Patterns and drivers of terrestrial arthropod biodiversity in northern Canada

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Abstract

The overarching goal of this thesis was to describe patterns of terrestrial arthropod biodiversity and community structure in northern Canada, and to explore the underlying drivers and mechanisms that are responsible for these patterns. The term "biodiversity" is used here in a broad sense that includes both taxonomic (TD) and functional (FD) diversity. Ground-dwelling arthropods, especially beetles (Coleoptera), were used as model taxa, and were collected using standardized methods from twelve locations in the three northernmost ecoclimatic zones of Canada.

Beetle biodiversity changes over time and space. Over the course of one active season, rapid species and functional turnover were observed in two major habitats in one subarctic location (Kugluktuk, Nunavut). While some functional groups were apparent only for brief periods of time, entomophagous predators consistently dominated the assemblage structure in biomass and abundance. This dominance by carnivores was observed consistently throughout the study, regardless of spatial or taxonomic scope. This inverted trophic structure suggests that predators may rely on alternative, non-epigeic prey items. A natural history study of previously unknown host-parasite interactions between beetles and nematomorphs (*Gordionus* n. sp.) suggests that beetles use alate insects with aquatic larval stages as an important nutrient subsidy.

Across the entire study region, beetle TD and FD, as well as overall assemblage structure, display strong negative relationships with latitude, which conforms to the classical latitudinal gradient of diversity. After considering many spatial, environmental and climatic variables, the most significant driver of beetle biodiversity and assemblage structure over time and space was climate, particularly temperature.

When the taxonomic scope of the research was expanded to include all ground-dwelling macroarthropod taxa, and the functional scope refined with a multidimensional functional trait-based approach, the same patterns and processes were observed. Additionally, it was found that functional redundancy was greater in the high arctic than in the warmer ecoclimatic zones further south, despite a paucity of taxa in the high arctic. This supports the hypothesis that environmental constraints are more important in regions with harsh climates, and play a greater role in diversity and community assembly processes than niche differentiation.

The biodiversity (TD and FD) and structure of terrestrial macroarthropod communities in northern Canada have several consistent patterns: (1) large-scale negative relationships between biodiversity/assemblage structure and latitude; (2) strong correlations between TD and FD; and (3) the dominance of active predatory taxa. The most important finding of this study is that climate (temperature) gradients provide the best explanation for the variability observed in arthropod biodiversity and assemblage structure over time and across space. Lastly, the effects of climate on biodiversity and community assembly seem to be more pronounced in the high arctic than in more southerly biomes. Given the rapid and significant rise in temperature projected for northern biomes and the fact that predatory taxa are often more sensitive to changes in their environments, major changes to arthropod diversity are expected in the north, with implications for the stability of northern ecosystems.

Résumé

L'objectif principal de cette thèse est de décrire les patrons de biodiversité des arthropodes terrestres, la structure de leurs communautés dans le Nord du Canada, et d'explorer les forces et les mécanismes responsables de ces patrons. Le terme «biodiversité» est utilisé ici dans un sens large qui comprend à la fois la diversité taxonomique (DT) et fonctionnelle (DF).Les arthropodes vagabonds, en particulier les coléoptères (Coleoptera), utilisés comme taxon modèle, ont été recueillies à l'aide de méthodes normalisées dans douze sites répartis dans les trois zones écoclimatiques les plus septentrionales du Canada.

La biodiversité de coléoptères varie dans l'espace et le temps. Au cours d'une saison active, un changement taxonomique et fonctionnel rapide a été observé dans les deux habitats étudiés à Kugluktuk, Nunavut, dans la région subarctique. Alors que certains groupes fonctionnels n'étaient observés que pour de brèves périodes de temps, les prédateurs entomophages dominaient constamment la structure de l'assemblage en biomasse et en abondance. La prépondérance des carnivores en Arctique a été observée régulièrement pendant toute l'étude, quelle que soit la portée spatiale ou taxonomique. Cette structure trophique inversée suggère que les prédateurs pourraient se nourrir de proies non vagabondes. Une étude de l'histoire naturelle des interactions hôte-parasite précédemment inconnues entre les coléoptères et les nématomorphes (*Gordionus* n. Sp.) suggère que les coléoptères consomment des insectes ailés avec des stades larvaires aquatiques comme une source importante de nutriments.

À travers toute la région d'étude, la DT et la DF des coléoptères, ainsi que la structure globale d'assemblage, étaient négativement corrélées avec la latitude, ce qui est conforme au gradient latitudinal classique. Après avoir examiné de nombreuses variables spatiales, environnementales et climatiques, la force qui semble influencer le plus la biodiversité et la

structure de l'assemblage des coléoptères au Nord, et ce, dans l'espace ou dans le temps, est le climat, en particulier la température.

Lorsque tous les taxons de macroarthropodes terrestres vagabonds ont été inclus, et que la variabilité fonctionnelle est décrite à l'aide de plusieurs traits fonctionnels, les patrons de biodiversité et de structure observés ainsi que les forces sous-jacentes étaient similaires. La redondance fonctionnelle était plus grande dans l'Extrême-Arctique que dans les zones écoclimatiques plus au sud, et ce, en dépit d'un manque de taxons dans l'Extrême-Arctique. Cela confirme l'hypothèse que les contraintes environnementales sont plus importantes dans les régions au climat rigoureux, et jouent un rôle plus important dans la variation de diversité et d'assemblage que la force de différenciation de niche écologique.

La biodiversité (DT et DF) et la structure des communautés de macroarthropodes terrestres dans le Nord du Canada ont plusieurs patrons compatibles: (1) relations négatives à grande échelle entre la biodiversité / la structure d'assemblage et la latitude; (2) de fortes corrélations entre DT et DF; et (3) la domination des taxons prédateurs actifs. La conclusion la plus importante de cette étude est que le climat (température) semble être la force qui explique le mieux la variabilité observée dans la biodiversité des arthropodes et la structure d'assemblage dans le temps et dans l'espace. Enfin, les effets du climat sur la biodiversité et l'ensemble de la communauté semblent être plus prononcés dans l'Extrême-Arctique que dans les biomes plus au sud. Compte tenu de la hausse rapide et importante de la température prévue pour les régions nordiques et le fait que les taxons prédateurs sont souvent plus sensibles aux changements dans leur environnement, des changements majeurs de la diversité des arthropodes sont attendus dans le nord, avec des implications importantes pour la stabilité des écosystèmes nordiques.

Translation: Sarah Loboda

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Thesis format, contributions of authors, and contributions to knowledge

Format

This thesis is presented as a collection of published manuscripts and chapters written in manuscript style. Chapter 2 has been published in *The Canadian Entomologist* (see Appendix A1-3), Chapter 3 will be submitted to *The Journal of Parasitology*, Chapter 4 is in press in *PLoS ONE* (see Appendix A2-2), and Chapter 5 will be submitted to *Ecology*. Chapter 1 and 6 introduce the thesis and its objectives, provide a review of the literature, summarize the main finding of the research and discuss directions for future work.

Contributions of authors

I wrote all of the original manuscripts. My advisor, Dr. Christopher M. Buddle (McGill University), is co-author on the manuscripts for Chapters 2 to 5 and participated actively in the conceptualization of the research program and editing of manuscripts. Chapter 3 is additionally co-authored by Dr. Ben Hanelt of the University of New Mexico, who contributed the species determination and description of the parasite. The sampling protocol used to collect arthropod specimens was developed by members of the Northern Biodiversity Program. The analyses conducted for each manuscript were selected and performed by me, in consultation with Dr. Buddle and members of our lab. I performed all the arthropod sampling for the study described in Chapter 2, and contributed to the large-scale collection efforts and sample sorting as a NPB team member. I identified all beetle specimens at least to family (often to subfamily or genus), and identified all Carabidae (the most abundant taxon) to species. All other contributions by colleagues and taxonomic experts are outlined in the acknowledgement sections of each chapter.

Contributions to knowledge

- Taken together, the data and analyses presented in this thesis represent the largest standardized, field-based study of terrestrial biodiversity patterns and processes, and is among very few that have examined the relationships between TD, FD, and mechanistic processes at this scale.

- Over 11,000 beetle specimens – including uncommon, rare, or new species - have been identified and properly curated, and are being incorporated into three internationally significant entomological research collections.

- Multiple lines of evidence that temperature is one of the most important drivers or mechanisms responsible for patterns of terrestrial arthropod biodiversity: the positive temperature-biodiversity relationship is not only temporal, but it also operates over large latitudinal gradients (Ch. 2,4,5)

- Evidence that that niche complementarity plays an important role in shaping arthropod community structure at a large spatial scale, but is overridden by environmental constraints in the high arctic (Ch. 5)

- Evidence that northern arthropod communities may conform to an uncommon trophic structure known as an inverted pyramid (Ch. 2,4,5)

- The first description of host-parasite relationships between ground beetles and horsehair worm parasites in any arctic or subarctic system, which provides significant indirect information about the prey and dietary breadth of northern carabids, and about the importance of nutrient subsidies from aquatic habitats for terrestrial carnivores (Ch. 3).

- This study highlights that fact that northern terrestrial diversity is dominated by a rich and unique arthropod fauna that reflects environmental (particularly climate) changes in their diversity, distribution, and assemblage structure, making them ideal taxa for targeted long-term diversity monitoring in the arctic.

Acknowledgments

Since the moment that I confessed to my wife that I had a real desire to return to school and pursue an academic career, Kim has supported and encouraged this mad and wonderful adventure. Without her willingness to accept the inherent challenges and risks, her excitement and optimism about our future, her unwavering encouragement and support, and her gentle reminders to take a break and enjoy a drink on the back deck on a warm summer evening, this thesis would not exist.

I am extremely fortunate to have had Dr. Christopher Buddle as my advisor. He provided the guidance, support, and professional opportunities I needed to succeed, not only as a researcher, but also as a teacher, and as a person. He stood by me through difficult stretches of time, and cheered with me when things went really well. He has been an incredible mentor for many aspects of my professional and personal growth, and I don't know if I can ever thank him properly for everything, but I'll try my best by doing him proud in the future.

One of the most valuable lessons I have learned while completing this work is the value of collaboration. The scope of the research contained in these pages would not have been nearly as extensive without the hard work of many, many individuals. First, my team members of the Northern Biodiversity Program must be recognized for the many hours spent away from home in distant northern regions collecting arthropods, and also for the weeks and months spent sorting samples (T. Wheeler, D. Currie, S. Loboda, K. Sim, L. Timms, M. Blair, A. Solecki, P. Schaeffer). My study of host-parasite relationships, a fascinating and unexpected outcome of this research, has been greatly enriched by the contributions of my collaborator, Dr. Ben Hanelt, from the University of New Mexico. I had many keen and hard-working undergraduate volunteers work with me in the lab; I was thrilled to provide them with opportunities to get some hands-on

experience with ecological/entomological research, and in return the “Bug Army” saved me many hours of microscope work. Four residents of Kugluktuk, Nunavut, deserve special mention: A. Pedersen, K. Kuodluak, J. Bolt and A. Niptanatiak were of enormous help in the field, acting as guides, chauffeurs, teachers, field assistants, and bear-keeper-away-ers. The contributions of the students of Kugluktuk High School are also greatly appreciated, and I thank their teachers for the opportunity to work with those amazing young people.

Even in the arctic, the diversity of the Coleoptera is daunting! Therefore, I must extend my deepest and most sincere gratitude to the many taxonomists who helped me with the very difficult task of identifying some important groups of beetles, and confirming those I did myself: R. Anderson, Y. Bousquet, A. Davies, H. Douglas, J. Klimaszewski, L. Lesage, C. Maier, T. MacRae, S. Peck, A. Smetana, and C. Wood. Henri Goulet, especially, spent many hours working with me one-on-one, and I am grateful for the experience and knowledge he has passed on to me; it was a joy to work in the shadow of one with a lifetime’s worth of passion for insects.

My labmates, past (Joey, Raph, Katie, Dory) and present (Sarah, Shaun, Chris, Jessica, Elyssa), are an incredible group of scientists whose collective knowledge and skills are astounding and enriching, and whose friendships I came to value very deeply. I enjoyed every moment in my lab surrounded by these people, and I am going to miss them and my academic home away from home terribly.

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Chapter 1: Introduction, literature review, and objectives

1.1 Introduction

The overarching goal of community ecology is to describe, and find explanations for, patterns of biodiversity across different spatial scales and over time. Community ecology is a science that is still maturing. It is also complex and multidimensional, and considers vast temporal and spatial extents, all of which make data collection challenging and analyses even more so. However, in an era where biodiversity is steadily declining, and anthropogenic stressors are on the rise, there is a greater need than ever to understand and monitor the distributions of living organisms (Sala et al. 2000, Tilman 2000, Butchart et al. 2010, Bellard et al. 2012).

In a separate camp, ecosystem ecologists have focused on, among other things, the important matter of ecosystem function. Decomposition, pollination, pest suppression, primary productivity, and carbon sequestration, are responsible for the maintenance of ecosystem stability and the provision of ecological services. Until quite recently, a gap existed between community ecology (the study of species diversity) and ecosystem ecology (which considers ecological function). The biodiversity–ecosystem function (BEF) studies of the 1980s made important strides towards bridging this gap by beginning to relate biodiversity with ecosystem function (Thompson et al. 2012).

Recently, criticisms have arisen from both factions regarding the limited scope of the BEF paradigm, which tends to focus on single functions performed by, or that influence, narrowly-defined groups of organisms. There has been a call to consider the biodiversity-function relationship in a way that incorporates multiple processes and interacting organisms that span a breadth of trophic levels and taxa (Hooper et al. 2002, Hooper et al. 2005, Thompson et

al. 2012), as traditional approaches continue to be largely unproductive in terms of the development of generalizable ecological theories (McGill et al. 2006).

As a result, significant efforts have been made in community ecology to expand the scope of biodiversity research to include alternative or complimentary genetic, morphological or functional measures of diversity alongside the traditional taxonomic metric of species richness; these have begun to offer new insights and opportunities (Magurran 2004). There is now widespread understanding that taxonomic diversity and ecological function are inextricably linked, and that biodiversity loss results in reduced or less efficient ecological function (Tilman 2000, Cardinale et al. 2012). Conversely, it is understood that organisms' functional traits may play an important role in influencing species diversity patterns: trait-based biotic interactions and responses to environmental gradients can influence niche availability and occupancy (Lamanna et al. 2014). The inclusion of functional diversity in ecological studies may ultimately yield more powerful tests of biodiversity theories (McGill et al. 2006, Beck et al. 2012, Lamanna et al. 2014). In short, with the multitude of new theories, insights and analytical approaches, it is an exciting time to be a community ecologist.

In 2010, a multi-institutional initiative, the Northern Biodiversity Program (NBP), began conducting standardized arthropod sampling in the boreal forests and arctic regions of Canada (Buddle 2011). The objective of this program was, in part, to assess current patterns of arthropod diversity across a large area of the far north. As a student member of this initiative, I had the opportunity to use arthropods as a model taxon to study biodiversity patterns and processes in the context of this modern upsurge of new paradigms and research methods. And so, I have embraced the challenge of working with the most diverse phylum of organisms on Earth with the

aim of making meaningful contributions to the ongoing and increasingly exciting biodiversity dialogue, during a time of great ecological importance and crisis.

The chapters in this thesis are presented in an order that reflects the progressively enlarging scope of my research, as I sought different lines of evidence to identify generalizable patterns and processes of biodiversity at different temporal and spatial scales. In Chapter 2, I describe temporal patterns in the biodiversity and structure of ground-dwelling beetle assemblages at a local scale, in two habitats in one subarctic location. In Chapter 3, I explore the nature of novel host-parasite relationships between beetles and horsehair worms, and in doing so provide evidence of diet breadth and nutrient subsidies that may help explain some patterns I observed in the trophic structure of terrestrial beetles. In Chapter 4, I expand the geographic scope of my beetle biodiversity studies to include 11 additional sites from across northern Canada, spanning a large latitudinal gradient that encompasses three different biomes. In Chapter 4, I examine patterns and drivers of biodiversity among all ground-dwelling arthropod taxa collected by the NBP, and incorporate a trait-based approach in order to help elucidate community assembly mechanisms. This work, taken as a whole, provides multiple levels of evidence for relationships between taxonomic and functional diversity, and reveals the underlying climatic and community mechanisms responsible for large-scale patterns of arthropod biodiversity in northern systems.

1.2 Literature Review

1.2.1 Patterns of terrestrial diversity

The number of species and the manner in which organisms assemble in time and space is generally not uniform (Gaston 2000). The observation and the study of this simple fact have

captivated scientists since the earliest natural historians began to take note of the diversity of life around them (Conniff 2011). The combined efforts over many years of countless researchers who painstakingly documented the identities and whereabouts of different organisms have accumulated enough evidence to support some fairly generalizable patterns of diversity.

The species-area relationship that features prominently in island biogeography theory dictates that larger land areas support greater numbers of species than small areas. This pattern is so well evidenced that it is arguably one of the few actual "laws" of ecology (Gotelli 2008), even amidst new evidence of exceptions among extremely small areas (Lomolino 2000). The closely related distance effect reliably creates less speciose communities in land areas that are geographically separated from other land masses that could otherwise act as sources of new species or individuals (Gotelli 2008).

Perhaps the best-known pattern is that of the latitudinal gradient of species richness: communities found in tropical regions at or near the equator boast richly diverse life forms, and communities become increasingly species-poor as they draw nearer to the poles (Gaston 2000). This pattern has attracted a tremendous amount of research, and a multitude of explanatory hypotheses have been brought forth. Willig (2003) reviews these hypothesis and those which are best supported by current evidence, including the geographic area hypothesis, the productivity hypothesis and the ambient energy hypothesis. The geographic area hypothesis proposes that high species richness at the equator is due to the large size of the land area encompassed by the tropics, and the continuity of that area (as opposed to disjunct temperate or polar land areas) – there are obvious ties to the species-area relationship described above. The productivity hypothesis suggests that more productive areas (measured as a function of the amount of solar radiation that enters the system) support greater diversity, and the related ambient energy

hypothesis considers the positive effects of solar radiation on organisms' physiological responses. The ambient energy hypothesis acts as something of a proxy for climate- or environment-based mechanisms: if climate/environmental conditions are physiologically challenging or costly, they will produce communities that are less diverse. These mechanisms could conceivably operate at smaller spatial or temporal scales, as well as across large latitudinal gradients.

All of these well-studied diversity patterns have one thing in common: their focus on the number of species (i.e., species richness). Historically, the term "biodiversity" has been understood to mean the number or abundance of species present in a community (i.e., taxonomic diversity, TD) (Naeem and Wright 2003, Magurran 2004). Some have argued that traditional taxonomic approaches make it difficult to compare assemblages in different regions or at different successional stages (Voigt et al. 2007) or to develop general principles about community assembly (McGill et al. 2006).

1.2.2 A paradigm shift in ecology

Given these shortcomings, it is clear that the concept of biodiversity must be expanded to include additional or complementary measures (e.g., phylogenetic relationships, ecological function) in order to advance our understanding of diversity patterns and processes (McGill et al. 2006, Schleuter et al. 2010). Since functional approaches operate independently of any particular taxonomic composition, they can be used to facilitate the study of diversity and assemblage structure and function over large spatial scales.

Functional diversity (FD) is not a new idea (e.g., Elton 1927, Lindeman 1942, Hairston et al. 1960). Functional diversity refers to the components of diversity that influence how an

ecosystem operates or functions (Tilman 2001) and therefore considers organisms in terms of their ecological roles regardless of their taxonomic or phylogenetic identities or relationships. FD is important to the study of biodiversity, as it is the component of diversity responsible for ecosystem dynamics, stability, productivity, nutrient balance, among other elements of ecosystem functioning (Mason and de Bello 2013). The manner by which the functional diversity of communities is operationally defined has evolved considerably over time.

Hutchinson's seminal studies on species diversity and community assembly asked the simple question, "why are there not more different kinds of animals?" His conclusion that niche occupation was limited by organisms' competition for shared resources was based on observations that organisms differed in traits associated with resource acquisition (Hutchinson 1959). This led to the idea that communities were composed of groups of organisms that shared similar traits (Blondel 2003). Concepts like "guilds" (Root 1967, Root 1973) and "functional groups" (Cummins 1974) were later adopted to describe these groupings. While the terms are similar and are often used interchangeably, it should be noted that the former refers more explicitly to competitive resource use among species within a taxon, and the latter to ecosystem function resulting from resource use across taxa (Blondel 2003). Since guilds and functional groups are generally broadly defined by a single function (e.g., "pollinator"; "nitrogen fixer"), they offer the advantage of rapid FD assessment (Mason and de Bello 2013). FD is thus sometimes defined as the number of groups or guilds in a community of interest.

Organisms can also be grouped by feeding-related function into different trophic levels, an approach initially popularized by Lindeman's trophic-dynamic model (Lindeman 1942) . Trophic structures are based on the direction and magnitude of nutrient flow among interacting organisms; when different trophic levels are linked they collectively describe the trophic

structure of a community. Typical terrestrial trophic structures generally include three to five discrete levels: primary producers (plants), primary consumers (herbivores), then secondary, tertiary, and quaternary consumers (carnivores). Trophic structures can also include less discrete (intermediate) levels or non-linear relationships, such as those represented by saprophages, omnivores and cannibals. The functional diversity or structure of an assemblage can be therefore be defined by the relative contributions of and relationships between trophic levels.

Over the last decade or so, the study of functional diversity has evolved rapidly, with a growing emphasis on trait-based measures of FD. Natural history traits – measurable features of morphology, behaviour, reproduction, feeding mode, phenology, and physiology, among others (e.g., Bremner et al. 2003, Bishop 2012, Schirmel et al. 2012, Pedley and Dolman 2014) – directly determine productivity and fitness, habitat and food requirements, and the nature of interactions (predator-prey, competition, etc.) with other taxa (Cadotte et al. 2011). Trait-based assessments of diversity patterns and process may ultimately be more practical and meaningful (i.e., for land managers, conservationists, and decision-makers), as they permit greater levels of generality and predictability than highly case-specific taxonomy-based approaches (McGill et al. 2006). Trait-based methods provide a natural bridge between the often disparate realms of community and ecosystem ecology.

