**" to my procedure. I still follow the entire protocol, but the samples are sometimes plagued by organic debris. This can be mitigated by using a higher % of ETOH during the float, but it will also pick up less arthropods. This results in needing more consecutive floats per sample (I get 90-95% of all micro arthropods after 3 floats at 70%). So in general if there is a lot of organic debris in the floated sample sorting/ cleaning is a lot of work. Sorting a sample (not ID-ing, just manually separating the arthropods from the debris) can take 4-8 hours depending on how bad it is). I now do an additional float of 15 minutes in the (glass) storage vial of the already floated sample. This is just to make the sorting go faster. Done right, an extra 15 minute float will give you a clean sample and a pile of debris with VERY few arthropods to go through.

11. There will be large amounts of junk ETOH. Do no flush this down your drain. Please contact your hazardous waste/ chem. department. They may want the kero and ETOH separated. You can do a crude separation by dumping everything in a vat that has a small tap at the bottom. This way you can leave the kero separate from the ETOH and remove the ETOH from underneath.

*As a last note, based on floatation curves (cumulative # of arthropods per consecutive float) I have roughly assessed that the 1st float get's you about 75-80%, 2nd up to 85-90% and a 3rd get's you all the way up to 95% of the possible extractable micro arthropods. I have opted to drop the 3rd float this year because it's too time consuming. I am doing 2 floats now but ID-ing only the first. If my stats show me that I need higher numbers I will sort and ID the 2nd float. I don't see any taxa that are extracted on 2nd, 3rd or 4th floats that are not in the first. Only thing to note is that the larger the arthropod (large Oribatids in particular) the less you extract from them. Looking at those accumulation curves you see all taxa topping out (curve becoming a lot less steep) after 3 floats, with Oribatids this is not the case. This might be an artifact of my general low Oribatid numbers at my site but other literature confirms my observations.

**Using the vacuum chamber is optional. It can increase your extraction efficiency, particularly if you have much plant debris. However, kerosene floats work fine without the vacuum too.

†I use a modified 10 mL pipette (see Figure 2) with part of the tip cut off for a larger bore (3 mm). The larger bore makes it easier to pick up the floated sample, but also makes it easier to spill. Exercise caution!

Further reading:

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Faraji, F, Bruin, J, and Bakker, F, 2004. A new method for mite extraction from leaf samples. Experimental and Applied Acarology 32: 31–39.

Geurs, M, Bongers, J, and Brussaard, L. 1991. Method for assessing population of soil-inhabiting invertebrate- Improvements to the heptane flotation method for collecting microarthropods from silt loam soil. Agriculture, Ecosystems & Environment 34: 213-221.

Kethley, J, 1991. A procedure for extraction of microarthropods from bulk soil samples with emphasis on inactive stages. Agriculture, Ecosystems and Environment 34: 193-200.

Macfadyen, A, 1961. Improved Funnel-Type Extractors for Soil Arthropods. Journal of Animal Ecology 30: 171-184.

McSorley, R, and Walter, DE, 1991. Comparison of soil extraction methods for nematodes and microarthropods. Agriculture, Ecosystems and Environment 34:

201-207. Proctor, H. 2001. Extracting aquatic mites from stream substrates: a comparison of three methods. Experimental and Applied Acarology 25: 1–11

Walter, DE, Kethley, J and Moore, JC. 1987. A heptane flotation method for recovering microarthropods from semiarid soils, with comparison to the Merchant-Crossley high-gradient extraction method and estimates of microarthropod biomass, Pedobiologia 30**:** 221–232.

Wood, T. G. (1965). Comparison of a funnel and a flotation method for extracting Acari and Collembola from moorland soils. Pedobiologia, 5, 131-9.

Figure III.1: Notice the small air bubbles inside after 15 minutes in the vacuum chamber. Also, more importantly, the ETOH-kerosene interface is clearly visible (brown muck); this is what you siphon up.

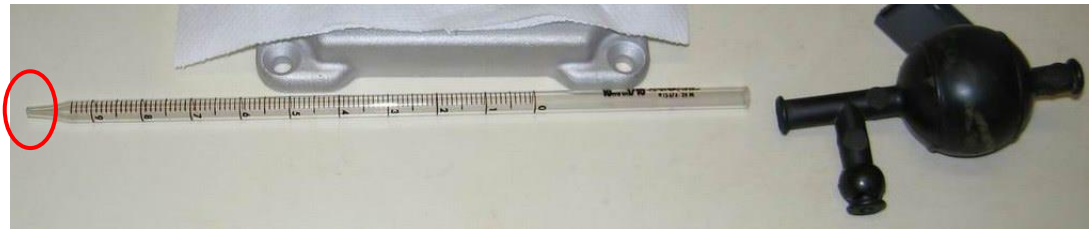

Figure III.2: A modified 10 ml pipette with pipette bulb. Tip has been cut off to increase bore size to 3mm.