Functional traits can be classified as "effect" traits or "response" traits. Functional effect traits are those that determine how species affect ecosystem properties and processes, while response traits dictate how species respond to environmental change (Hooper et al. 2005). Effect and response traits may be correlated, and single traits may fall into both categories. The relationships among functional response and effect traits are not yet well understood, but it may be important to consider both types of traits simultaneously in order to understand the dynamics

of ecosystem function (Hooper et al. 2002, Hooper et al. 2005). The study of functional traits is proving to be an important means of assessing and of predicting how environmental gradients or changes (e.g., land use changes, introduced species, climate change) affect communities and assembly processes, and the consequences of these community-level changes on biodiversity, and ecosystem processes and functions (Hooper et al. 2002, Naeem and Wright 2003, Fontana et al. 2014, Pearson et al. 2014).

Even since the initiation of this thesis, much has changed in the world of FD research methods. New multidimensional trait-based analyses are being developed, tested, criticised and refined at a staggering rate (Petchey and Gaston 2006, Villéger et al. 2008, Laliberte and Legendre 2010, Mouchet et al. 2010, Pavoine and Bonsall 2010, Schleuter et al. 2010, Mason and de Bello 2013, Mason et al. 2013). Designed to be similar (and thus familiar) in concept to the traditional species diversity metrics of taxonomic diversity (TD), functional diversity now includes measures of richness, evenness, and divergence, among others, that provide detailed information about the way that species occupy trait (or niche) space in their communities.

Mason et al. (2005) defined FD as "the distribution in functional trait space of the species presence and abundance in a community, including three components: (1) the amount of functional trait space filled by species in the community (functional richness); (2) the evenness of abundance distribution in filled trait space (functional evenness); and (3) the degree to which the distribution of species abundances maximizes divergence in functional traits (functional divergence)". This definition has been widely adopted, and used as a framework for the development of analytical methods that may offer insight into the effects of different environmental, spatial, temporal or climatic variables on diversity and community structure.

1.2.3 Mechanisms underlying biodiversity patterns

There has been increased interest in not merely describing patterns of biodiversity and community structure, but also in elucidating the causal mechanisms behind these patterns (Willig et al. 2003, Ricklefs 2004, McGill and Nekola 2010, Beck et al. 2012, Keith et al. 2012). Environmental, spatial, and climatic factors, as well as interspecies interactions, can affect changes in taxonomic and functional diversity; these changes are often expressed disproportionately among certain taxa or functional groups (Petchey et al. 1999, Voigt et al. 2003, Voigt et al. 2007, Tylianakis et al. 2008) and seem to be dependent on scale. Some animals may be constrained by primary productivity (i.e., the availability or abundance of a basal plant food source) or the structure of the plant community (Root 1973, Wright et al. 1993, Trotter et al. 2008, Blaum et al. 2009, Bowden and Buddle 2010, Pakeman and Stockan 2014). Spatial gradients (e.g., altitude, latitude) have been linked to biodiversity as discussed earlier, but the intensity and direction of these effects varies between taxonomic and functional groups, and are assumed to be mediated by other correlated factors, especially climate. Climate – in particular, temperature – has been broadly recognized as a key variable associated with both terrestrial and aquatic biodiversity and function (e.g., Hawkins 2004, Field et al. 2009, Gilman et al. 2010, Thomas 2010, Boyero et al. 2011, Bellard et al. 2012, Spasojevic et al. 2014, Proulx et al. 2015).

The search for mechanisms has been challenging. Although a broad range of climatic, evolutionary, biotic, and spatial hypotheses have been put forth (reviewed by Gaston 2000, Willig et al. 2003), no single factor has been identified as "the" key mechanism. It seems plausible that the diversity of organisms, and the way they assemble over space and time, are the result of multiple interacting ecological and evolutionary factors (Quinn and Dunham 1983, Gaston 2000, Condamine et al. 2012). Diversity patterns are likely to vary depending on the

spatial scale of interest, processes at different scales are likely to influence each other, and it stands to reason that even fairly generalizable patterns will be subject to exceptions or variations depending on the relative importance of different causal mechanisms (Gaston 2000).

1.2.4 Biodiversity in northern ecosystems: change and opportunity

Questions about large-scale patterns in biodiversity and community structure may be answered effectively in the expansive boreal and arctic ecosystems found at high latitudes. Representing over 40 % of Canada's land area, the arctic is a massive region of tremendous social, economic, and ecological importance (Government of Canada 2009), but relatively few ecological studies have been conducted in these regions compared to other Canadian biomes.

Climate models over the past two decades have consistently predicted a 1.8 - 4.0 °C increase in global mean surface temperatures by the end of the 21st century. This does not bode well for biodiversity in the far north, where the effects of climate warming are expected to be significantly more pronounced and rapid (Maxwell 1997, Sala et al. 2000, IPCC 2007, 2014). The rapid rate of change in the arctic, and the greater vulnerability of arctic species to these changes (Anisimov et al. 2007), are likely to create unprecedented changes in species distributions, assemblages, and their associated ecological functions, making the arctic and its component species a prime target for early detection of the effects of environmental change on Earth (Wookey 2007). Given these projections, it is critical to not only determine the current status of biodiversity in northern ecosystems (Magurran et al. 2010), but to also understand how climate and other drivers shape communities and their associated ecological functions. These data are critical for long-term ecological monitoring and for making decisions regarding the mitigation of the impacts of climate change.

The tracking of species' responses to environmental change and the expansion and maintenance of monitoring programs are among most commonly cited recommendations for biodiversity management in the face of climate change (reviewed in Heller & Zavaleta, 2009). While the number of terrestrial arctic species is low compared to the species richness found in temperate or tropical biomes, the contributions of those species to the stability and functioning of the arctic ecosystem nevertheless remains high (Johnson et al. 1996, Martens et al. 2003). Accordingly, a number of monitoring programs are currently under development or in early stages of implementation in the north, including multinational initiatives such as the CAFF Arctic Terrestrial Biodiversity Monitoring Plan, the Circumpolar Biodiversity Monitoring Plan, the Arctic Breeding Bird Conditions Survey, and the Program for Regional and International Shorebird Monitoring (see review of scope and aims of these and other programs in Buddle 2013).

Among the major practical elements that these and other monitoring programs in the arctic and elsewhere must consider is the selection of appropriate indicator taxa. A review by Hilty and Merenlender (2000) lists 16 biological, behavioural and ecological attributes on which the selection of indicator taxa are commonly based, including: clear taxonomic status; known correlations with ecological changes; non-migratory; small home range; small body size; high reproductive rate; widespread distribution; easy to find; low or medium trophic level. A meta-analysis of 100 vertebrate and 32 invertebrate taxa documented as indicators of ecosystem health reveals that invertebrates typically possess more of these attributes than vertebrates (Hilty and Merenlender 2000), which may explain the global popularity of arthropods as indicators of the effects of environmental change on diversity in a wide variety of habitats and ecosystems (e.g., Kremen et al. 1993, Madden and Fox 1997, Willett 2001, Bale et al. 2002, Cartron et al. 2003,

Convey et al. 2003, Longcore 2003, Andrew and Hughes 2004, Langor and Spence 2006, Maleque et al. 2006, Nakamura et al. 2007, Rohr et al. 2007, Høye and Forchhammer 2008a, Høye and Forchhammer 2008b, Midega et al. 2008, Blaum et al. 2009, Missa et al. 2009, Schuldt et al. 2009, Schuldt and Assmann 2010). Beetles (Coleoptera), in particular, have been featured as focal taxa in a number of studies and monitoring plans, due to their diversity, abundance, and ease of capture.

1.2.5 Arthropods in northern ecosystems

Terrestrial arthropods have been highlighted as appropriate indicators of environmental change in the arctic context (Danks 1992b, Strathdee et al. 1995, Hodkinson and Bird 1998, Hodkinson et al. 1998, McGeoch et al. 2006, Høye and Forchhammer 2008a, Høye and Forchhammer 2008b, Buddle 2013, Christensen et al. 2013, Ernst and Buddle 2013). In addition to meeting many of the named indicator attribute criteria, insects and other arthropods comprise roughly one third of all terrestrial arctic life forms, including plants, fungi, and vertebrates (Wookey 2007). They also exhibit diverse functional traits and perform many critical ecological functions, including plant pollination, decomposition, and provision of food for highly valued vertebrates, and they also act as key nuisance pests for wildlife and humans (Christensen et al. 2013).

The generation of high-quality baseline data, collected in a standardized and therefore replicable way, is crucial to the initiation and success of any long-term monitoring program (Magurran et al. 2010). Arthropods in northern Canada have been broadly sampled, particularly through the activities of the Canadian Northern Insect Survey (NIS) (e.g., Downes 1964, McAlpine 1964, Oliver et al. 1964), but the majority this work has been inventorial and not

standardized (Danks 1981a). Therefore, before biodiversity monitoring can be effectively performed in the arctic, baseline information – distributions, abundance, richness, community structure – must be collected.

Carefully-designed field sampling of diverse arthropod communities over a broad spatial scale will also contribute new information that may improve our understanding of large-scale patterns of taxonomic and functional diversity, and their relationships with different climatic and environmental conditions. Although the arthropods of northern regions have developed physiological, morphological and behavioural adaptations to cope with harsh environmental conditions (see reviews in Downes 1965, Ring and Tesar 1981, Strathdee and Bale 1998), they are still subject to the influences and variability of arctic climate (i.e., annual or longer-term meteorological measurements and patterns) and weather (i.e., daily or shorter-term patterns).

Different climatic or environmental variables seem to have an influence on the diversity and community structure of arthropods at a local or regional scale. For example, Hoye and Frochhammer (2008) found that the abundance of flying insects (many of which were likely haematophagous or pollen-feeders) in Zackenberg, Greenland, was influenced most heavily by air temperature, while ground-dwelling (most likely entomophagous predators and decomposers) arthropod activity was primarily affected by solar radiation. Ground-dwelling arthropod activity in Taimy, Sibera, however, was mainly affected by air temperature, and secondarily by precipitation and wind (Tulp and Schekkerman 2008). A long-term survey of arthropods on four Canadian high arctic islands found that the varability in flying and ground-dwelling arthropod abundance and biomass were best explained by mean daily temperature and the timing of spring thaw (Bolduc et al. 2013). Temperature is commonly cited as an important driver of arthropod diversity, and likely warrants continued investigation.

There remains a need to examine patterns and processes of arthropod biodiversity and community structure at a larger spatial scale. This information could be used to make predictions about changes in biodiversity, community structure, and associated ecological functions in response to future and ongoing changes in the north, such as climate warming.

1.4 Research objectives and scientific approach

The overarching goal of this thesis is to describe patterns of terrestrial biodiversity and community structure in northern Canada, and to determine the underlying drivers or mechanisms that are responsible for these patterns. Here, I use "biodiversity" in a broad sense, including both taxonomic and functional diversity. Ground-dwelling arthropods, especially beetles (Coleoptera), are used as model taxa, and are collected from twelve locations in the three northernmost ecoclimatic zones of Canada. The research program has four main objectives and associated hypotheses.

1.3.1 Temporal changes in beetle biodiversity and assemblage structure in the subarctic

The first objective is to uncover temporal changes in the biodiversity and assemblage structure of beetles in two important habitats that are ubiquitous in northern ecosystems, and to test the influence of short-term changes in climate on these patterns.

Hypotheses 1: the biodiversity and structure of beetle assemblages will vary throughout the active season, and will differ between habitats.

Hypothesis 2: regardless of habitat, seasonal patterns in beetle assemblage structure will be most strongly associated with short-term changes in temperature.

1.3.2 Intertrophic relationships: novel high arctic host-parasite interactions and their implications for arthropod trophic structure

The second objective is to conduct a natural history study of previously unknown relationships between carabid beetles and nematomorphs in arctic and subarctic regions of Canada. The goal is to increase our understanding of species distributions, host-parasite interactions, the relationships between taxa in terrestrial and aquatic habitats, and the implications of these for arctic arthropod trophic structure. This was not a hypothesis-driven project. Rather, it was included in this thesis in recognition of the importance of documenting novel ecological relationships that may provide insight into complex interactions that shape biodiversity and the structure of communities. The research questions addressed in this study are:

Question 1: what hairworm-carabid associations exist in subarctic and arctic Canada, and where are they found?

Question 2: what are the relationships between host traits or environmental factors and the infection status of possible hosts?

Additionally, this study will result in the description of a new species of hairworm; diagnostic morphological characters will be discussed.

1.3.3 Large-scale latitudinal gradients and drivers of beetle diversity

Objective three was to determine large-scale latitudinal patterns of beetle biodiversity across multiple northern biomes, and to establish which climatic and/or environmental variables were responsible for these patterns.

Hypothesis 1: beetles will conform to classical latitudinal gradients of biodiversity, with greater richness at lower latitudes.

Hypothesis 2: beetle assemblages will show latitudinal gradients of similarity between ecoclimatic zones.

Hypothesis 3: patterns of biodiversity will be most strongly associated with climatic factors, which mediate the effect of latitude.

1.3.4 Terrestrial macroarthropod biodiversity and large-scale mechanisms of community assembly

The last objective is to determine the significance of environmental filtering and niche complementarity in large-scale arthropod diversity and community assembly, by linking ecological and climatic gradients, taxonomic diversity, and trait-based functional diversity.

Hypothesis 1: terrestrial macroarthropod TD and FD are correlated at large spatial scales, with higher FD in communities with higher TD (support for niche complementarity).

Hypothesis 2: patterns of terrestrial macroarthropod TD and FD are associated with climatic gradients, with lower diversity in colder ecoclimatic zones.

Hypothesis 3: environmental filtering will play a more important role in shaping biodiversity in zones with harsher (colder) climates.

1.4 Connecting Statement

The literature review and statement of research objectives in Chapter 1 have provided the context for this thesis, and for the research projects that will be described in the next four chapters. In Chapter 2, I document changes in beetle biodiversity and assemblage structure in different habitats and over time in the subarctic region of Kugluktuk, Nunavut. I also begin to explore the possibility that environmental, spatial or climatic variability is responsible for these changes. This study acted as an important "jumping-off" point for Chapters 4 and 5, which describe patterns of diversity involving larger spatial scales and more diverse taxa.

Chapter 2: Seasonal patterns in the structure of epigeic beetle (Coleoptera) assemblages in two subarctic habitats in Nunavut, Canada

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2.1 Abstract

Seasonal patterns in the taxonomic and functional structure of epigeic Coleoptera assemblages in wet and mesic habitats were studied in Kugluktuk, Nunavut. Using pan and pitfall traps, 2638 beetles were collected between 21 June and 13 August 2010. Fifty species (including 17 new territory records) in 11 families were identified. The biomass of each specimen was estimated, and each was assigned to a functional group. Species composition differed between habitats throughout the active season and there was a rapid compositional turnover even though species diversity was similar in both habitats and among sampling periods. The functional beetle assemblages in the two habitats were different, and both assemblages experienced seasonal turnover in function; this effect was more pronounced in the mesic habitats. The beetle fauna in both habitats was predominantly entomophagous. We also examined the influence of seasonal weather patterns on assemblage structure: there is a significant relationship between mean daily temperature and assemblage structure. This relationship indicates that changes in weather (or longer-term changes in climate) could affect the diversity and ecological function of insects in this system. Given the significance of insects in the north, this could result in important changes to northern ecology.

2.2 Introduction

Arthropods perform many important tasks in arctic ecosystems, including pollination, herbivory, and decomposition (Leborgne et al. 2011). They are also an important food source for highly valued vertebrates. Tulp and Schekkerman (2008) demonstrated that the seasonal availability of arthropod prey is critical to the growth and survival of many arctic shorebirds. As the major food source for some 50 species of arctic birds (Meltofte et al. 2007) and a component of mammalian diets including those of Mustelidae (Mammalia) and arctic fox (*Vulpes lagopus* (Linnaeus); Mammalia: Canidae) (Elmhagen et al. 2000, Hoekstra et al. 2003), it is critical to understand the seasonal availability of energetically significant epigeic macroarthropods.

The phenology patterns of some individual arctic arthropod species have been well studied (e.g., Danks 1978, Danks 1999, Sovik et al. 2003, Mjaaseth et al. 2005) but we know relatively little about how entire assemblages vary seasonally (but see Høye and Forchhammer 2008a, Høye and Forchhammer 2008b, Tulp and Schekkerman 2008). It is important to recognise that relationships between species often lead to community responses that contradict predictions generated from single-species models (e.g., Davis et al. 1998, Tylianakis et al. 2008, Van der Putten et al. 2010). In other words, patterns of assemblage structure can be strongly influenced by interactions (de Ruiter et al. 2005). It is therefore important to consider phenological changes in entire assemblages.

The phenology of an entire assemblage can be estimated using capture rates (*e.g.*, the number of individuals or biomass per sampling period). These rates may change throughout the active season in response to weather-mediated effects on activity levels (Briers et al. 2003). Although arthropods in northern regions have developed physiological, morphological, and behavioural adaptations to cope with harsh arctic weather conditions (see reviews in Downes

1965, Ring and Tesar 1981, Strathdee and Bale 1998, Danks 2004), they are still responsive to the inherent variability of seasonal weather patterns. While temperature seems to be a critical influence on seasonal arthropod activity in the far north (e.g., Høye and Forchhammer 2008a, Høye and Forchhammer 2008b, Tulp and Schekkerman 2008) the responses of ground-dwelling northern arthropod assemblages to seasonal weather patterns requires further study.

In addition to revealing changes in taxonomic assemblage structure, arthropod capture rates can act as a proxy for the effects of environmental variation on the functional contributions of arthropods to an ecosystem. Although guilds (Root 1967, Root 1973) are often used to describe assemblages on the basis of competitive resource use, the parallel term "functional group" (FG) (Cummins 1974) is more accurately used to describe animals that are equivalent in terms of their ecological roles or processes (Blondel 2003). The functional structure of an assemblage can be defined by the relative contributions (*e.g.*, abundance and/or biomass) of individuals in specific functional groups (FGs). Functional groups based on feeding behaviours, food types, or feeding relationships can be particularly useful for describing dynamic insect communities and their responses to environmental variation, as has been demonstrated recently in the literature (e.g., Lassau et al. 2005, Noriega et al. 2007, Choi et al. 2010).

We examine changes in the taxonomic and functional assemblage structure of epigeic insects collected in Kugluktuk, Nunavut, over the course of the active season. Beetles are used as the model ground-dwelling insect taxon in this study, because they are diverse, abundant, have diverse ecological functions, and respond rapidly to environmental change (Nelson 2001). The data are used to test four hypotheses: (1) the taxonomic structure of beetle assemblages will vary during the active season, (2) the functional structure of beetle assemblages will vary during the

active season, (3) seasonal patterns in beetle assemblage structure will differ between habitats, and (4) weather variables will explain seasonal variations in the assemblage structure of beetles.

2.3 Methods

2.3.1 Experimental Design

Beetles were collected in Kugluktuk, Nunavut, Canada (67.82°N, 115.09°W). The landscape beyond the limits of the town centre is open, largely undisturbed tundra, interspersed with occasional rocky outcrops of Canadian Shield. The region falls within the southern bounds of the subarctic ecoclimatic zone (Strong et al. 1989) and has a semi-arid climate, receiving approximately 250 mm of precipitation per year. Winters are long and cold, with an average temperature of -16.9 °C between September and May, while summers are short and cool, averaging 8.2 °C between the months of June-August (*i.e.*, the active period for most terrestrial arthropods).

Two broadly delimited but ecologically distinct habitat types were investigated in this study. “Mesic” habitats were characterised by elevated topography and well-drained soils. The dominant vegetation was dwarf woody shrubs, especially willows (*Salix reticulata* Linnaeus and other *Salix* Linnaeus species (Salicaceae)), birch (*Betula glandulosa* Michaux (Betulaceae)), arctic heather (*Cassiope tetragona* (Linnaeus) Don (Ericaceae)), mountain avens (*Dryas integrifolia* Vahl (Rosaceae)), Labrador tea (*Ledum decumbens* Small (Ericaceae)), and various berries (*Vaccinium* Linnaeus species (Ericaceae)), and perennial forbs (*e.g.*, *Lupinus arcticus* Watson (Fabaceae)), as well as moss and lichen cover, with occasional bare patches. “Wet” habitats were located in adjacent low-lying regions and had saturated or very poorly drained

soils. The vegetation in the wet habitats consisted primarily of sedges (*Carex* Linnaeus species and *Eriophorum* Linnaeus species (Cyperaceae)) some grass, and mosses.

2.3.2 Sampling and specimen processing

Between 21–22 June 2010, sampling sites were established at three different locations within 8 km of each other. Each site consisted of one wet and one mesic habitat. Within each habitat, three 75 m trap lines were set, spaced 15 m apart. Three pitfall traps and three pan traps were placed in a random sequence at 15 m intervals along each trap line, creating a 15 x 75 m grid with a total of 18 traps (nine of each type) per habitat (108 traps in total, for all habitats and sites). Pitfall traps consisted of a plastic cup 10 cm in diameter and 7 cm deep, nested in a second cup of the same diameter that was 15 deep, and into which drainage holes had been punched. Pitfall traps were covered by a 12 x 12 cm square piece of corrugated plastic positioned 3 cm above each trap. Pan trap were bright yellow, 20 cm in diameter and 3 cm deep. Traps were dug into the soil or vegetation so that the top edge of the trap was flush with the ground surface. Propylene glycol (diluted 2:1 with water) and a drop of surfactant were placed in each trap to capture and preserve arthropods.

Traps were serviced once per week, for a total of eight collection periods between 22 June and 13 August 2010. Samples were subsequently placed in 95% ethanol and returned to the laboratory. Adults were pinned and identified to species or morphospecies, and data were pooled by habitat type and sampling period. Based on information available in the literature regarding feeding preferences (of the species if available; if not, then of the lowest possible taxonomic resolution), each beetle was assigned to one of seven functional groups (see Table A1-1). Voucher specimens of all species are deposited in the Lyman Entomological Museum (Ste-

Anne-de-Bellevue, Québec, Canada) and/or at the Canadian National Collection of Insects, Arachnids and Nematodes (Ottawa, Ontario, Canada).

2.3.3 Weather data

Weather data were obtained online from the Canadian National Climate Data and Information Archive (http://climate.weatheroffice.gc.ca, climate station ID # 2300902). Since this was a short-term study and because there was some variability in the length of the sampling periods, it was determined that daily weather data would be used to generate mean weather values for each sampling period. Mean values were determined for the following variables: mean daily temperature (°C), mean daily wind speed (km/hour), atmospheric pressure (kPa), and total precipitation (mm rain or snow). These variables were selected based on previous seasonal studies that supported their effects on insect activity in the arctic (*e.g.*, (Høye and Forchhammer 2008a, Høye and Forchhammer 2008b). Maximum and minimum daily temperatures were also considered, but both were found to be highly correlated with the mean daily temperature; they were thus excluded to prevent difficulties associated with autocorrelation. Given their proximity to each other (within 8 km), all sampling sites were considered to have about the same weather conditions.

2.3.4 Data Analyses

The biomass of each beetle was estimated by measuring the specimen length and using length:biomass regressions for Coleoptera (Jarosik 1989, Hodar 1996). To account for slight variations in the length of sampling periods and disturbed traps, abundance and biomass data were standardised to the number of active traps per day per sampling period. To compensate for

zero counts and large differences in abundance and biomass between samples, data were log+1 transformed prior to analyses.

The total beetle biomass and abundance for each sampling period in each habitat was determined. We tested whether sample period and/or habitat had an effect on the total biomass and the total abundance of beetles via repeated measures analysis of variance (ANOVA). The dependent variable was either total biomass or total abundance (adjusted values, pooled by replicate, sample period, and habitat); sample period was treated as the within-subjects factor; and habitat was treated as the between-subject factor. The ANOVA was conducted using the ezANOVA function in the ez package (Lawrence 2011) in R version 2.10.0 (R Development Core Team 2012).

Species richness in each habitat was determined. However, species richness tends to increase as more individuals are added to a sample. Larger samples can be standardised to smaller samples via random sampling (Sanders 1968), so that the species richness of all samples is based on a constant number of individuals (*i.e.*, rarefaction). Rarefaction was therefore used to generate an unbiased estimate of the expected number of species (rarefied species richness, S) (Forbes et al. 2001) in each habitat at each sampling period using the rarefy function in the vegan package (Oksanen et al. 2010) of R version 2.10.0 (R Development Core Team 2012).

To test the hypotheses that (1) taxonomic and (2) functional beetle assemblages changed over time, assemblages from each sampling period in each habitat were visualised with non-metric multidimensional scaling (NMDS), using the rich (Rossi 2011) and vegan (Oksanen et al. 2010) libraries of R version 2.10.0 (R Development Core Team 2012). Non-metric multidimensional scaling is an indirect ordination approach maximising the rank order correlation between distances in a distance matrix. Assemblages that are more similar to each

other are arranged more closely in ordination space. In this case, the ordinations were conducted using Bray-Curtis distance matrices generated from the species (42 species, standardised and log + 1 transformed abundances) and functional (eight feeding groups, standardised and log-+1 transformed biomass) matrices. Since biomass integrates functional characteristics of assemblages (*e.g.*, energy and nutrient flow) (Saint-Germain et al. 2007, Wang et al. 2009), it was used as the metric to describe the functional assemblage (*i.e.*, rather than abundance). Changes in the functional assemblage over time were additionally visualised using stacked bar graphs showing the total biomass of beetles in each feeding group. Due to great differences in biomass between functional groups, the data were log + 1 transformed and displayed on a non-logarithmic scale. Untransformed values are presented in Table A1-2. To test the hypothesis that beetle assemblages changed over time in response to seasonal weather patterns, weather variables were overlaid on the NMDS plots as vectors , using the envfit function in the vegan (Oksanen et al. 2010) library in R version 2.10.0 (R Development Core Team 2012). The direction of each vector indicates the direction of the gradient (that of the most rapid change), and the length of the vector is proportional to the strength of the correlation between the variable and the ordination. This function allows a more objective interpretation of the results of unconstrained ordination analyses and generates a measure of fit as well as a significance value based on a permutation test (1000 permutations). Using this function, the significance of the relationship between each weather variable and the assemblages at each sampling period was tested.

2.4 Results

A total of 2638 terrestrial adult beetles was captured between 23 June and 13 August 2010. These represented 50 species or morphospecies in 11 families (Table A1-1). The dominant taxon was the ground beetles (Carabidae), with 2466 individuals and 16 species. More species of rove beetles (Staphylinidae) were found (22 species), but they were much less abundant (58 individuals). All other families were represented by three or fewer species, and less than 50 individuals (Table A1-1). The beetles collected in this study include 17 new species records for the territory of Nunavut, and probably two species unknown to science (Table A1-1).

In both habitats, the number of beetles is greatest during the first three sampling periods (albeit with a pronounced "dip" in abundance during sampling period 2); abundance exhibits a steep decline in sampling period 4 that continues for the remainder of the active season. More beetles were collected from mesic habitats than from wet habitats during each sampling period (Fig. 2.1a) and overall (1693 and 945, respectively). Wet habitats supported more total beetle biomass than mesic habitats over the course of the season (Fig. 2.1b). The total beetle abundance and biomass from the pooled samples were found to differ significantly by sampling period ($P < 0.001$) (Table 2.1), but not by habitat type. Although fewer beetles were trapped in the wet habitats, they tended to be larger (range of mean beetle biomass/sampling period = 9.4 ± 1.2 to 19.5 ± 1.7 mg) than those caught more abundantly in dry habitats (range of mean beetle biomass/sampling period = 6.2 ± 0.5 to 12.0 ± 1.7 mg) (Fig. 2.1c).

Overall capture rates for individual species (Table A1-1) indicate that, while some species can be found in either habitat, most display either a strong preference for one habitat type (*e.g.*, *Cymindis unicolor* Kirby (Carabidae), *Pterostichus haematopus* Dejean (Carabidae) – mesic; *Carabus vietinghoffi* Adams (Carabidae), *Pterostichus vermiculosis* Ménétries

(Carabidae) – wet) or are found exclusively in one habitat (*e.g.*, *Notiophilus borealis* Harris (Carabidae)*, Quedius fellmani* Zetterstedt (Staphylinidae), all Leiodidae, Coccinelidae, and Elateridae – mesic; *Blethisa catenaria* Brown (Carabidae) and most other Staphylinidae – wet). The NMDS ordination of the taxonomic beetle assemblages (Fig. 2.2, stress = 6.199, solution found after two iterations) indicates a difference in the overall species composition of beetles in the wet habitat compared to those in the mesic habitat. The arrangement of assemblages from each sampling period within habitats suggests a rapid turnover in species composition throughout the season. Despite the apparent turnover, rarefied species richness within and between habitats remained nearly consistent throughout the season (Fig. 2.1c). The only exception to this occurred in week six, when rarefied estimates of species richness decreased in both habitats.

The NMDS based on functional groups (Fig. 2.3, stress = 8.98141, solution found after 3 iterations) confirms that the beetle assemblages in the two habitats were functionally distinct throughout the active season. Similar to the taxonomic NMDS, the functional ordination also indicates a seasonal functional turnover in both habitat types, although this pattern is more evenly gradual in the wet habitats; there is a pronounced change in the functional assemblages between sampling periods 4 and 5 in the mesic habitats.

The beetle biomass in both wet (Fig. 2.4, Table A1-2) and mesic (Fig. 2.5, Table A1-2) habitats was dominated by entomophagous fauna throughout the active season. Among the non-carnivorous FGs, florivores are relatively well represented in both habitats from the beginning of the season to approximately sampling period 5, whereas bryophages are more commonly collected early in the season. Folivores are generally scarce in wet habitats (Fig. 2.4), but in mesic habitats display two peaks of activity in the first three and final three sampling periods (Fig. 2.5). Granivore biomass is consistent throughout the season in mesic habitats (Fig. 2.5), but

becomes almost negligible after sampling period 5 in wet habitats (Fig. 2.4). Necrophages were infrequently represented in traps.

Vectors of the weather data were plotted on the taxonomic (Fig. 2.2) and functional (Fig. 2.3) NMDS ordination space. Mean temperature was the only variable found to be significantly related to the taxonomic ($r^2 = 0.616$, $p = 0.002$) and functional ($r^2 = 0.435$, $p = 0.020$) assemblage structures throughout the sampling periods.

2.5 Discussion

In this study, ground-dwelling beetles were quantitatively sampled for eight weeks in two habitat types in a subarctic region, to determine how their taxonomic and functional assemblage structures changed over time and in response to seasonal weather patterns. Our results show that, while some species were found in both habitats sampled, many displayed strong preferences for one particular habitat. As a result, the hypothesis (3) that the beetle assemblages in the two habitats would be taxonomically distinct throughout the active season was supported. This could be attributed largely to differences in the diversity and structure of the vegetation in each habitat. Assemblages of other ground-dwelling arthropods in the far north have been shown to be best explained by associated plant communities (e.g., spiders; see Bowden and Buddle 2010) or by structural vegetational boundaries (e.g., Carabid beetles, see Nelson 2001).

Species in both habitats exhibited rapid seasonal turnover, supporting our first hypothesis, which was that the taxonomic assemblage structure would change throughout the active season. This is to be expected given the very brief summers of the subarctic region: northern species have adapted to the short summers, cold temperatures and unpredictable food supplies by displaying short periods of seasonal activity, resulting in an extension of their

lifespan and development (compared to southern species) (Danks 1992c, Lovei and Sunderland 1996). Although the species composition changed throughout the season, rarefied species richness remained relatively stable, and there was little difference in richness between the two habitats. In light of this stability, and given the inherent paucity of resources in the far north (Danks 2004), the assumption might be made that temporal resource partitioning is taking place. It has been surmised that in some ground beetle assemblages interspecific competition between individuals relying on similar resources or prey items (*i.e.*, functional groups) can be reduced by their minimally-overlapping or non-overlapping periods of emergence and activity (Niemelä 1993). Although comprehensive studies of the life cycles of northern species are scarce, some generalisations may be made. For example, while some arctic arthropods respond to the brief availability of resources and favourable weather by emerging as early as possible in spring and completing their development in a single season, others display greater flexibility in terms of the timing of their emergence and the duration of their development (Danks 1999). These different strategies, and the resulting variability in faunal composition at any given time, may permit a temporal "staggering" of resource exploitation by species reliant on similar resources.

Functionally, the beetle assemblage demonstrated a seasonal turnover, supporting our second hypothesis that the functional assemblage structure would change throughout the active season. Generally, the seasonal turnover effect was more pronounced in the mesic sites, due to the fact that the diversity of functional groups was generally lower in the wet sites. The two habitats were functionally distinct throughout the active season (supporting our third hypothesis). Both the mesic and the wet sites were overwhelmingly dominated by entomophagous beetles throughout the active season. However, mesic sites consistently had greater biomass and greater diversity of herbivorous functional groups; this was especially pronounced by sampling period 6,

when herbivores were all but absent from wet sites. With the exception of sporadic appearances of necrophagous scavengers, saprophages were absent from the samples.

The vegetation in the two habitats may be the most likely factor explaining these results. The wet habitats in this study were dominated by graminoids, while the mesic sites supported a variety of shrubs and forbs. In a feeding preference study involving 42 common arctic plants, MacLean and Jensen (1985) found that herbivorous insects (Lepidoptera and Hymenoptera larvae) consistently selected deciduous shrubs while rejecting evergreen and graminoid species. Deciduous shrubs tend to grow on more nutrient-rich soil, and therefore exhibit rapid growth, high leaf turnover, and little investment in chemical or physical defence; conversely, graminoids grow in nutrient-poor soils, grow more slowly, have low leaf turnover and tend to favour more investment in defence (MacLean and Jensen 1985). It is likely that the vegetation in mesic sites provided more favourable food sources for herbivorous beetles. While reduced leaf senescence in the wet habitats might explain why few saprophages were collected there, the apparent absence (or paucity, at least) of generalist saprophages from the mesic sites is interesting given the abundance of senesced deciduous leaves from the previous season. In addition to senescence, other plant phenology patterns may explain other functional trends. For example, plant communities in the far north exhibit a single, compressed flowering season, as opposed to plants in temperate or tropical regions that display periodic or ongoing flowering (Thórhallsdóttir 1998). The florivorous beetles in this study similarly display a short, intense period of activity in the early summer.

The foraging and activity levels of certain insect species can be reduced by high wind speeds in exposed habitats such as open tundra (Downes 1969, Service 1980, Totland 1994). Wind speed can also be a factor in habitat selection by some ground beetles, which generally

prefer lower wind speeds (e.g., Penney 1966). Atmospheric pressure can also alter flight and foraging activities in some insects (Lanier and Burns 1978, Drake and Farrow 1988). In our study, seasonal changes in the structure of the entire beetle assemblage were not significantly related to wind speed, precipitation, or atmospheric pressure. Epigeic fauna may be less affected by wind and atmospheric pressure - which are closely related - due to shelter afforded from vegetation, or because of their flightlessness (many species of beetles above the tree line are apterous). There was little total accumulation of precipitation across the season (68.7 mm total) and rain events were frequent (21 days) but not significant (mean = 1.4 mm; the largest single rain event deposited only 15.6 mm). While flash floods or periods of heavy rain might affect the availability of food or the suitability of habitats, the minimal rainfall in this semi-arid region is not likely to affect short-term changes in the activity of ground-dwelling fauna.

We did uncover a significant seasonal relationship between the beetle assemblages and mean daily temperature. We can therefore partially accept hypothesis four: mean daily temperature appears to play an important role in the taxonomic and functional assemblage structure of insects. This is consistent with other work from northern regions. For example, seasonal ground-dwelling arthropod activity in Taimy, Sibera, Russia was found to increase most strongly in response to increased temperatures, and secondarily to lower precipitation and wind (Tulp and Schekkerman 2008). Ground-dwelling arthropod activity in Zackenberg, Greenland, was most strongly influenced by solar radiation levels and secondarily by temperature (Høye and Forchhammer 2008a). Solar radiation data were not available for this study. The influences of temperature on the species composition and functions of epigeic assemblages in Kugluktuk indicate that changes in weather (or, by proxy, longer-term changes in climate) could affect the biodiversity and ecological function of insects in this system (and other similar systems). Given

the significance of insects in the north (Leborgne et al. 2011), such changes could result in important modifications to northern ecology.

A final point of interest is the carnivore-heavy trophic structure evident in this study system: an apparent "inverted trophic pyramid" (Odum 1971). One possible explanation is that beetle predators are supported by something other than non-carnivore beetle prey. Mites (Acari), Collembola, Hemiptera, Orthoptera, and Lepidoptera larvae were also present in traps, but in low numbers and minimal biomass. Alternate explanations are intratrophic predation or cannibalism, or it could be that beetles are consuming "aerial plankton"; wind-dispersing arthropods may provide important influxes of food in the arctic (Coulson et al. 2003). Future work will seek to uncover which of these trophic interactions (if any) support carnivorous arthropods in the far north. Uncovering the mechanisms behind the trophic structure may prove to be important: since carnivores represent the greatest biomass in the assemblage, their functional role and availability as a food source for other animals may be affected if weather and long-term climate patterns continue to change.

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Table 2.1 Summary of repeated measures ANOVA testing for the influence of habitat type (wet or mesic) and sample period (1–8) on total biomass and total abundance (adjusted, pooled values). Degrees of freedom (df) for the numerator and denominator (n, and d, respectively), F and P values. P values with an asterisk (*) indicate significance.

Replicate	Effect	df (n,d)	Total Biomass (g)		Total Abundance	
			F	***P* < 0.05**	***F***	***P* < 0.05**
1	Habitat	1, 4	0.243	0.648	2.738	0.173
2	Sample period	7, 28	15.726	< 0.001*	13.687	< 0.001*
3	Habitat:Sample period	7, 28	1.0870	0.399	1.8289	0.1209

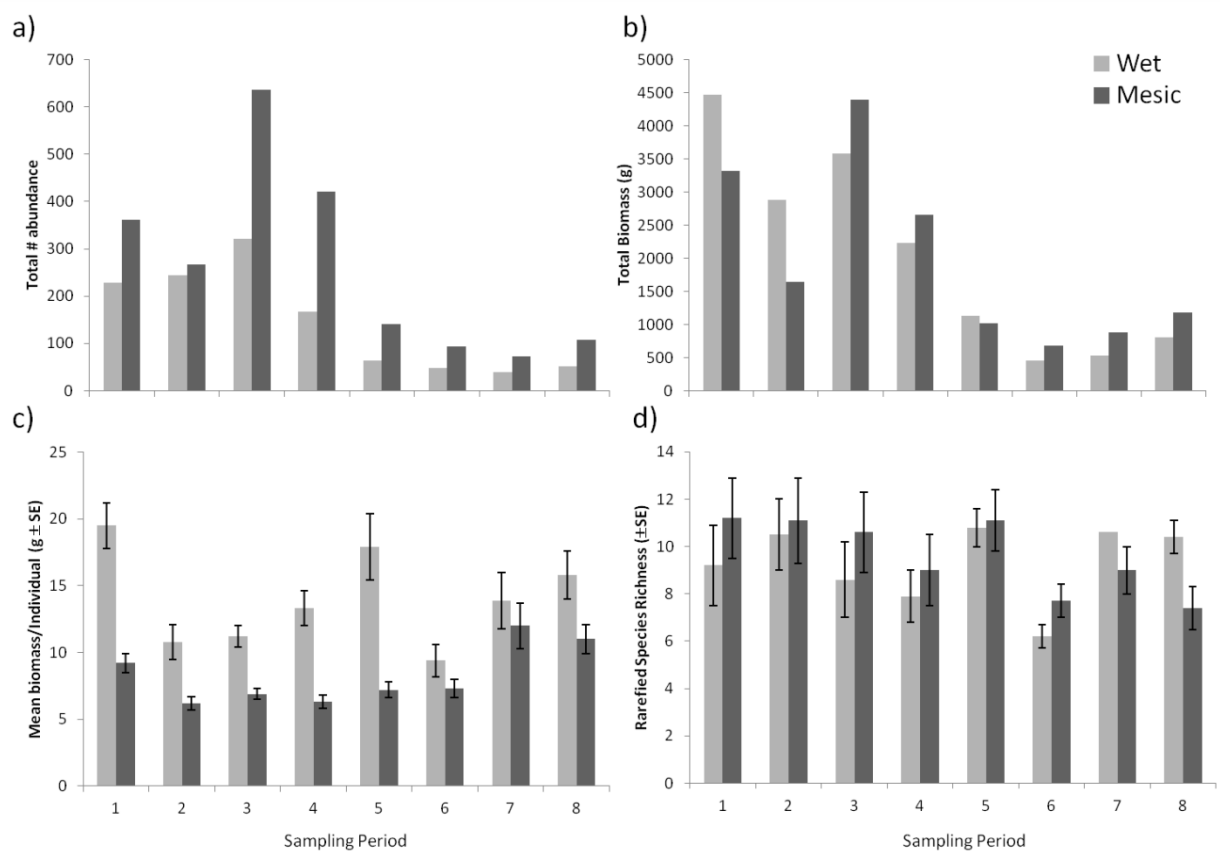

Figure 2.1 Changes in a) total abundance; b) total biomass (g); c) average biomass (g); and d) rarefied species richness of beetles collected from wet (grey) and mesic (black) habitats across sampling periods from June to August 2010.