Appendix IV

Kerosene-flotation and Tullgren performance

Here I present results of a test of the efficacy of kerosene flotation done during my thesis, in order to determine how many floats were necessary to provide a reasonably complete picture of the number of microarthropods present in a sample. Table IV.1 and IV.2 show the mite and springtail abundance per kerosene float per sample, respectively, while Figure IV.1 and IV.2 show accumulation curves based on the cumulative proportion of the total number of mites and springtails extracted after 3 floats. Note that 100% does not imply 100% of all mites or springtails in a soil sample. The accumulation curve shows that after two floats relative few extra mites are extracted by consecutive floats.

Also, after doing the Tullgren extraction for my 2009 data (see Chapter 5 for details), I collected the dehydrated soil sample left in the extractor, rehydrated it for a week in ethanol, and proceeded to do a kerosene floatation extraction. Surprisingly a very large proportion of mites, and an even higher proportion of springtails, were collected from this residue (Figure IV.3). While these were relatively crude Tullgren extractors (compared to high-gradient extractors) with hot halogen bulbs, it does clearly show a very strong possible bias. Without this knowledge an observer would conclude that there are very few or no springtails present in the studies area. This is also the first time to my knowledge that someone has used kerosene flotation to test the efficiency of a Tullgren extractor in this manner.

Table IV.1: Table of absolute abundance of mites per kerosene float per sample (C: control, W: warming, N: no defoliation, L: low intensity defoliation, H: high intensity defoliation, A: ambient precipitation, -: reduced precipitation)

	Mites		
	Float 1	Float 2	Float3
W, N, -	358	108	18
W, L, -	392	101	14
W, N, A	343	56	19
C, N, -	600	92	48
W, H, A	703	106	22
W, H, -	188	31	14
C, L, -	460	80	48
C, L, A	353	122	22
W, L, -	71	122	50
W, L, -	229	104	31

Table IV.2: Table of absolute abundance of springtails per kerosene float per sample (C: control, W: warming, N: no defoliation, L: low intensity defoliation, H: high intensity defoliation, A: ambient precipitation, -: reduced precipitation)

	Springtails		
	Float 1	Float 2	Float3
W, N, -	30	9	3
W, L, -	55	4	0
W, N, A	19	0	0
C, N, -	85	11	2
W, H, A	33	4	1
W, H, -	30	9	3
C, L, -	40	5	0
C, L, A	144	14	2
C, H, -	**39**	**14**	**2**
C, N, A	**13**	**4**	**1**

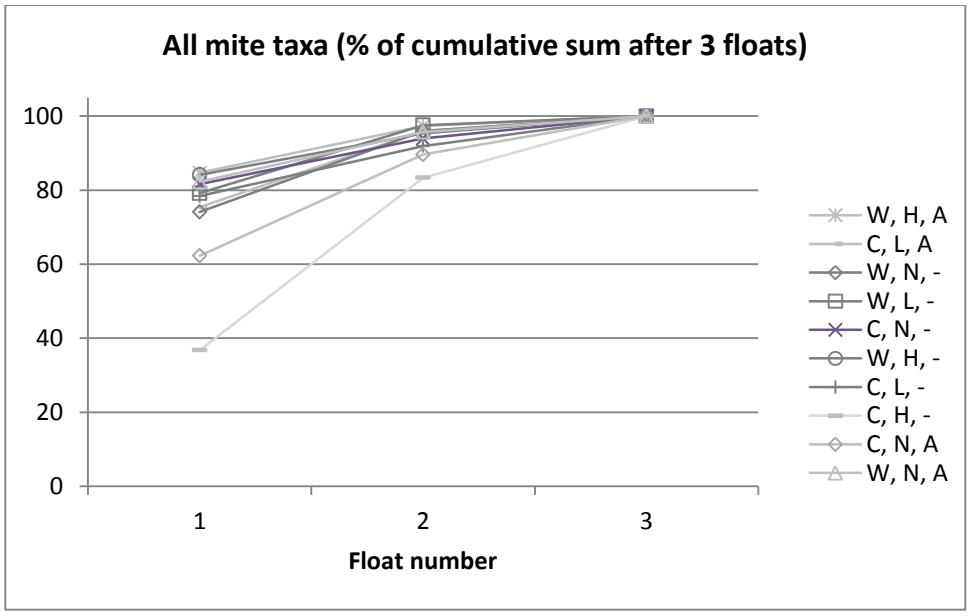

Figure IV.1: Accumulation curve of the total proportion of mites collected after 3 consecutive kerosene-flotation extractions (C: control, W: warming, N: no defoliation, L: low intensity defoliation, H: high intensity defoliation, A: ambient precipitation, -: reduced precipitation).