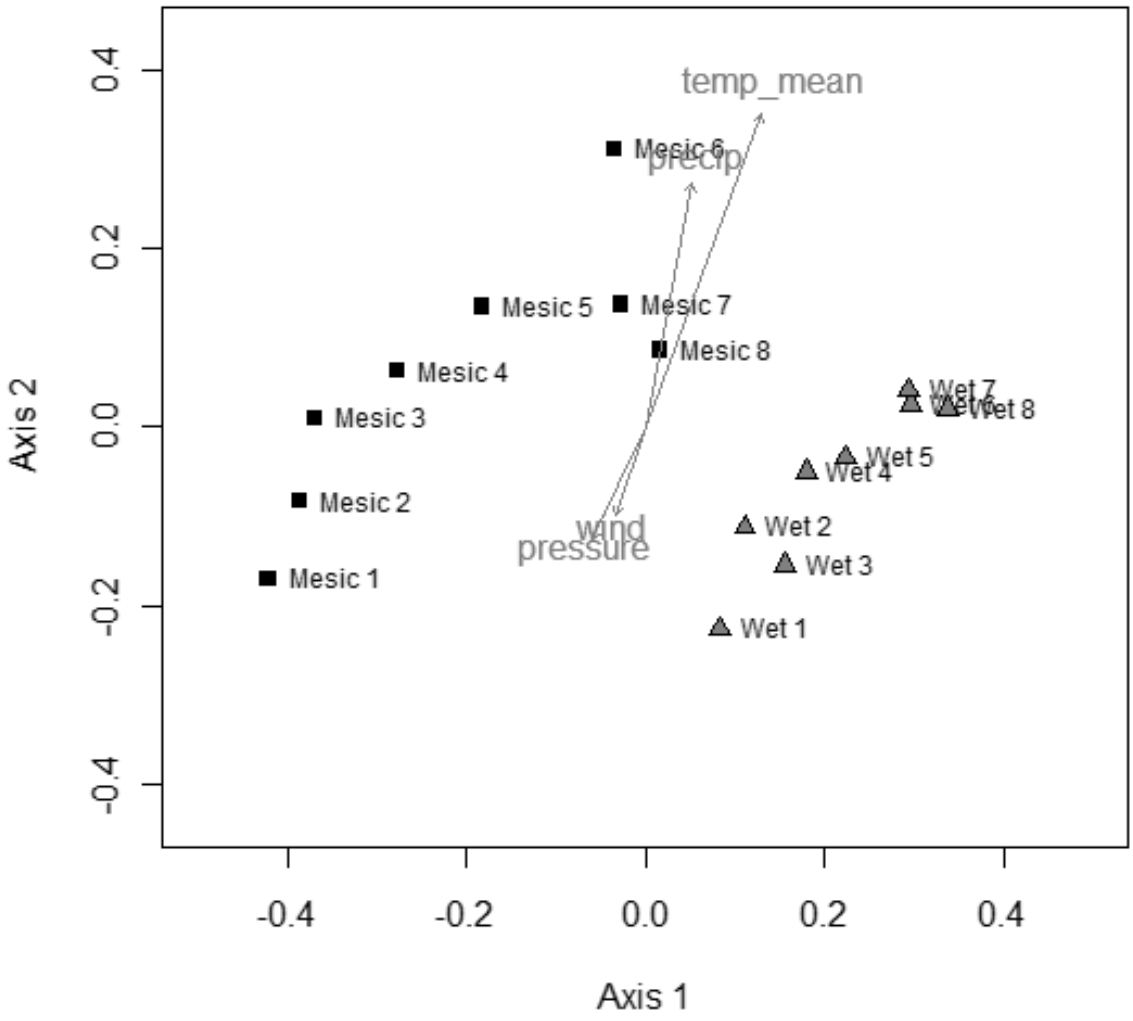

Figure 2.2 Non-metric multidimensional scaling of 50 beetle species (log + 1 abundance) collected in wet (triangles) and mesic (circles) habitats across sampling periods (denoted by numbers) from June to August 2010. Overlaid on the figure are the weather variables, visualized as vectors.

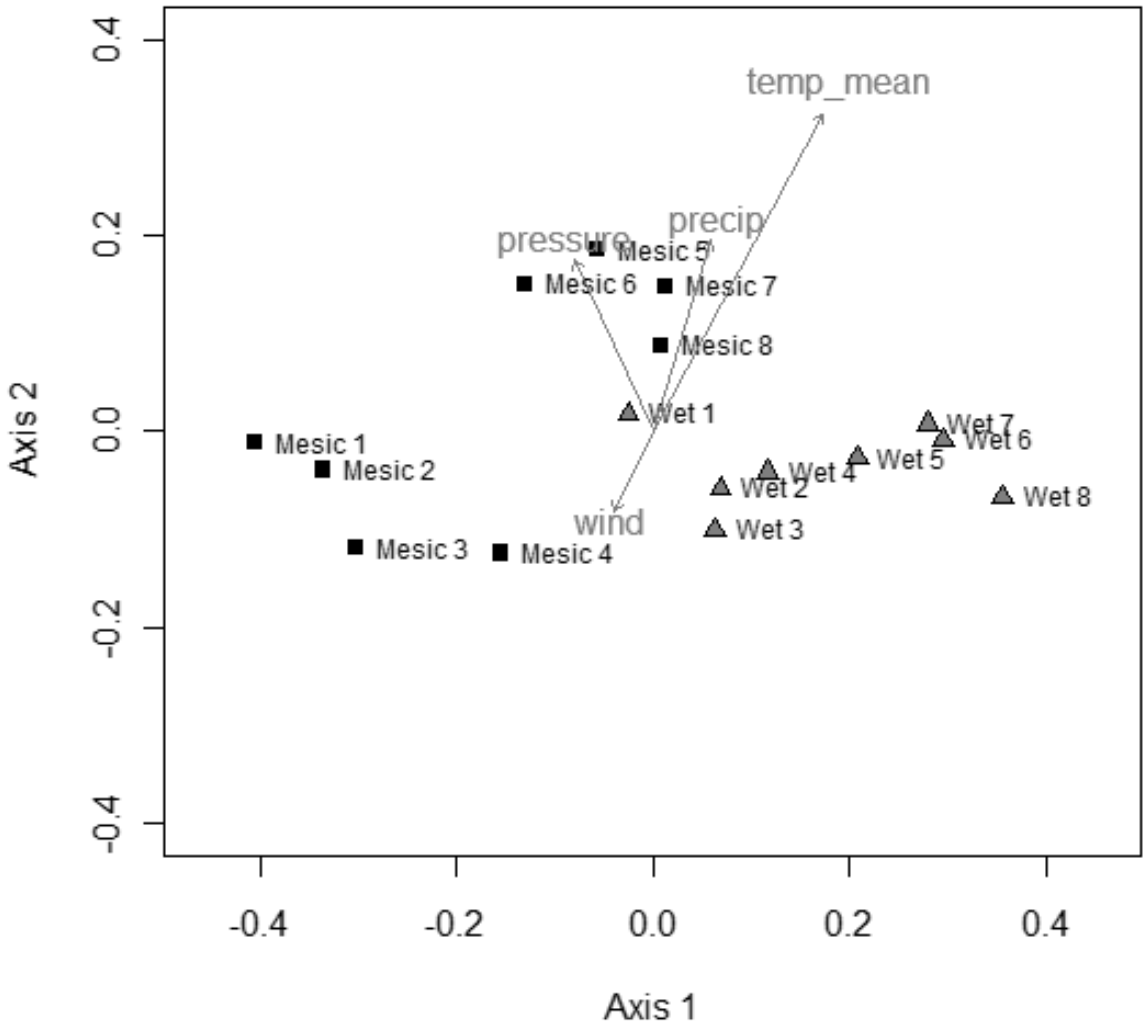

Figure 2.3 Non-metric multidimensional scaling of seven beetle functional groups (log + 1 biomass) collected in wet (triangles) and mesic (circles) habitats across eight sampling periods (denoted by numbers) from June to August 2010. Overlaid on the figure are the weather variables, visualised as vectors.

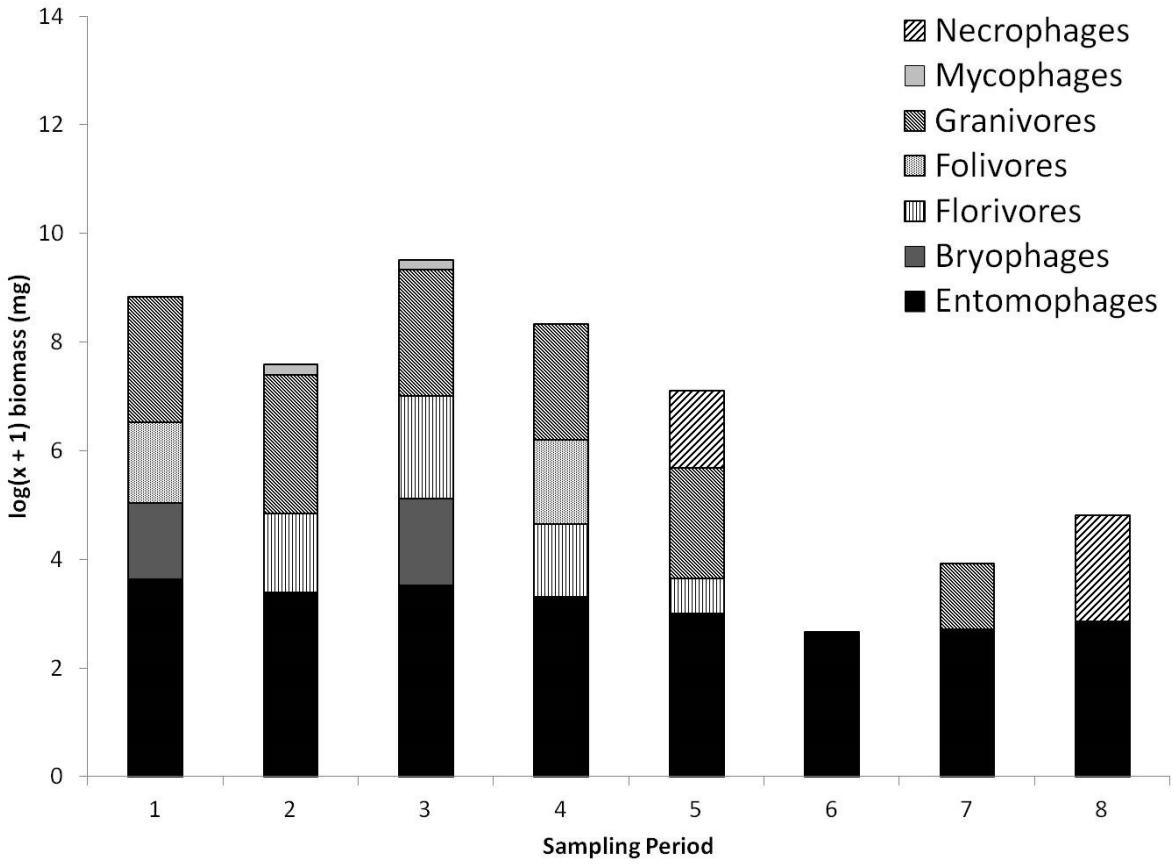

Figure 2.4 Stacked bar graph showing the total biomass (log + 1 transformed) of beetles from each functional group collected eat each sampling periods from June to August 2010, in mesic habitats. Note that the y-axis is not a logarithmic scale.

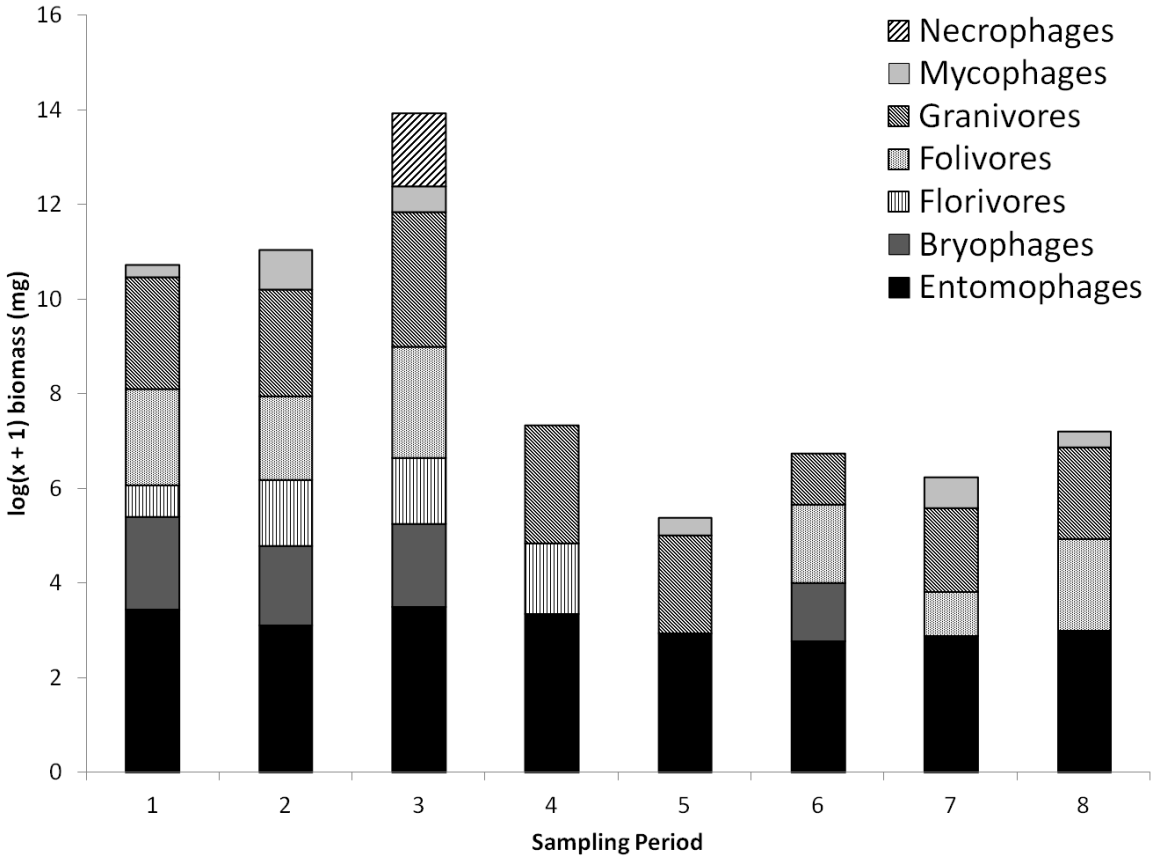

Figure 2.5 Stacked bar graph showing the biomasses (log + 1 transformed) of all feeding groups collected across sampling periods from June to August 2010, in wet habitats. Note that the y-axis is not a logarithmic scale.

2.7 Connecting Statement

The results from Chapter 2 revealed, in part, high numbers (and biomass) of carnivores in the epigeic beetle assemblages of both habitat types, suggesting that this trophic tructure may be an ubiquitous condition of northern food webs. Given an apparent paucity of herbivorous prey on the ground, I was left wondering what alternative sources of food these carnivores might be relying on. I made an unexpected discovery while processing beetle specimens from other locations during the field seasons subsequent to the one described in Chapter 2, which shed some light on this issue of predator diet. Many beetles from different high and subarctic locations were visibly affected by a parasite known to infect terrestrial insect hosts via ingestion of the alate adult forms of aquatic insects, such as mosquitoes. The following Chapter describes these novel host-parasite associations between ground beetles (Carabidae) and a new species of horsehair worm (Nematomorpha). These associations provide new information about the prey and diet breadth of terrestrial beetles, and suggest important nutritional links between aquatic and terrestrial habitats.

Chapter 3: Parasitism of ground beetles (Coleoptera: Carabidae) by hairworms (Nematomorpha: Gordiida) in arctic Canada

Crystal M. Ernst, Ben Hanelt and Christopher M. Buddle

3.1 Abstract

The host-parasite associations between ground beetles (Coleoptera: Carabidae) and hairworms (Nematomorpha: Gordiida) collected from the arctic (a novel and ecologically important region) is described. Carabids and their parasites were collected from twelve sites spanning the three northernmost ecoclimatic zones of Canada (north boreal, subarctic and high arctic) using standardized methods. The beetles and hairworms were identified using traditional morphological approaches. Six beetle species are recorded as hosts: *Amara alpina, Pterostichus caribou*, *P. brevicornis*, *P. tareumiut*, *P. haematopus*, and *Notiophilus borealis*. All represent new host records (increasing the known North American host list from 14 to 20), and this is the first record of hairworm infection in the genus *Notiophilus.* Beetles from Banks Island, NWT, were infected in high numbers and were used as an ecological case study. At Banks Island, 11-19% of all beetles were infected at each sampling period, and 20% of those were infected with two or more mature worms. There was no significant relationship between infection status and host species, body size or sex. Beetles collected in wet habitats were more likely to be infected, which indicates that the paratenic hosts do not disperse very far from the original body of water containing the parasites. Morphological examinations to date indicate that the hairworms collected from all locations represent a single, new species of *Gordionus*, making it only the sixth hairworm species and the third species of that genus found in Canada. Hosts are unknown

for all other Canadian (and one Alaskan) *Gordionus* species. Given the life cycle of the parasite, which consists of both aquatic and terrestrial stages, this study provides evidence that some omnivorous and predatory terrestrial beetles are using flying insects as an important nutrient subsidy in the far north.

3.2 Introduction

Parasites and their roles in ecosystems are poorly understood, despite arguments that parasites are critical components of biodiversity and positive indicators of ecosystem health (Marcogliese and Cone 1997, Hudson et al. 2006, Lafferty et al. 2008b). Parasites can influence food web chain length, stability, and connectance (Lafferty et al. 2008a, Dunne et al. 2013). They have the capacity to regulate host populations, and may represent important determinants of community structure (Marcogliese and Cone 1997). Concerted sampling efforts targeting specific host taxa in a variety of habitats and unique localities are likely to provide important new information about host-parasite associations, their ecological functions, and their influences on community structure.

Gordiid nematomorphs are a poorly known group of parasitic roundworms found in freshwater habitats worldwide, with the exception of the Antarctic (Poinar 2008). Over 300 species of Gordiids have been identified and there are 18 recognized species in North America (Hanelt et al. 2005, Poinar 2008). Only five species have been reported in Canada from six provinces (NB, ON, QU, AB, SK, BC) and one territory (YK) (Schmidt-Rhaesa et al. 2003). The northernmost limit of the known distribution of nematomorphs in North America is represented by specimens of *Gordius attoni* collected from Old Crow, Yukon (67°34′0″ N, 139°48′0″ W) (Redlich 1980, Schmidt-Rhaesa et al. 2003).

Commonly called “hairworms” due to their very slender, elongated shape, Gordiids infect a variety of terrestrial arthropod hosts including flies, crickets, mantids and beetles (Schmidt-Rhaesa and Ehrmann 2001, Poinar and Weissman 2004, Hanelt et al. 2005). Ground beetles (Coleoptera: Carabidae) are common definitive hosts for hairworms. Globally, 79 species of ground beetles have been found to be infected (Looney et al. 2012). Recent work by Looney et al. (2012) in Washington State (USA) increased the known North American ground beetle host list from 8 to 14 species.

The worms have free-living aquatic stages and a terrestrial parasitic stage (Hanelt et al. 2005). All hairworms require at least one, and usually two, hosts (Hanelt et al. 2005; see Fig. 3.1). Larval hairworms first enter an aquatic paratenic host, such as a larval fly, generally via consumption. The larvae form cysts that cause no harm to the host, and the cysts survive their hosts’ metamorphosis from aquatic larva to terrestrial adult (Hanelt and Janovy 2004). Consumption of a cyst-bearing paratenic host results in the infection of a definitive host, which is typically an omnivorous or carnivorous terrestrial insect. Inside the alimentary tract of the definitive host, the hairworm grows until its length is many times that of its host, effectively filling a large portion of haemocoel. At this point the mature worm leaves its host to return to fresh water. Hairworms can alter the definitive hosts’ behaviour, compelling them to seek and enter water, so the mature worm can then escape the hosts’ haemocoel and enter the aquatic environment (Thomas et al. 2002).

In this study we examine host-parasite associations in a novel and ecologically important region: arctic Canada. Despite the harsh environmental conditions of arctic and subarctic ecosystems, over 2000 arthropod species are found above the tree line (Danks 1981b). Closely associated with these is a suite of invertebrate and fungal parasites that prey on arthropods (e.g.,

Wharton 1986, Meyling et al. 2012), some of which are hyperdiverse and abundant. Hairworms, however, are poorly represented in our contemporary understanding of parasitic arctic fauna. The three objectives of this research were to: (1) describe hairworm-carabid associations and distributions in arctic and subarctic Canada; (2) use a case study of beetles on Banks Island, Nunavut, to test the relationships between host traits or environmental factors and the infection status of hosts; and (3) to describe a new arctic hairworm species.

3.3 Materials and Methods

3.3.1 Study sites and sampling design

In 2010 and 2011, ground-dwelling beetles were collected at 12 different locations (Fig. 3.2, Table 3.1) in northern Canada as part of a larger research project (the Northern Biodiversity Program, NBP, see e.g., Ernst and Buddle 2013, Timms et al. 2013a) At each location, three replicates were established within approximately 15 km of each other. Each replicate contained two broadly delimited but ecologically distinct habitats. “Mesic” habitats are characterized by higher elevations and well-drained soil, while “wet” habitats have saturated or very poorly drained soils, and can be found in adjacent low-lying regions. The vegetation of mesic sites was a discontinuous cover of dwarf shrubs, perennial forbs, and lichens. Wet habitats contained continuous cover of moss, sphagnum, saxifrages and sedges. In order to ensure consistency of sampling in both habitats across all locations, all replicates were established in open areas with no tree canopy cover; some dwarf black spruce were encountered in some of the more southern sites.

Replicated grids of pitfall and yellow pan traps were established in each habitat, in each replicate, at each of the twelve locations (Ernst and Buddle 2013). Traps were serviced once

every four days over a period of two weeks, for a total of three collection periods (see Table 3.1 for collection dates). Beetle and hairworm samples were subsequently placed in 95% ethanol and returned to the laboratory.

3.3.2 Beetle identification and infection status

Adult beetles were removed from the trap catches. Those without signs of hairworm infection were pinned; those with obvious infections (i.e., with one or more hairworms partially emerged from the posterior end) were retained in 95% ethanol so that the parasites could be extracted and identified. All beetles, regardless of infection status, were identified to species as per Lindroth (1961-1969). Their sex was determined via examination of the protarsi, and their body length was measured using an ocular micrometer.

Voucher specimens of the beetles are deposited at the Lyman Entomological Museum of McGill University's Macdonald Campus in Sainte-Anne-de-Bellevue, Quebec, Canada.

The high infection rate at one location (Banks Island, Nunavut; BAN on Figure 3.2) provided an opportunity to quantify the infection status of beetles in this region, and to determine whether any host traits or other factors were related to infection status. Fisher's Exact Tests were used to test for independence between infection status and: a) habitat type (wet and mesic); b) trap type (yellow pan and pitfall); c) sampling period (1 - 3, see Table 3.1) and; d) sex (male and female). A logistic regression was used to determine if there was an association between body size and infection. The analyses were performed using R version 2.15.1 (R Development Core Team 2012).

3.3.3 Parasite identification

For each worm, length and colour was recorded before each was divided with a razor blade into four pieces. Three pieces – the anterior, posterior, and a small portion of midsection – were preserved in 70% ethanol for scanning electron microscopy (SEM) work and stored at room temperature. The remaining tissue was preserved in 100% ethanol for future molecular work and stored at -80°C.

For SEM, ethanol-preserved tissues were dried using two methods. In the first method, samples were placed in acetone and then dried with CO_2 in a CPD-1 critical point dryer (Denton Vacuum, Moorestown, NJ). Many samples processed using this first method collapsed, making some morphological features difficult to visualize. Therefore, samples were also dried via increasing concentrations of hexamethydisilazane. Tissues were then mounted on stubs with carbon tape and coated with gold-palladium in an EmiTech K950 turbo-pumped vacuum coater with a gold-palladium sputter coater attachment (Quorum Technologies, West Sussex, England). Observations were made and digital images were taken using a JEOL 5800LV SEM at 15kV (JEOL Ltd, Tokyo, Japan).

Nematomorph voucher specimens are deposited at the Museum of Southwestern Biology, Division of Parasitology, University of New Mexico, Albuquerque, New Mexico, USA.

3.4 Results

3.4.1. Beetle hosts

Ground beetles were collected in high numbers from all 12 sampling locations, but beetles with visible hairworm infections were found only in four locations: one is located in the

subarctic Tombstone Mountain range in the Yukon Territory (TOM), while the other three are located on high arctic islands: Iqaluit, Nunavut (IQA); Cambridge Bay, Nunavut (CAM); and Banks Island, Northwest Territories (BAN) (Fig. 3.2).

Parasites were found in a total of 97 beetle hosts, in six species from the family Carabidae: *Amara alpina* Paykull, *Pterostichus (Cryobius) caribou* Ball, *Pterostichus (Cryobius) brevicornis* Kirby, *Pterostichus (Cryobius) tareumiut* Ball, *Pterostichus (Stereocerus) haematopus* Dejean, and *Notiophilus borealis* Harris (see Fig. 3.2 for distribution and abundances, and images of infected beetles in Fig. 3.3).

At three of the locations, four or fewer beetles were parasitized, and always by a single hairworm (Fig. 3.2). However, traps from the northernmost location (Banks Island, NT) yielded 157 hairworms. One hundred and seven of these hairworms parasitized a total of 87 beetles: 17 beetle specimens had more than one parasite (2 worms, N = 14; 3 worms, N = 3). The remaining 50 hairworms had fully emerged from the beetles into the preservative fluid in the traps, and therefore could not be associated with a particular beetle host.

Parasitism rates at Banks Island were high: 87 out of a total 652 ground beetles, or 13.3%, had an emerging parasite. Beetles collected in wet habitats ($p < 0.0001$, CI = 0.096 – 0.292, odds ratio = 0.171) and those collected in yellow pan traps ($p < 0.0001$, CI = 1.69 – 5.44, odds ratio = 2.966) were significantly more likely to be parasitized (Table 3.2). There was no significant relationship between a beetle's sex or the sampling period (Table 3.2), or the insect's body length and its infection status ($p = 0.801$, $p = 0.800$, and $p = 0.406$, respectively).

3.4.2 Nematomorphs

Hairworms were collected in the free-living, post-parasitic, adult stage, and from within the definitive host. The majority of the adult nematomorphs were collected from beetles or in traps at Banks Island and Cambridge Bay between July 7-19, 2011. Others were collected at Tombstone from June 27-July 1, 2011, and at Iqaluit from July 7-19, 2010. A total of 28 individuals (14 males, 14 females) were examined from a variety of sites using light microscopy. The anterior, posterior, and midsection of six individuals (three males, three females) individuals were examined by SEM.

3.4.2.1 Description of male

Adult males (N = 14) varied in length from 80 mm to 129 mm ($\bar{x}$ = 99 mm). Males were monochromatically dark brown, but several worms were uniform cream brown or had dark brown posterior ends and cream brown/brown midsections and anterior ends. The male posterior end consists of a distinctive bifurcating end, a subterminal, round cloacal opening, bristle fields, and postcloacal cone-like spines (Fig. 3.4A). Starting roughly 50 µm apart and roughly 150 µm anterior to the cloacal opening are numerous rows of bristles arranged in a V-shaped formation. Bristles continue posterior towards the bifurcating end for roughly 175 µm, ending abruptly in line with the start of the bifurcation. Adhesive warts are absent.

Postcloacal spines are found on the ventral surface of the tail lobes and on the ventral part of the interior of the tail lobes (Fig. 3.4A). Postcloacal spines are roughly 5 µm in width, and vary in shape. The round cloacal opening is roughly 25 µm in diameter, and contains numerous short spines.

The cuticle shape of the male worms is uniform along the length of the worm. Areoles are generally polygonal (Fig. 3.4 B-E), and are roughly 10-15 μm in diameter. The worms contain only one type of areole, and no areole ornamentation was noted. Areoles are smooth and without knobs. Interareolar furrows are absent; however, areoles are connected by thin, thread-like, interareolar structures (Fig. 3.4 C). In males, each areole is superficially striated parallel with the length of the body (Fig. 3.4 A-E).

3.4.2.2 Description of female

Females (N = 14) varied in length from 46 mm to 107 mm ($\bar{x}$ = 68 mm). Their colour ranged from monochromatically dark brown, cream brown and light brown to pattern variations of those three colours along the body length, with one having a grey/dark brown pattern. As in the male, areoles are similar along the length of the body (Fig. 3.5 C-E). Areoles are polygonal in shape and are connected to surrounding areoles by thin extensions between areoles (Fig. 3.5 D,E).

3.4.1.3 Diagnoses and taxonomic comments

The shape of the areoles, including the connections between the areoles within the interareolar space, in combination with the bristle field and post-cloacal spines, make this species unique. All other *Gordionus* spp. found in Canada are morphologically distinct from the species described above. *Gordionus sinepilosus*, described from British Columbia, lacks bristles anterior to the cloaca, contains adhesive warts, has rounded areoles and interareolar bristles. *Gordionus platycephalus*, described from Quebec, contains long slender tail lobes, lacks bristles and spines

on the posterior end, and interareolar bristles are present. Finally, *G. alascensis*, from Alaska, contains irregular areoles (in form and size) and has a distinctive parabolic integumentary ridge.

3.5 Discussion and Conclusion

Important, interesting, and poorly understood associations between ground beetles and parasitic hairworms are described from arctic Canada. Six species of Carabid hosts were identified, none of which have previously been reported in the literature. One photograph of an infected specimen of *A. alpina* exists, but the location and date of this record was not published (M. Bolek, pers. comm.). Although other species of *Amara* and *Pterostichus* are known to be hairworm hosts (Poinar et al. 2004), this study provides the first record of a hairworm infection in any species of beetle in the genus *Notiophilus*. This study increases the known Carabidae hosts to 85 species worldwide, and increases the list of North American Carabid hosts from 14 to 20. Given the number of new host associations that have been discovered in recent years (including those reported here), it is likely that more remain to be described in the arctic and elsewhere.

Prior to this study, hairworms had not been recorded from Nunavut or the Northwest Territories; we have therefore contributed two new territorial records to the known Canadian distribution of hairworms. In doing so, we have expanded the known distribution of Gordiids in North America northward by approximately 5.68 degrees of latitude, or about 630 km. Three of the sites at which hairworms were found were on high arctic islands. These locations are subject to geographic isolation and harsh climatic conditions. The presence of hairworms at these sites raises questions of their mode of dispersal and cold tolerance mechanisms, among others. In a laboratory study of an Argentinian hairworm, 100% of *Chordodes nobilii* eggs and 89% of adults were killed by 48 hour exposure to temperatures of -3°C; larvae, on the other hand, largely

survived and remained infective (Achiorno et al. 2008). Another study involving a North American species, *Paragordius varius,* found that storage at -80°C for 7 months had no effect on the viability of larvae (Bolek et al. 2013), and storage at -20°C had no effect on the viability of *P. varius* cysts, nor of those of a related African species, *P. obami*. These studies indicate that, while free-living nematomorphs may be vulnerable to cold temperatures, non-free-living stages are capable of surviving long periods of extreme cold beyond what would be experienced in the wild, even in the high arctic. Extreme temperatures likely impose environmental constraints on the distribution of hairworms in Canada: only very cold-hardy species would be able to survive.

High levels of infection were found in the ground beetles collected on Banks Island, NT. While we have estimated the infection rate there to be approximately 13.3%, this figure could arguably be as high as 21% if each of the 50 parasites with no determinable host association came from a unique host (these were not included in our analyses). Additionally, we made no attempt to dissect beetles that lacked obvious sign of infection. We expect that some of these beetles were infected with immature or encysted hairworms and our estimated infection rates are therefore probably conservative. That said, the total number of infected beetles collected in traps could have been inflated by behavioural modification of the hosts by the parasites (Thomas et al. 2002): parasites may have compelled infected beetles to enter traps, which contained a preservative fluid, at a rate greater than non-infected beetles were entering traps by chance alone. Additional studies would need to be performed to determine whether trapping methods influence capture rates.

More beetles were collected from pitfall traps than from pan traps, yet a greater proportion of beetles in pan traps were infected. The pitfall traps used in this study included a plastic cover set a few centimeters above the trap itself (primarily to exclude flying insects),

while the pan traps were uncovered and their liquid preservative contents were clearly visible. As mentioned above, the prevalence of infected beetles in pan traps may be indirect evidence of behavioural manipulation of the beetle hosts by the parasites. Thomas et al. (2002) demonstrated that water-seeking behaviour of hairworm-infected orthopterans is directed by their mature parasites. The definitive hosts are presumably compelled by the parasite to enter bodies of water so that the parasite can return to an aquatic habitat to complete its life cycle (i.e., mate and lay eggs, see Fig. 3.1). Additionally, there are many examples of hairworm-infected terrestrial insects being found in artificial bodies of open water of different sizes, including swimming pools (Thomas et al. 2002), bathtubs (Spiridonov et al. 1992), toilet bowls (Herter and Nesse 1989) and pet water dishes (Hanelt et al. 2005). The uncovered yellow pan traps used in this study provide similar sources of fluid into which beetles may have been compelled to enter by their mature parasites.

Ground beetles on Banks Island were infected regardless of their sex, body size, or species. All three ground beetle species collected on the island had hairworm infections. There is a fourth species known to be present on the island (*Pterostichus haematopus*) (Lindroth 1961-1969) and while we did not collect any specimens on Banks Island in this study, we did collect infected *P. haematopus* at Tombstone and Cambridge Bay. This indicates that all ground beetles - important carnivores in the terrestrial food web - can potentially become infected on Banks Island. The implications of this are not known, but it would be worthwhile to examine the effects of hairworm infection on the beetles' fitness and on behaviours such as dispersal and predation.

The lower numbers of infected beetles at the other sites are probably due to the short window during which they can be effectively sampled from active definitive hosts – a reflection of their short life cycles and brief periods of emergence and activity (Hanelt et al. 2005). This

rapid and seasonally brief life cycle may make hairworms particularly well-suited for life in the far north, where other invertebrates are known to display similarly abbreviated periods of activity in response to the very short summers that are characteristic of higher latitudes (Danks 2002, Danks 2004).

Fewer beetles were collected from wet habitats than from mesic habitats, yet a greater proportion of beetles in the wet habitats were infected. This is intuitive since both the parasites and the paratenic hosts are aquatic for part of their development. Mosquitoes and other paratenic hosts with similar life cycles do naturally disperse from their natal bodies of water after undergoing metamorphosis to their terrestrial adult forms. Wind can also trigger or otherwise influence the dispersal of arctic flies after emergence (Service 1980). Natural and wind-based dispersal of cyst-bearing paratenic hosts to drier areas can explain the presence of infected beetles in mesic habitats. However, dispersal of paratenic hosts can be somewhat limited and can vary considerably (e.g., Jenkins and Hassett 1951). Taken together with the fact that host characteristics do not appear to influence infection status, this suggests that infection of the definitive beetle hosts is primarily dependent on successful infection, dispersal and ultimate consumption of the paratenic hosts.

When a parasite requiring multiple hosts is found infecting one host, it indicates that the other required host(s) must be present in the community (Marcogliese and Cone 1997). Additionally, if a host is infected late in the parasite's life cycle, the parasite's presence can be indicative of direct links in the food web, thereby identifying the hosts' prey (Marcogliese and Cone 1997). The presence of nematomorph parasites in terrestrial beetles provides some of the first evidence of a direct link between the arthropod food webs of aquatic and terrestrial habitats in the arctic. The prevalence of infected beetles suggests that flying insects with aquatic larval

stages (i.e., the paratenic hosts) are becoming prey items for ground-dwelling beetles, providing an important prey subsidy in a food web that otherwise seems to be prey-poor (Ernst and Buddle 2013).

The presence of parasites can additionally be evidence for omnivory in taxa that might otherwise be assumed to be herbivores (Marcogliese and Cone 1997). *Amara*, for example, is a genus consisting largely of seed-feeding beetles; in cases where their feeding habits have not been directly observed, their rounded mandibles (Lindroth 1961-1969) are not suggestive of a predatory lifestyle (Larochelle and Lariviere 2003). The infection of *Amara alpina* is evidence for omnivorous feeding habits, if not outright carnivory. Omnivory is likely a more common feeding strategy than traditionally assumed (Coll and Guershon 2002, Thompson et al. 2007), and may be particularly important in high arctic regions where primary productivity is low and prey items are comparatively scarce (Danks 1981a). Little is known about the feeding habits of most arctic arthropods, so the information that can be gleaned from host-parasite interactions in this region warrant continued study. On the other hand, it has been demonstrated that hairworm-infected hosts provide significant energetic inputs for fish predators in streams, thanks to the behavioural manipulation that compels the hosts to enter water (Sato et al. 2011). It stands to reason that infected arctic beetles are also compelled to enter the many ponds, streams and rivers that characterize the wetter habitats of the tundra landscape, thereby similarly contributing energetic subsidies to aquatic arctic habitats.

The hairworm in this study will be only the third *Gordionus* species described from Canada (molecular confirmation of the morphological determinations is currently underway), with one other species known in Alaska. None of the hosts are known for any of these other *Gordionus* hairworms, and this research represents the first host-based study of any *Gordionus*

from arctic or subarctic biomes. In addition to making a significant contribution to existing knowledge about the hosts and geographic range of nematomorphs, this study is a novel illustration of the utility and importance of considering the roles of parasites in studies of food web or community ecology.

3.6 Acknowledgements

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Table 3.1 Locations and sampling dates of four sites where hairworm-infested ground beetles were collected from in northern Canada (see Fig. 2.2 for map).

Site	Latitude, Longitude	Sampling Periods (dates) 1	2	3	Sampling Year
Banks Island, NT (BAN)	73.22412, -119.55255	7-11.vii	11-15.vii	15-19.vii	2011
Cambridge Bay, NU (CAM)	69.12177, -105.41688	7-11.vii	11-15.vii	15-19.vii	2011
Tombstone Mtns., YT (TOM)	64.60629, -138.35637	21-24.vi	24-27.vi	27.vi-01.vii	2011
Iqaluit, NU (IQA)	63.76144, -68.57352	17-21.vii	21-25.vii	25-29.vii	2010

Table 3.2 Summary of infected (IB) and non-infected (NIB) beetles found on Banks Island, NWT. The number (and proportion, % of total) of beetles are shown by sex, as well as by habitat, trap type, and sample period (1: 7-11.vii.2011; 2: 11-15.vii.2011, 3: 15-19.vii.2011) in which they were collected.

Infection status	**Habitat**		**Trap Type**		**Sex**		**Sample Period**		
	Mesic	**Wet**	**Pitfall**	**Pan**	**Female**	**Male**	**1**	**2**	**3**
IB	21 (5.4 %)	66 (25.0 %)	18 (6.7 %)	69 (17.7 %)	63 (13.6 %)	24 (12.6 %)	41 (11.4 %)	33 (18.9 %)	13 (10.7 %)
NIB	370 (94.6 %)	198 (75.0 %)	248 (93.3 %)	320 (82.3 %)	401 (86.4 %)	167 (87.4 %)	318 (88.6 %)	142 (81.1 %)	121 (89.3 %)
Total	**394**	**264**	**266**	**389**	**464**	**191**	**359**	**175**	**121**

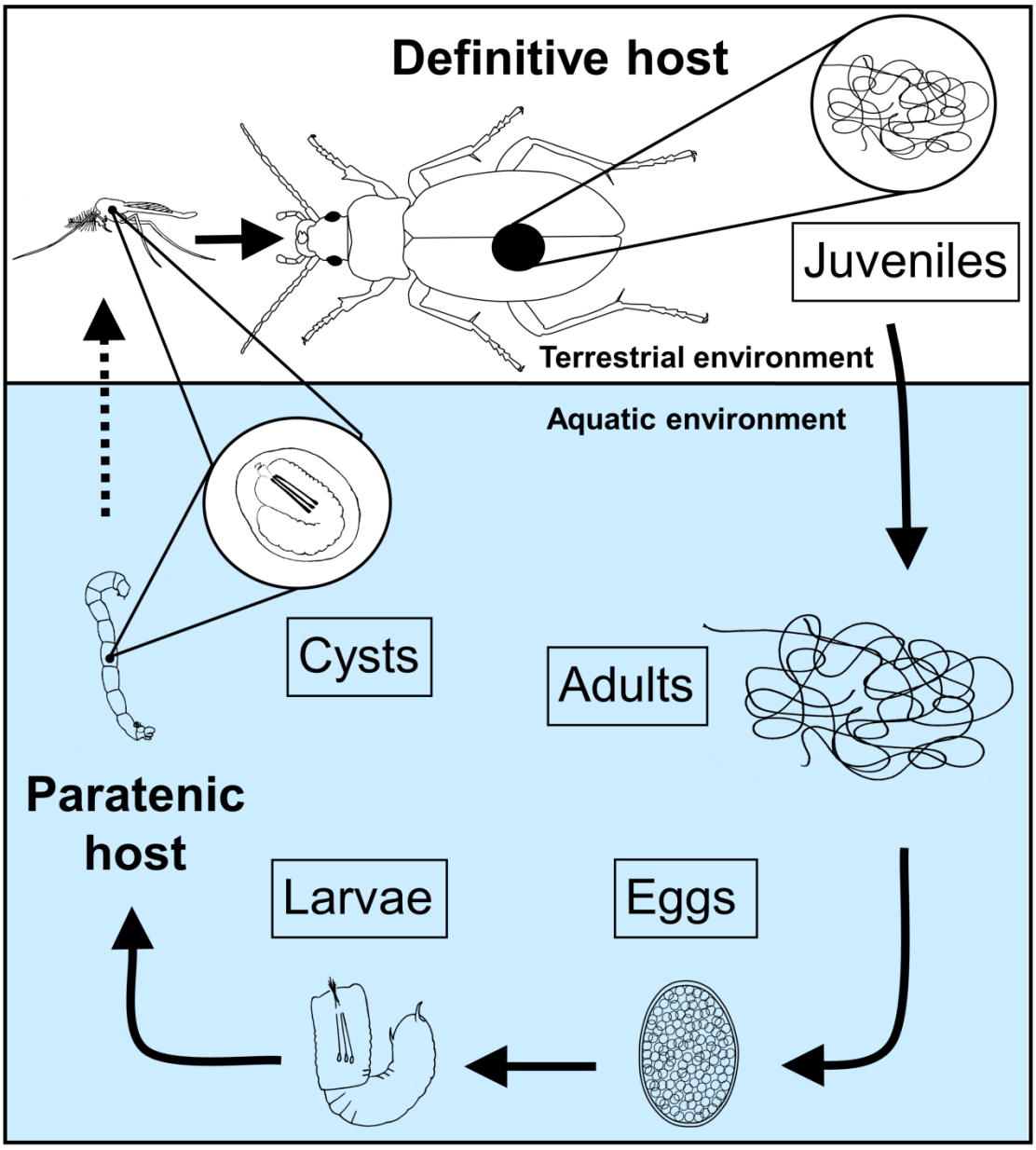

Figure 3.1 The life cycle of a horsehair worm (adapted from Hanelt et al. 2012). Gordiid adults mate and oviposit in freshwater habitats. Hatched larvae are consumed by, and encyst in, a variety of aquatic animals (here, a midge larva). The cysts are transported to terrestrial habitats after metamorphosis (dashed line), where the paratenic hosts and its cysts are consumed by a definitive host (here, a beetle), where the larvae excyst, penetrate the gut and develop within the haemocoel. When mature, the worms manipulate the host's behavior and compel it to enter water, enabling the worms to make a successful return from the terrestrial to the aquatic environment.