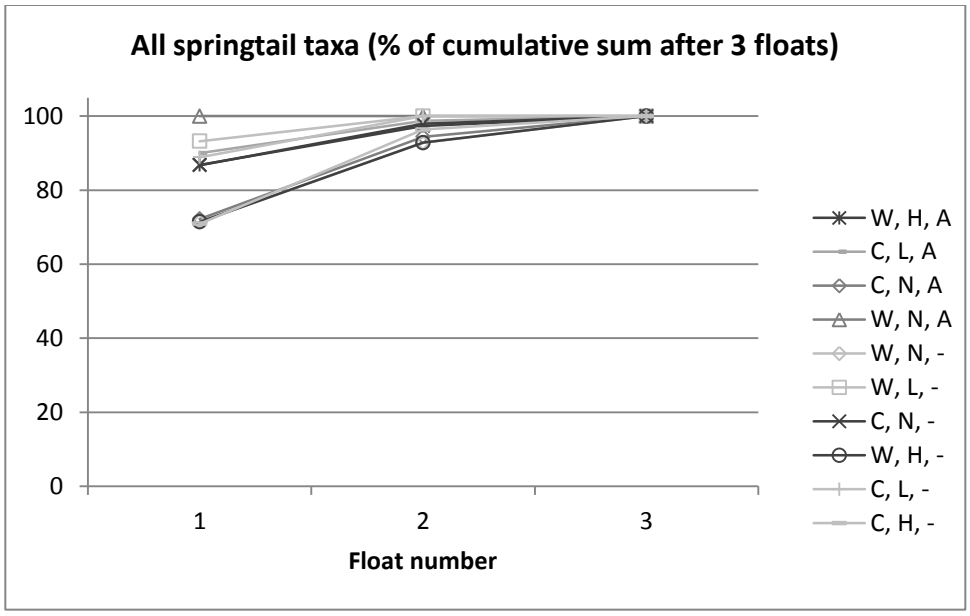

Figure IV.2: Accumulation curve of the total proportion of springtails collected after 3 consecutive kerosene-flotation extractions (C: control, W: warming, N: no defoliation, L: low intensity defoliation, H: high intensity defoliation, A: ambient precipitation, -: reduced precipitation).

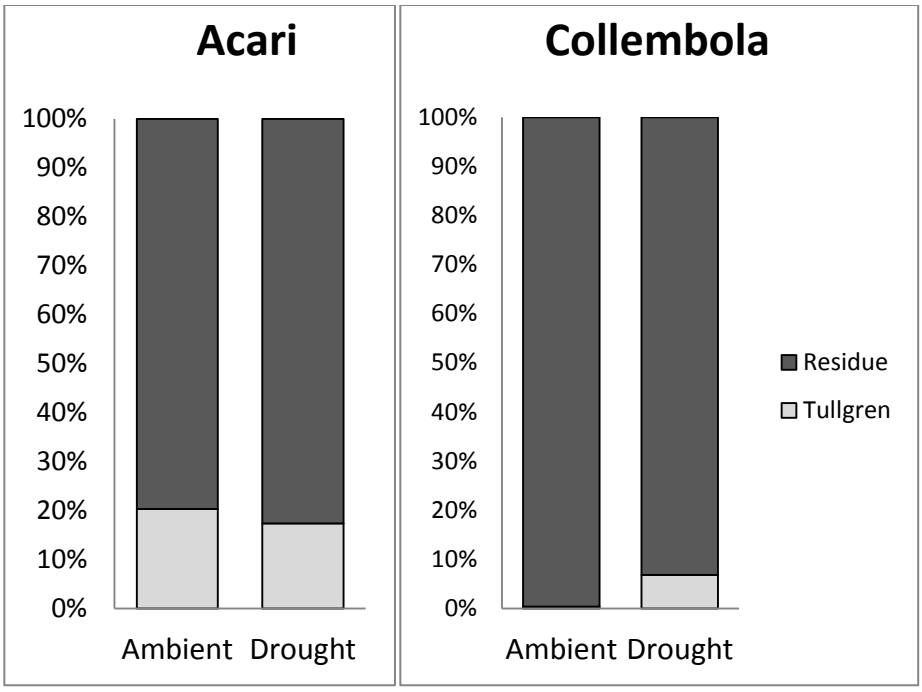

Figure IV.3: Proportions of total abundance of mites and springtails. Residues are Kerosene floated "Tullgren residues".