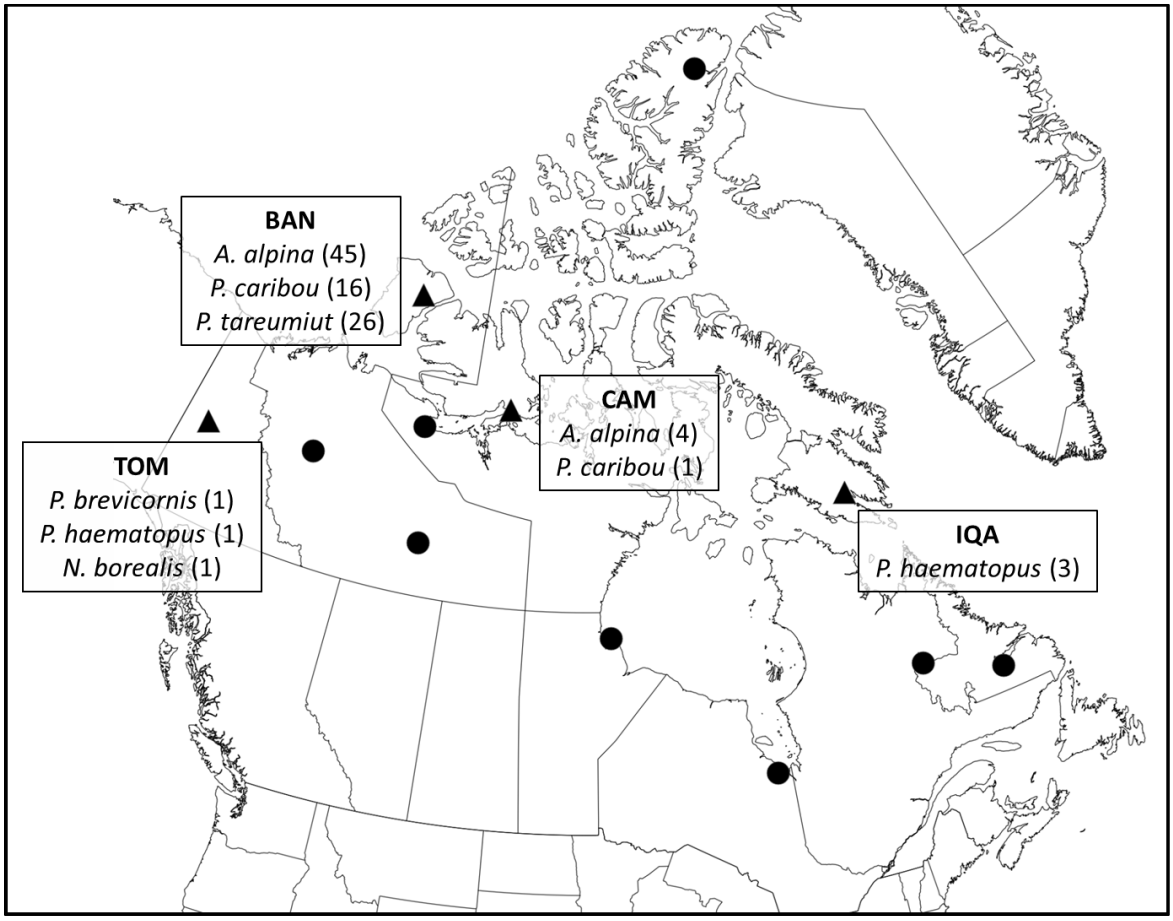

Figure 3.2 Locations that were sampled for ground-dwelling beetles as part of the NBP protocol. Locations (see Table 2.1 for more information and site abbreviations) marked with a triangle had one or more obviously parasitized beetle. Species names of infected hosts are shown in boxes, with total number of parasitized individuals of each species in parentheses.

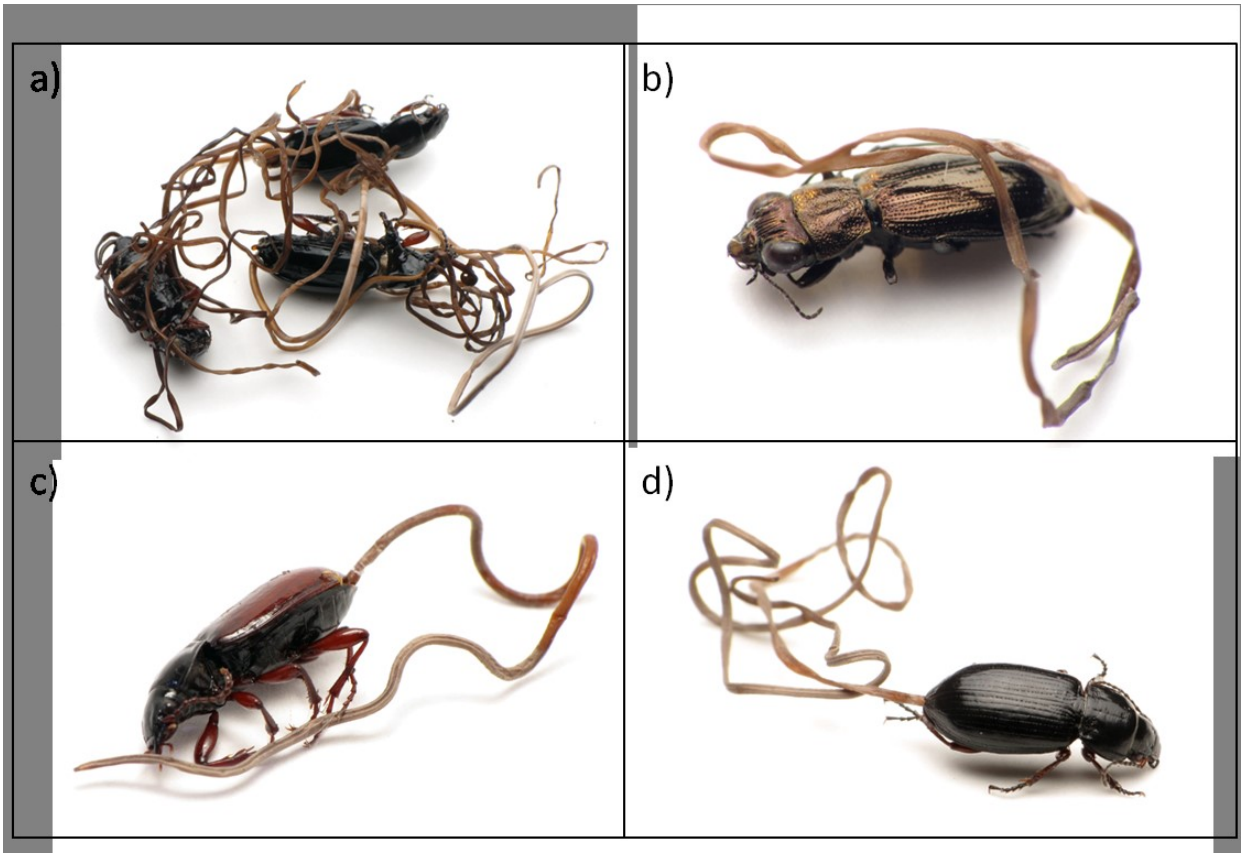

Figure 3.3 Four examples of infected beetle hosts: a) three specimens of *Pterostichus (Cryobius) tareumiut* pulled from one trap (Banks Island); b) *Notiophilus borealis* (Tombstone); c) *Pterostichus (Stereocerus) haematopus* (Iqaluit); d) *Amara alpina* (Banks Island).

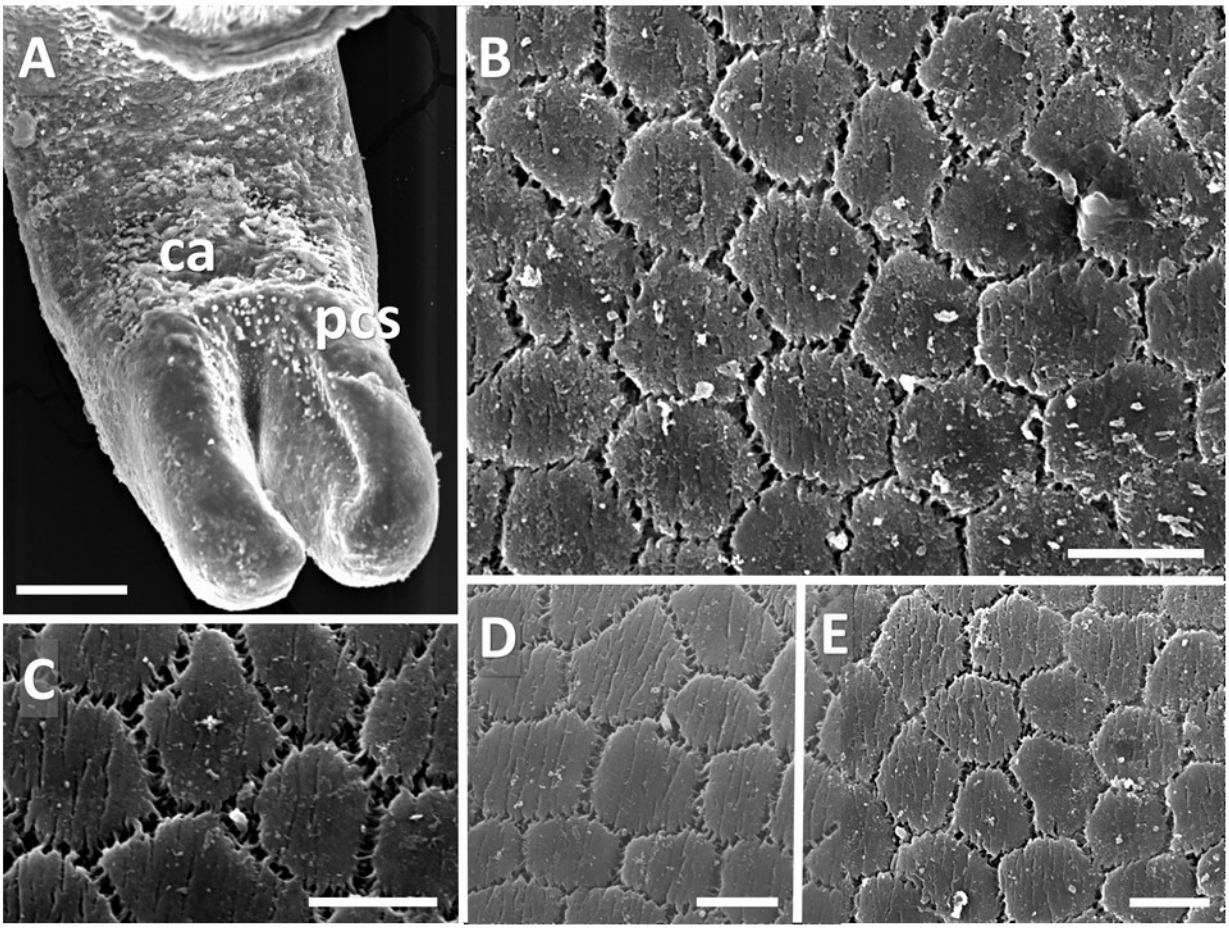

Figure 3.4 *Gordionus* **n. sp.** male. (A) Posterior end with bifurcating ends, cloaca (ca), and postcloacal spines (pcs). (B) Cuticle on lateral side near posterior end. Note the lack of adhesive warts. (C) Close up of cuticle on lateral side near posterior end showing interareolar space. (D) Cuticle at midsection of body on ventral side. (E) Cuticle at midsection of body on lateral side. Note that most areoles are striated parallel to the length of the body. Scale bars = 10µm, except (A) where scale bar = 100µm.

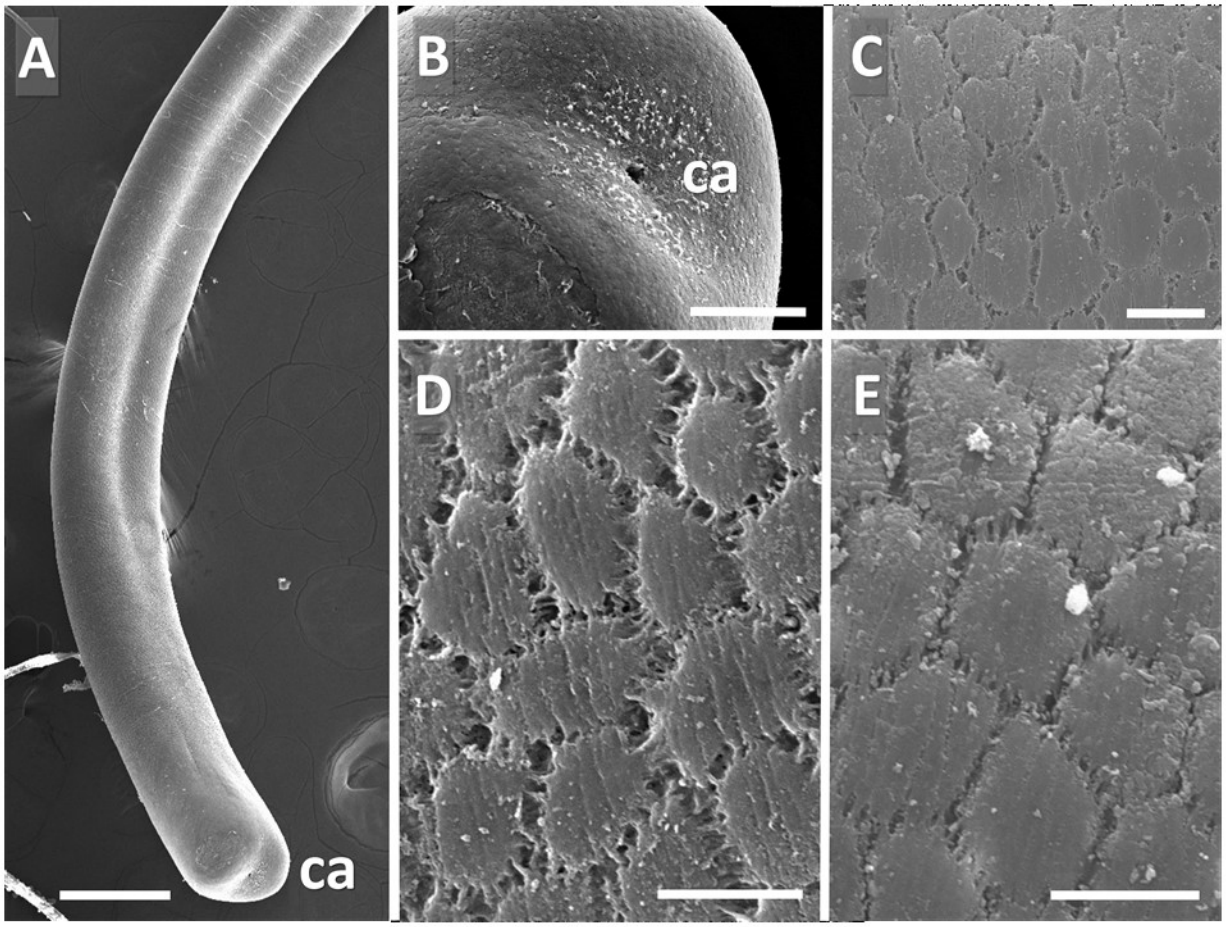

Figure 3.5 *Gordionus* **n. sp.** female. (A) Posterior end with cloaca (ca). (B) Close up of the posterior end. Note the slightly indented and bifurcating shape of the tip. (C) Cuticle at midsection of body on ventral side. Note the shallow interareolar space. (D) Cuticle on lateral side near posterior end showing interareolar space. Note that only areoles in this area are striated parallel to the length of the body. (E) Cuticle at midsection of body on lateral side. Scale bars = 10µm, except (A) where scale bar = 250µm, and (B) where scale bar = 50µm.

3.6 Connecting Statement

Having conducted a focused study of temporal changes in beetle biodiversity and assemblage structure in a single subarctic region (Chapter 2), and having explored one novel component of the terrestrial arthropod food web involving the dominant beetle predators of northern assemblages (Chapter 3), I wished to examine biodiversity patterns of beetle assemblages and their underlying mechanisms across a large geographic extent. In Chapter 4, I describe the diversity, distribution and assemblage structure of beetles collected from 12 locations across northern Canada (spanning three ecoclimatic zones), with consideration for both TD and FD. To ascertain the underlying mechanisms behind biodiversity patterns, I tested the relationships between community structure and different spatial, biotic and climatic gradients.

Chapter 4: Drivers and patterns of ground-dwelling beetle biodiversity across northern Canada

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4.1 Abstract

Many macroecological patterns of biodiversity, including the relationship between latitude and species richness, are well-described. Data collected in a repeatable, standardized manner can advance the discipline beyond the description of patterns, and be used to elucidate underlying mechanisms. Using standardized field methods and a hyper-diverse focal taxon, viz. Coleoptera, we aim to: (1) describe large-scale latitudinal patterns of taxonomic diversity, functional diversity, and assemblage structure across northern Canada, and (2) determine which climatic, spatial and habitat variables best explain these patterns. We collected terrestrial beetles at twelve locations in the three northernmost ecoclimatic zones in North America: north boreal, subarctic and high arctic (51-81ºN, 60-138ºW). After identifying beetles and assigning them to a functional group, we assessed latitudinal trends for multiple diversity indices using linear regression, and visualized spatial patterns of assemblage structure with multivariate ordinations. We used path analysis to test causal hypotheses for species and functional group richness, and used a permutational approach to assess relationships between assemblage structure and 20 possible climatic and environmental mechanisms. Over 9,000 beetles were collected, representing 464 species and 18 functional groups. Species and functional diversity have significant negative relationships with latitude, which are likely explained by the mediating effects of temperature, precipitation and plant height. Assemblages within the same ecoclimatic

zone are similar, and there is a significant relationship between assemblage structure and latitude. Species and functional assemblage structure are significantly correlated with many of the same climatic factors, particularly temperature maxima and minima. At a large spatial extent, the diversity and assemblage structure of northern beetles show strong latitudinal gradients due to the mediating effects of climate, particularly temperature. Northern arthropod assemblages present significant opportunities for biodiversity research and conservation efforts, and their sensitivity to climate make them ideal targets for long-term terrestrial diversity monitoring.

4.2 Introduction

Macroecologists have successfully described large-scale spatial patterns of biodiversity and species distributions. Among them, the latitudinal gradient of species richness, in which fewer species are found at high latitudes compared to at the equator, has captivated researchers for many decades (Gaston 2000). Over the past decade, there has been increased interest in elucidating the causal mechanisms behind latitudinal diversity patterns (Willig et al. 2003, McGill and Nekola 2010, Beck et al. 2012, Keith et al. 2012). The search for likely mechanisms has been challenging, however, and although a broad range of climatic, evolutionary, biotic, and spatial hypotheses have been put forth (reviewed by Willig et al. 2003), no single factor has been identified as a key mechanism. It seems plausible that the number of species found at different latitudes, and the way these species assemble over space and time, is the result of multiple interacting ecological and evolutionary factors (Quinn and Dunham 1983, Condamine et al. 2012). Despite the challenge of teasing apart the relative contributions of different factors to patterns of diversity, climate – in particular, temperature – has been broadly recognized as a key

element in both terrestrial and aquatic systems (Hawkins 2004, Field et al. 2009, Boyero et al. 2011) and is worthy of additional testing.

Recently, some workers have begun including alternative or complimentary genetic, morphological or functional measures of diversity alongside the traditional taxonomic metric of species richness (Magurran 2004). Function may play a particularly important role in influencing species diversity patterns, as species richness may be limited by biotic interactions, differences in life history traits, and environmental gradients that influence niche availability (Lamanna et al. 2014). The inclusion of functional diversity in macroecological studies may ultimately yield more powerful tests of biodiversity theories (McGill et al. 2006, Beck et al. 2012, Lamanna et al. 2014).

In addition to expanding the lens with which we examine diversity patterns beyond taxonomy, we can also use the framework established by earlier macroecological studies as a platform from which to broaden the scope of future work. Some authors have identified avenues of research that hold great promise for the advancement of macroecological theory, namely, the inclusion of: (1) standardized, repeatable faunal sampling, (2) broader taxonomic or functional scopes, (3) broader ecological scopes (e.g., multiple habitats or biomes), and/or (4) underrepresented yet ecologically significant biomes (aquatic systems and polar regions) and taxa (invertebrates, non-vascular plants and fungi (Willig et al. 2003, Beck et al. 2012). While some of these advancements present logistical challenges, working to overcome them may generate sufficient quantitative data to test and support generalizable statements about large-scale patterns and processes of diversity (Stevens et al. 2003, Safi et al. 2011). Understanding the underlying processes responsible for patterns of diversity will provide powerful mechanisms for

predicting the effects of climate change and other anthropogenic disturbances on biotic communities and their component species (Beck et al. 2012).

Testing large-scale biodiversity patterns and processes requires using a focal taxon that is diverse, easily sampled, representative of different processes and functions, taxonomically well understood, and sensitive to environmental or ecological changes (McGeoch 1998). Beetles are an ideal study taxon: they are one of the most taxonomically and functionally diverse groups of animals (Slipinski et al. 2011), and are the most abundant, diverse and ecologically significant epigeic (i.e., living predominantly on the ground surface) insect taxon in northern systems (Danks 1981a, Chernov et al. 2014). Beetles are also easily caught using passive trapping methods that can be standardized and thus permit comparisons of assemblages across time and space (Spence and Niemelä 1994, Lemieux and Lindgren 1999, Missa et al. 2009), and show rapid responses to environmental change (Danks 1992a, Hilty and Merenlender 2000, Rainio and Niemelä 2003). These factors make northern beetles ideal focal taxa for conducting a comprehensive examination of terrestrial diversity and assemblage structure.

The overall objective of our research was to conduct a standardized, species-level assessment of both taxonomic and functional biodiversity patterns across multiple biomes, using beetles as a focal taxon. Our specific goals were to: (1) quantify latitudinal patterns in diversity and assemblage structure (taxonomic and functional), and (2) establish the climatic and/or environmental factors associated with taxonomic and/or functional assemblage structure across a large geographic extent, which was twelve locations in the three northernmost ecoclimatic zones of North America (Table 4.1). We hypothesized that: (1) beetles will conform to classical latitudinal gradients of diversity, with greater species and functional richness at lower latitudes; (2) species richness is directly influenced by climatic variables, which are influenced by latitude;

(3) species and functional assemblage structures will display latitudinal gradients of similarity; (4) variations in assemblage structure will be best explained by climatic, rather than spatial or biotic, variables.

4.3 Methods

4.3.1 Study region and sampling locations

In 2010 and 2011, as part of a larger research project (e.g., Ernst and Buddle 2013, Timms et al. 2013a) we collected terrestrial beetles at twelve locations in the three northernmost ecoclimatic regions of northern Canada (Strong et al. 1989): four locations were in the north boreal region, four in the subarctic and four in the high arctic (Table 4.1). The extent of the study consists of a latitudinal gradient of 51-81ºN and a longitudinal gradient of 60-138ºW. Permits were granted by the following agencies to conduct sampling in the northern territories: Nunavut Research Institute (Scientific Research Licence), Nunavut Department of the Environment (Wildife Research Permit), Yukon's Department of Tourism and Culture (Scientists and Explorers Licence), Aurora Research Institute of the Northwest Territories (Scientific Research Licence), Parks Canada Agency (Research and Collection Permit; for the Lake Hazen location, which falls in the Quttinirpaaq National Park of Canada, NU). In no instance did our work involve the collection endangered or protected species. In light of this fact, and since no other sampling was conducted in provincial parks or wildlife reserves, no specific permits were required to sample on public land in the other locations.

At each location, we established three replicates within about 15 km of each other. In consideration of the fact that habitat selection by northern arthropods is highly dependent on moisture and vegetation (Kevan and Danks 1986, Danks 2004), each replicate contained two

broadly delimited and ecologically distinct habitats. “Mesic” habitats are characterized by higher elevations and well-drained soil, while “wet” habitats have saturated or poorly drained soils, and can be found in adjacent low-lying regions. The mesic vegetation was a discontinuous cover of dwarf shrubs, perennial forbs, and lichens. Wet habitats contained continuous cover of moss, sphagnum, saxifrages and sedges. In order to ensure consistency of sampling in both habitats across all locations, we established all replicates in open areas with no tree canopy cover; we encountered some dwarf black spruce in some of the more southern sites.

4.3.2 Insect sampling and specimen processing

In all replicated habitats at each location, we set nine pitfall and nine yellow pan traps in three transects as a 30 x 75 m grid. We deployed 108 traps per location, and 1296 traps in the entire sampling design and we serviced them three times over two weeks (see Table 4.1 for collection dates, and for a complete description of trapping and collection protocols, see Ernst and Buddle 2013). To account for phenology, we sampled the southernmost locations first, and the northernmost last, so that insect activity would be approximately equal at all locations. We placed specimens in 95% ethanol and returned them to the laboratory for sorting, and identified adult beetles to species or morphospecies using traditional morphological approaches.

We assigned each beetle to a functional group based on its predominant food source and mode of feeding (see, e.g., Stevens et al. 2003). Since biomass integrates functional characteristics of assemblages such as energy and nutrient flow (Saint-Germain et al. 2007; Wang et al. 2009), we used it as the metric to describe assemblages functionally (i.e., rather than abundance). We estimated the biomass of each beetle using length:biomass regressions (Jarosik

1989, Hodar 1996), using measured body length or a known average length of common species collected previously (Ernst and Buddle 2013).

Voucher specimens of all species are now contained in at least one of the following collections: Lyman Entomological Museum (Sainte-Anne-de-Bellevue, Québec, Canada), Canadian National Collection of Insects, Arachnids and Nematodes (Ottawa, Ontario, Canada), Canadian Museum of Nature (Ottawa, Ontario, Canada).

4.3.3 Environmental variables

We quantitatively assessed the plant community at each location by randomly establishing five 1 m^2 quadrats in and adjacent to the trap grid in each habitat replicate. To characterize the vegetation in each quadrat we used a % cover classification system, the Braun-Blanquet scale (Braun-Blanquet 1964). We assigned plants to a class (forbs, shrubs, graminoids, mosses, lichens), gave each class a Braun-Blanquet score of 1 to 6, and determined the mean score for each class for each location. We measured the maximum height of the vegetation of any class (MaxVegHt) in each quadrat, and determined an average of these heights for each location.

Climate data are available online (Canadian National Climate Data and Information Archive (http://climate.weatheroffice.gc.ca). We used climate normals (calculated using at least 15 years of data taken between 1981-2010) recorded at the weather station closest to each location to obtain the following: mean annual temperature (MeanTemp), mean maximum temperature (MaxTemp), mean minimum temperature (MinTemp), mean temperature of warmest month (WarmMean), mean temperature of coldest month (ColdMean), mean total annual precipitation (TotPrecip), mean degree days above zero (DDA0), mean degree days

below zero (DDB0), mean wind speed (Wind), mean annual days with sunshine (SunDays), mean annual total sunshine hours (SunHrs), and number of frost-free days (Frost). Given their proximity, we considered all replicates at the same location to have the same climate conditions.

4.3.4 Data analyses

We conducted all analyses using R, version 3.1.1 (R Core Team, 2014). We described the total abundance of beetles at each location. While our sampling was standardized, the resulting sample sizes were unequal and there were many rare species. Therefore, in addition to calculating the observed species richness, observed functional group richness, Simpson's diversity, and Pielou's evenness, we also used the Chao1 index (Chao 1984), an asymptotic estimator, to generate unbiased estimates of expected species richness at each location (all performed using the vegan package; Oksanen et al. 2010).

To test whether beetles would conform to predicted latitudinal gradients of diversity, we used linear regressions to test the relationship between each diversity index and latitude. The indices were log-transformed prior to running the models to ensure data met assumptions of normality. We removed extreme outliers to improve model fit: IQA for observed species richness, Chao1 and functional richness, and NOR for evenness and Simpson's index.

In addition to identifying latitudinal diversity patterns, we wanted to determine if latitude has an indirect effect on diversity that is mediated by other biotic, climatic or spatial factors. Confirmatory path analysis is one method of testing multivariate causal hypotheses that cannot be tested through randomized experiments (Shipley 2000). We used Shipley's d-separation test of causal hypotheses (Shipley 2000, 2009) to analyse the relationships between latitude, diversity, and mechanistic factors. In this analysis, the causal hypotheses are represented by a set

of structural equations that are visualized as a path model (or directed acyclic graph; DAG), and these causal relationships imply independence relations between other pairs of variables (a basis set), either directly or after conditioning on other variables. Using the package `ggm` (Marchetti et al. 2014) we developed three alternative DAGs with hypothesised relationships between latitude, species and functional diversity, and several mechanistic variables, then generated the basis sets of the conditional independencies resulting from the models.

The initial list of mechanisms considered included the climate and vegetation variables described in the previous section. In order to avoid issues associated with autocorrelation and to achieve the most parsimonious DAG, we reduced the number of variables in the model by considering the statistical and ecological relationships between the variables. First we visualized the data with scatterplots of all pairwise combinations of variables. All temperature and sun-related variables were correlated, so MeanTemp was selected as a proxy for all temperature measures. There were some missing Wind values so this variable was omitted. Precipitation was moderately correlated with MeanTemp, but since it captures a very different component of climate, and because moisture can be a constraint for northern arthropods (Danks 1981a, Danks 2004), it was retained. All vegetation class Braun-Blanquet scores were retained, as was MaxVegHt. Next, we examined the variance inflation factors using the vif function in the HH package (Heiberger 2014). Some inflaction factors were high due to relationships between different vegetation classes, suggesting we should select one representative vegetation variable. We additionally performed stepwise AIC model selection, which selected MeanTemp, MaxVegHt and TotPrecip as independent variables. These steps and results led us to conclude the selection with these three ecologically significant, noncolinear (VIF between 2.2 and 3.5) variables.

We considered three plausible alternative models to test the relationship between latitude and speices richness (Fig. 4.2 A-C). These included the simplest model (Fig. 4.2 A), where only latitude acts on the mediating effects, and two models where interactions between mediating factors were considered. In model B, temperature (T) is directly influenced by latitude, which in turn affects plant height and precipitation. In model C, precipitation additionally influences vegetation height. For each DAG, we tested all hypothesized independences between these variables and then conducted overall tests of the models using Fisher's C tests. We performed a separate path analysis for functional group richness. Again, we developed three plausible models, using the best-fit DAG for species richness as a starting point (Fig. 4.2, Model 1), because it suggested that interactions between temperature, vegetation and precipitation were not important. Since functional group richness is likely to increase as more species are added (as shown earlier, there is a positive relationship between species and functional richness), we included species richness in the model. The three models we developed were designed to determine whether: a) latitude acts directly on functional richness, b) the effects of latitude are mediated by spatial or biotic variables, and/or c) species richness provides a second level of mediation (i.e., that the effects of temperature, vegetation and precipitation on functional richness are solely or additionally mediated by species richness).

We hypothesized that assemblages would demonstrate spatial (latitudinal) gradients of similarity. To test this, we visualized species and functional assemblages at each location with non-metric multidimensional scaling (NMDS) ordinations, using the rich (Rossi 2011) and vegan (Oksanen et al. 2010) packages. Non-metric multidimensional scaling is an indirect ordination approach that maximizes the rank order correlation between distances in a distance matrix, and the function we used (metamds) uses multiple random starting configurations to find a stable

global solution for the ordination. Assemblages that are more similar to each other are arranged more closely in the ordination space. In this case, we generated the ordinations using Bray-Curtis distance matrices of log+1 transformed abundances (species) or biomasses (functional groups). Because the species assemblages at HAZ were composed of only a single species, we omitted the location from the NMDS analyses. We were also interested in the relationship between species and functional assemblages, so we compared the congruence of the two ordinations using Procrustes rotation analysis, and assessed the correlation between then using a permutational statistic calculated by the function protest (Peres-Neto and Jackson 2001).

To test the relationships between assemblage structure and spatial, climatic and biotic factors, the envfit function in the vegan package was used to fit each factor on the ordinations as vectors. The direction of each vector indicates the direction in which the linear change in the variable is the fastest, and the length of the vector is proportional to the strength of the correlation between the variable and the position of the assemblages in ordination space. This function provides an objective interpretation of the results of unconstrained ordination analyses and generates a measure of fit as well as a significance value based on a permutation test (1000 permutations).

4.4 Results

We collected 9062 beetles: 2832 in the high arctic, 3275 in the subarctic and 2955 in the north boreal zone. Abundances varied between locations, ranging from 14 individuals collected from the northernmost location (Lake Hazen, NU), to 1696 individuals from Cambridge Bay, NU, also in the high arctic (Fig. 4.1). There was no relationship between latitude and abundance. Thirty-four families and 155 genera were represented in the collection. Over 80% of the

collection was comprised of three families: Carabidae (6221 individuals, 68.8% of total number of specimens), Staphylinidae (870, 9.6%), and Cryptophagidae (247, 2.7%). We found staphylinids at all locations, carabids at all locations with the exception of Lake Hazen, and cryptophagids only from locations in the subarctic and boreal zones. We provide a list of all taxa in Appendix A2-1, and a complete dataset of individual specimen records is available at http://doi.org/10.5886/5dvj8642.

Species-level identifications were done whenever possible, though we focused our efforts on identifying the most abundant and widespread taxa (e.g., Carabidae, Staphylinidae) and those that are taxonomically well known. In total, we identified 464 species and morphospecies, and richness ranged from a single species observed in Lake Hazen, to 115 in the north boreal location Moosonee, ON. Among the samples were 15 new provincial and/or territorial records (denoted by an asterisk, *, next to the species name in Appendix A2-1). Most species were found at three or fewer locations, but others were more widespread. For example, in the high and subarctic zones, *Pterostichus haematopus*, *P. brevicornis*, *P. caribou* and *Amara alpina* were particularly abundant and widely distributed; together, these four species represented 44.0% of the total catch.

Eighteen functional groups were identified, representing diverse specialist and generalist herbivores and carnivores, omnivores, and saprophages, with different food sources and modes of feeding (Table 4.2). Functional group richness ranged from 1 in Lake Hazen to 13 groups in two of the subarctic locations (Norman Wells and Yellowknife, NWT) and one boreal location, Moosonee. Carnivores comprised the majority of the biomass in all sites except Goose Bay, NFLD, which was the only location where herbivores had the greatest proportion of biomass (Fig. 4.1). Strict herbivores were largely absent from the subarctic and high arctic locations, but

were well represented in the boreal sites. Although Moosonee had very high species and functional richness, high numbers of two very large predacious carabid beetles were caught, *Carabus maeander* and *C. melanarius*, and these dominated the overall biomass (Fig. 4.1). Omnivores were exceptionally prominent in the high arctic, represented primarily by the opportunistically predacious granivore, *Amara alpina* (Fig. 4.1).

4.4.1 Diversity

Both observed species richness ($P = 0.002$, $R^2 = 0.6345$, $F = 18.36$, $df = 9$) and expected species richness ($P = 0.002$, $R^2 = 0.6411$, $F = 18.86$, $df = 9$) exhibited strong negative relationships with latitude. The Simpson's index similarly declined significantly with latitude ($P = 0.0043$, $R^2 = 0.5723$, $F = 14.38$, $df = 9$), but evenness had no significant spatial pattern ($P = 0.06$, $R^2 = 0.3078$, $F = 5.002$, $df = 8$). Functional group richness had a highly significant negative relationships with latitude ($P = 0.0007$, $R^2 = 0.7101$, $F = 25.49$, $df = 9$). Functional group richness and species richness have a very strong positive linear relationship ($P < 0.0001$, $R^2 = 0.9307$, $F = 148.6$, $df = 10$).

In our path analysis of species diversity, we opted to include MeanTemp, TotPrecip, and MaxVegHt, as mediating effects. Fisher's C tests (which simultaneously test all independencies in a DAG) indicated that, while all three models were good fits with no important dependencies missing, the first and simplest model (Fig. 4.2A) provided the best outcome (Fishers's $C = 3.637$, $P = 0.888$). The path analysis indicates that species richness is indirectly affected by latitude. MeanTemp, MaxVegHt and TotPrecip all decline as latitude increases. MeanTemp and MaxVegHt have positive effect on species richness, while TotPrecip has a negative effect. The strength and direction of the relationships determined by the path analysis for the best-fit model

are shown in Fig. 4.2 (Model 1). For functional diversity, Fisher's C tests indicated that all three models (D-F) were acceptable, but model F was the best fit (Fisher's C = 5.099, P = 0.984). In this path analysis we found that MeanTemp and species richness both had a positive effect on functional richness, and that latitude had an indirect negative effect through these mediating factors (Fig. 4.2, Model 2). Relationships between functional group richness, and MaxVegHt and TotPrecip, did not improve the model.

4.4.2 Assemblage structure

Solutions were reached for the NMDS ordinations of the species assemblages (stress = 0.079913, Fig. 4.3a) and the functional assemblages (stress = 0.05501, Fig. 4.3b). With the exception of CAM and BAN, whose species assemblages essentially overlap in the ordination space, all locations displayed distinct species and functional assemblages. The arrangement of the locations in the ordinations indicated that those in the same ecoclimatic zone had similar assemblages, and that there were clear delimitations between zones. Functional assemblages from the western and eastern part of the continent show a slight tendency to assemble closer together, even between ecoclimatic zones; this is more pronounced for locations in the north boreal and subarctic. A gradient of similarity was evident between ecoclimatic zones: assemblages in the subarctic were more like those found in the high arctic, while north boreal assemblages were more similar to subarctic than to high arctic assemblages. Species assemblage structure was significantly correlated with latitude (Table 4.3). According to the Procrustes rotation analysis, the species and functional ordinations were correlated (Procrustes sum of squares = 0.36157, Procrustes correlation, r = 0.7964, P = 0.001, 999 permutations).

Species and functional assemblage structure were significantly correlated with all temperature-driven climatic factors, with the exception that functional assemblages were not related to DDBO (Table 4.3). Both assemblage types were also significantly related to Frost. Species assemblage structure was additionally significantly related to TotPrecip, while functional assemblage also has significant relationships with SoilD, VarSoilD and GramCov. Otherwise, the plant community composition is not related to either species or functional assemblage structure. Variables that are significantly related to assemblage structure are plotted as vectors in Fig. 4.3 (only the temperature factor with the strongest relationship to assemblage structure is shown, for clarity).

4.5 Discussion

At a large spatial extent, the diversity and assemblage structure of northern beetles show strong latitudinal gradients, primarily due to mediating effects of climate, particularly temperature. Our research spanned a latitudinal gradient of 30º, included three ecoclimatic zones, and used standardized field sampling of terrestrial beetles to uncover biodiversity patterns across a large geographic extent. Macroecological studies with extents that range less than 20º of latitude are unlikely to show clear spatial patterns of species richness, even if such patterns exist (Willig et al. 2003); our findings should therefore provide an accurate portrayal of spatial biodiversity patterns in the far north. We found that beetle species richness (observed, predicted, and as measured by the Simpson's index) exhibits classical negative relationships with latitude. This aligns with general observations of beetle richness drawn from presence/absence data in arctic and northern boreal regions (Chernov et al. 2014) and with similar patterns described for

other insect taxa at a continental scale in temperate regions, including ants in Europe, and grasshoppers, butterflies and dung beetles in North America (reviewed by Willig et al. 2003).

Evenness showed a tendency to decline with increasing latitude, but the gradient was non-significant. Species richness and evenness can be, and often are, similar along latitudinal gradients, but they may also show no or even negative relationships with each other, as they may reflect different aspects of spatial variation in species assemblages and different responses to ecological factors (Stirling and Wilsey 2001, Ma 2005). Alternatively, if assemblages are more species-rich because they possess greater numbers of rare species, then we might expect latitudinal decreases in richness to be accompanied by greater evenness (Willig et al. 2003). While the majority of our rare species (singletons and doubletons) were indeed located in the more southerly locations, this did not translate to a positive latitudinal evenness trend.

In our study, functional group richness showed a very strong classical spatial gradient, decreasing sharply with increasing latitude. Studies on large-scale latitudinal patterns of animal functional diversity are scarce and their conclusions are variable. Stevens et al. (2003), for example, found that New World bat functional diversity, richness and dominance strongly increased towards the equator, and mammalian functional diversity generally appears to display the same pattern (Safi et al. 2011). Conversely, an analysis of invertebrates collected from 1000 stream monitoring stations in the US showed that functional richness decreased only weakly with increased latitude (Bêche and Statzner 2009).

Specific functional groups or guilds may display different latitudinal diversity patterns. For example, a large survey of the freshwater detriviorous shredder guild revealed much higher diversity at higher latitudes (Boyero et al. 2011). Similarly, among several functional groups of syrphid flies sampled across Europe, only saphrophage diversity was significantly related to

latitude (Keil et al. 2008), and this was also a positive relationship. Some evidence exists that trophic levels of beetles (i.e., carnivores, herbivores and saprophages) display latitudinal gradients. Examinations of selected groups of carnivorous and herbivorous beetles from island systems suggest that carnivores account for smaller proportions of the fauna in the southern hemisphere, increasing through the tropics into the far north, while the proportion of herbivores declines from northern latitudes to the equator, with little change further south (Brinck, 1948, as described in Gaston et al. 1992). Gaston's (1992) meta-analysis of carnivore:non-carnivore ratios in beetle fauna similarly found more predatory species in samples from northern temperate regions than from the tropics.

We found no significant relationship between latitude and abundance. However, abundance was especially low in the most extreme northern location, and generally higher further south (with notable exceptions), which aligns well with Danks' observation that in North America, beetles contribute fewer species to the overall pool of insect fauna at higher latitudes compared to mid-latitudes (Danks 1993). Gaston has suggested that an increase in non-beetle insects at higher latitudes may translate into an increase in food energy contained in the non-beetle part of the community, meaning there could be more potential energy available to predatory beetles (i.e., more non-beetles on which to prey) (Gaston et al. 1992). This might explain, in part, the greater proportion of carnivorous and omnivorous beetles collected in our study in high and subarctic locations (i.e., compared to boreal locations).

Ecoclimatic zones are defined by a variety of ecological characteristics, including climate, soil, humidity and vegetation communities (Strong et al. 1989). Since beetle assemblages were most alike when contained within the same ecoclimatic zone, it stands to reason that assemblages are highly dependent on at least some of these characteristics. A number

of recent studies suggest that temperature (Mjaaseth et al. 2005, Høye and Forchhammer 2008a, Bolduc et al. 2013, Ernst and Buddle 2013) and plant community composition (Bowden and Buddle 2010, Rich et al. 2013) are associated with temporal and spatial changes in arctic arthropod assemblage structure at the local or regional level. Northern insect activity levels can also be locally influenced by temperature (Danks 2004, Høye and Forchhammer 2008b)) or wind (Service 1980) .

Although the primary "causes" of the large scale relationships between biodiversity and latitude remain under dispute, there is nevertheless good evidence that they are climatic rather than biotic (i.e., involving species interactions), whether modern or on an evolutionary time scale (Rohde 1992, Willig et al. 2003, Condamine et al. 2012). We provide support for this with evidence that latitudinal patterns of beetle species and functional richness are mediated by mean annual temperature and total annual precipitation. We also demonstrate that beetle assemblage structure is strongly associated with multiple metrics of temperature minima and maxima, lending support to the idea that climatic gradients are key drivers of large-scale species assembly and ecological function.

The assemblage structure of northern beetles is linked at least in part to the depth of the active soil layer and the height of the surrounding vegetation, while functional assemblage structure is also related to the presence of graminoids; similar patterns have been observed for other macroarthropod assemblages (Frouz et al. 2004, Poyry et al. 2006). These associations are conceivably due to correlations between temperature, and soil depth and plant height. For example, experimental warming of plants by 1-3°C has been shown to significantly increase the height of shrubs and graminoids in the arctic tundra in under two years (Walker et al. 2006). Increased air temperature is well known to affect increases in soil temperature and active layer

depth, and to reduce permafrost stability in the Arctic (Kane et al. 1991, Hinkel et al. 2000, Smith et al. 2010). This may be additional support for climate (temperature) as a key determinant of terrestrial insect assemblage structure at large spatial scales.

In this study, we show that latitudinal gradients of species richness are correlated with those of functional richness. Additionally, we find that continental-scale patterns of functional assemblage structure are correlated with those of species assemblages, and that functional assemblages reflect climatic gradients just as strongly and in a near-identical manner as species assemblages. We suggest that climate change is likely to have significant effects on both the structure and function of ecological assemblages, and that function-driven examinations of assemblages are just as ecologically meaningful and informative as those using a traditional, species-level approach if the aim is to identify or track changes in biodiversity and assemblage composition over time or space.

The use of functional groups and functional diversity as complementary (Cardoso et al. 2014) or alternative metrics of biodiversity ("biodiversity surrogacy") has been supported by many authors for a variety of taxa and ecosystems (e.g., Voigt et al. 2007, Flynn et al. 2009, Buschke and Seaman 2011). There are multiple lines of evidence that indicate very strong ties between functional and taxonomic diversity (see review in Hooper et al. 2002) and that species-level responses to environmental changes or gradients are not lost at higher taxonomic resolutions (Timms et al. 2013b). From a practical perspective (e.g., in the context of ecological monitoring programs) most taxa can be assigned to a functional group or guild after being identified to subfamily, even family and occasionally order; a much more feasible undertaking for non-specialist workers, or volunteers.

4.6 Conclusion

Our data have provided a valuable test of macroecological diversity patterns and their underlying processes across the three northernmost ecoclimatic zones of North America, we collected over 9,000 beetles from diverse taxonomic and functional groups, and demonstrated that beetles conform to classical latitudinal gradients of diversity. Our data reveal a clear relationship between taxomomic and functional assemblage structure, both of which are strongly associated with latitude. Although climate appears to be a likely candidate for the key mechanism underlying these patterns, further field-based assessments are required.

To our knowledge, no other study has presented a quantitative examination of spatial patterns in species or functional assemblage structure across a spatial extent as large as the one we have presented here, using standardized field samples (i.e., including abundance or density). Although it seems intuitive that, if species-level spatial patterns exist, then assemblage-level patterns should similarly be displayed, it is nevertheless difficult to say whether the assemblage-level spatial patterns we have described here can be generalized to other systems, or whether they are specific to northern regions or biomes with extreme climates. We suggest that more effort must be made to assess not only the number of species present in ecosystems over large spatial scales, but also their relative contributions to the structure and functioning of their assemblages.

Northern terrestrial diversity is dominated by a rich and unique arthropod fauna. Terrestrial insects perform many critical ecological functions in northern biomes, including plant pollination, decomposition, and provision of food for highly valued vertebrates (Christensen et al. 2013). Their richness and ability to occupy a wide variety of functional ecological niches present significant opportunities for biodiversity research and conservation efforts. The imminent

threats of climate change in the fragile and susceptible regions of the Arctic (IPCC 2013) have prompted the conception of several international terrestrial biodiversity monitoring initiatives (e.g., Christensen et al. 2013). Beetles are highly sensitive to changes in climate and, as we have shown, reflect these changes in their diversity, distribution, and assemblage structure, making them ideal taxa for targeted long-term diversity monitoring.

4.7 Acknowledgements

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Table 4.1 Sampling locations, coordinates, ecoclimatic zone, and dates of sampling

Sampling Location	Latitude, Longitude	Ecoclimatic Zone	Sampling Periods (dates) 1	2	3	Sampling Year
Lake Hazen, NU	81.82975, -71.32244	High Arctic	19-23.vii	23-28.vii	-	2010
Banks Island, NWT	73.22412, -119.55255	High Arctic	7-11.vii	11-15.vii	15-19.vii	2011
Cambridge Bay, NU	69.12177, -105.41688	High Arctic	7-11.vii	11-15.vii	15-19.vii	2011
Iqaluit, NU	63.76144, -68.57352	High Arctic	17-21.vii	21-25.vii	25-29.vii	2010
Kugluktuk, NU	67.78157, -115.27824	Subarctic	22-26.vi	26-29.vi	29.vi-2.vii	2011
Tombstone Mtns., YT	64.60629, -138.35637	North Boreal	21-24.vi	24-27.vi	27.vi-01.vii	2011
Churchill, MB	58.73573, -93.79789	Subarctic	1-5.vii	5-9.vii	9-13.vii	2010
Schefferville, QC	54.75970, -66.71120	Subarctic	30.vi-3.vii	3-6.vii	6-9.vii	2010
Norman Wells, NWT	65.29112, -126.62262	Subarctic	7-11.vi	11-14.vi	14-17.vi	2011
Yellowknife, NWT	62.52110, -113.38174	North Boreal	7-11.vi	11-15.vi	15-18.vi	2011
Goose Bay, NFLD	53.21199, -60.45062	North Boreal	15-18.vi	18-21.vi	21-24.vi	2010
Moosonee, ON	51.28034, -80.64252	North Boreal	15-19.vi	19-23.vi	23-25.vi	2010

Table 4.2 Relative proportion of total beetle biomass from each of the 12 sampling locations, in each functional group. Molluscivores, Collembola and Mite Specialist Predators, Generalist Omnivores, Non-feeding Adults, Xylophages, and Micropolyvores have been omitted for clarity because their contributions to the biomass are extremely small (< 1% of total) in all locations.

Functional Group	**HAZ**	**BAN**	**CAM**	**IQA**	**KUG**	**TOM**	**CHU**	**SCH**	**NOR**	**YEL**	**GOB**	**MOO**
Generalist Predator	1.00	0.31	0.36	0.91	0.76	0.88	0.88	0.79	0.72	0.76	0.60	0.94
Carnivores (All)	**1.00**	**0.31**	**0.36**	**0.91**	**0.77**	**0.88**	**0.88**	**0.79**	**0.72**	**0.76**	**0.60**	**0.94**
Bryophage	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.01	0.00	0.03
Florivore	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.02	0.11	0.00
Folivore	0.00	0.00	0.02	0.00	0.02	0.00	0.05	0.00	0.02	0.01	0.19	0.01
Generalist Herbivore	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.03	0.01	0.07	0.04	0.01
Mycophage	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00
Saprophage	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
Herbivores (All)	**0.00**	**0.00**	**0.02**	**0.00**	**0.02**	**0.05**	**0.05**	**0.04**	**0.12**	**0.13**	**0.35**	**0.05**
Entomophage/Nectarivore	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.02	0.00
Opportunistic Granivores	0.00	0.69	0.63	0.09	0.21	0.01	0.04	0.17	0.01	0.05	0.02	0.00
Omnivores (All)	**0.00**	**0.69**	**0.63**	**0.09**	**0.21**	**0.01**	**0.07**	**0.17**	**0.02**	**0.05**	**0.04**	**0.00**
Detritivore	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
Carrion Feeder	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.15	0.04	0.00	0.00
Saphrophages (All)	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.06**	**0.00**	**0.00**	**0.15**	**0.05**	**0.00**	**0.00**

Table 4.3 Relationships between climatic and environmental factors, and the NMDS ordinations of species and functional assemblages at the twelve sites. R squared values and significance levels are obtained using a permutational approach.

Factors		Species				Functional			
		Axis 1	**Axis 2**	**R^2**	**Pr(>r)**	**Axis 1**	**Axis 2**	**R^2**	**Pr(>r)**
Climatic Factors	MeanTemp	0.756	0.655	0.95	**0.001**	0.514	-0.858	0.79	***0.024***
	MaxTemp	0.743	0.670	0.95	**0.001**	0.528	-0.850	0.79	***0.019***
	MinTemp	0.773	0.635	0.94	**0.001**	0.491	-0.871	0.78	***0.025***
	WarmMean	0.839	-0.544	0.94	**0.002**	0.998	0.060	0.96	**0.001**
	Coldmean	0.497	0.868	0.92	**0.001**	0.310	-0.951	0.70	***0.044***
	DDA0	0.995	-0.098	0.96	**0.001**	0.867	-0.498	0.94	**0.002**
	DDB0	-0.473	-0.881	0.92	**0.002**	-0.391	0.921	0.64	0.076
	TotPrecip	0.184	0.983	0.88	**0.005**	0.159	-0.987	0.60	0.114
	Wind	-0.724	0.690	0.36	0.310	-0.360	-0.933	0.47	0.228
	SunHrs	0.356	-0.935	0.54	0.121	0.332	0.943	0.59	0.128
	Frost	0.959	-0.282	0.91	**0.006**	0.876	-0.483	0.79	***0.024***
Environmental Factors	SoilD	0.173	0.985	0.20	0.538	0.065	-0.998	0.74	***0.047***
	VarSoilD	0.031	1.000	0.20	0.574	-0.064	-0.998	0.82	***0.015***
	MaxVegHt	0.815	0.579	0.42	0.265	0.558	0.830	0.62	0.092
	GramCov	-0.509	-0.861	0.67	0.076	-0.309	0.951	0.80	***0.019***
	ShrubCov	0.847	0.532	0.15	0.640	0.312	-0.950	0.29	0.402
	MossCov	-0.206	0.979	0.62	0.094	-0.782	-0.623	0.21	0.590
	LichCov	0.682	-0.732	0.23	0.505	0.261	0.965	0.28	0.421
	ForbCov	-0.597	-0.802	0.13	0.680	-0.240	0.971	0.30	0.393
	Lat	-0.218	-0.976	0.76	***0.048***	-0.239	0.971	0.51	0.174

Highly significant correlations ($P < 0.01$) are **bold**, significant correlations ($P < 0.05$) are in ***bold italics.*** Abbreviations used: MeanTemp, MaxTemp, MinTemp (mean annual, maximum and minimum temperature, respectively), WarmMean, ColdMean (mean

temperature of the warmest and coldest months), DDAO/DDBO (mean degree days above and below zero), TotPrecip (total annual precipitation, including snow), Wind (mean annual wind speed), SunHrs (mean annual number of hours of cloud-free sunshine), Frost (mean annual number of frost-free days), SoilD/VarSoilD (mean and variance of active soil layer depth), MaxVegHt (mean maximum height of vegetation), GramCov, ShrubCov, MossCov, LichCov, ForbCov (mean cover class of graminoids, shrubs, mosses, lichens, and forbs), Lat (latitude).

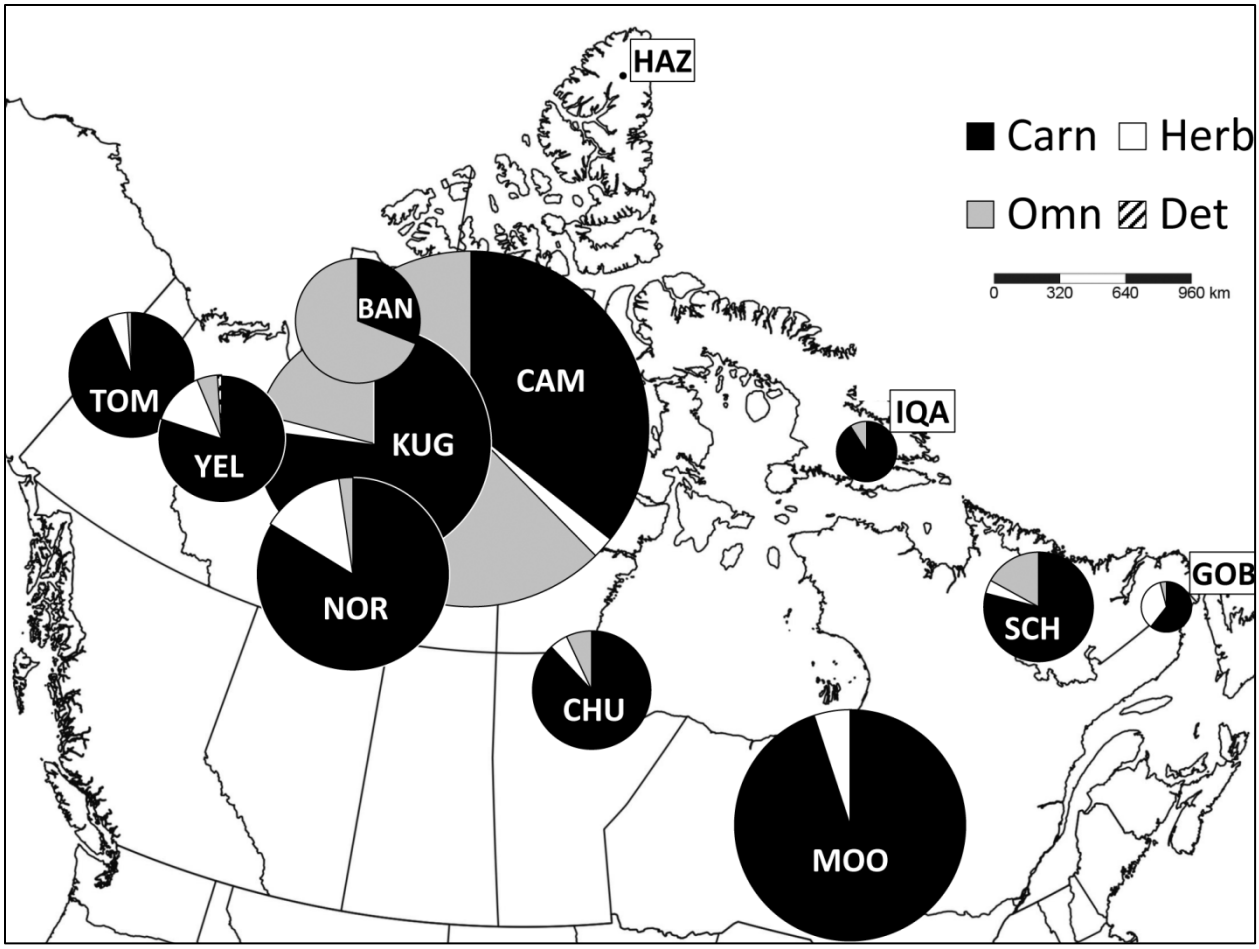

Figure 4.1 Map of the 12 study locations (North Pole Azimuthal projection), showing the spatial distribution of functional groups. FGs were pooled into trophic groups, and the pie charts show the proportion of the total site biomass represented by each trophic group: carnivore (black), herbivore (white), omnivore (grey) and detritivore (diagonal lines). Pie chart sizes are graduated according to the proportion of the entire study's beetles collected at that site. High arctic sites: HAZ (Lake Hazen, NU); BAN (Banks Island, NWT); CAM (Cambridge Bay, NU); IQA (Iqaluit, NU). Subarctic sites: KUG (Kugluktuk, NU); TOM (Tombstone Mtns., YT); CHU (Churchill, MB); SCH (Schefferville, QC). North boreal sites: NOR (Norman Wells, NWT); YEL (Yellowknife, NWT); GOB (Goose Bay, NFLD); MOO (Moosonee, ON).

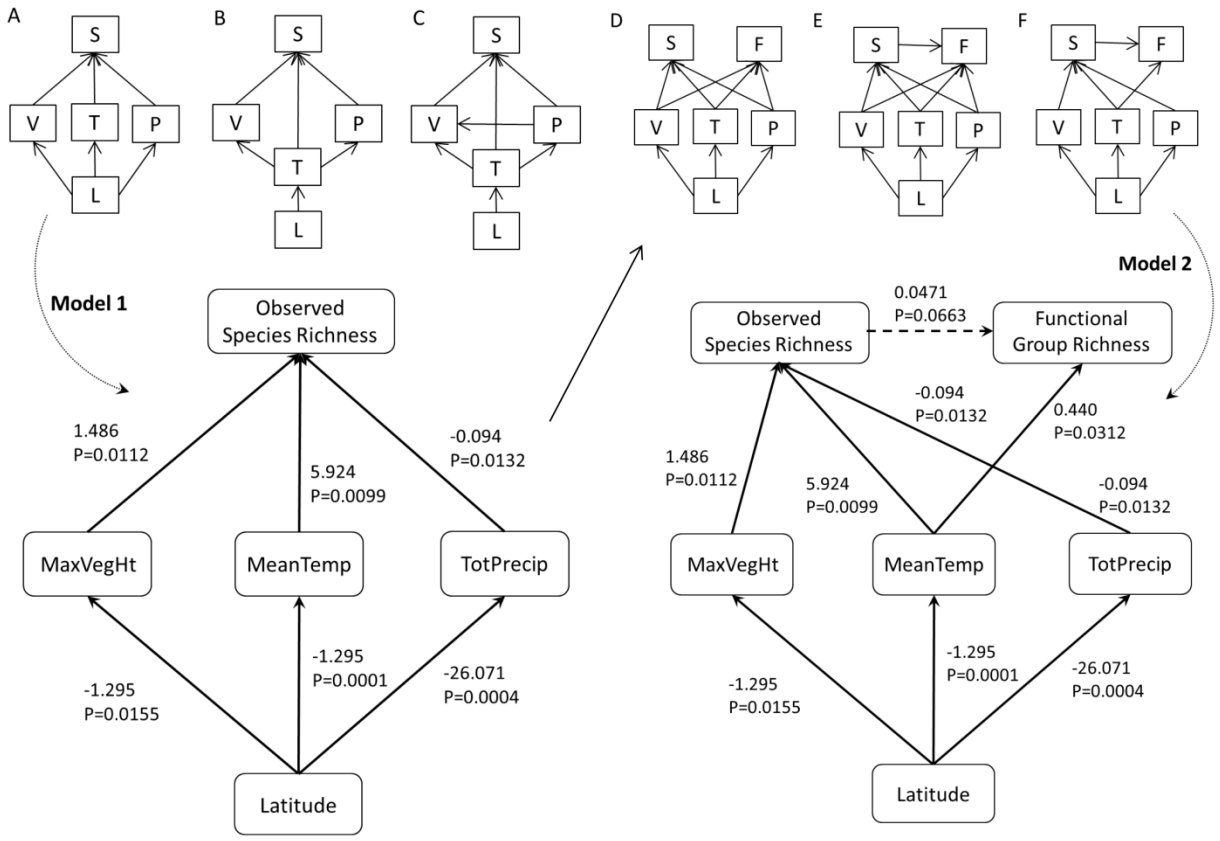

Figure 4.2 A, B and C are alternative directed acyclic graphs (DAG) of hypothesized direct and indirect effects on species richness (S). Model 1: results of best fit path model (derived from model A). D, E and F are alternative DAGs of hypothesized effects on functional group richness (F). Model: results of the best fit path model (from model F). The direction of the arrow indicates the direction of the relationship. Solid lines indicate a significant relationship. Estimated coefficients and P-values are shown for each relationship. Latitude (L), TotPrecip (P), MeanTemp (T) and MaxVegHt (V)

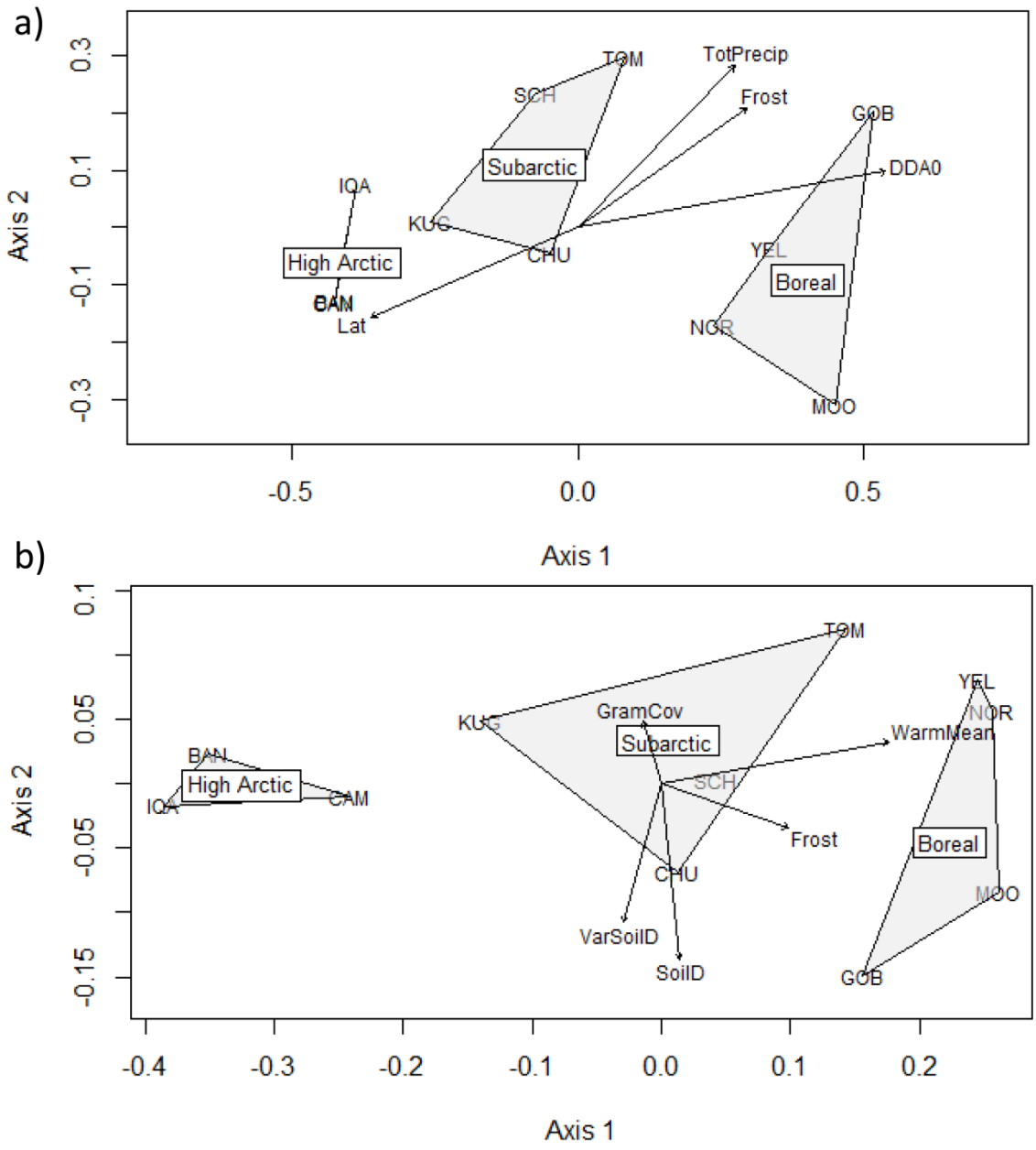

Figure 4.3 Non-metric multidimensional scaling ordinations showing similarities between a) species and b) functional assemblages from at each location. Shaded polygons are used to delimit the ordination space occupied by sites contained within the same ecoclimatic zone. Spatial, climatic, and biotic variables that are significantly correlated with the assemblages are plotted on the ordination space as vectors (for clarity, non-significant variables are omitted, and only the most important temperature-related variable is included for each ordination); the length of the

vector indicates the strength of the correlation. (HAZ has been omitted as an outler from both ordinations, as it contains only one, uncommon species).

4.8 Connecting Statement

In Chapter 4, I described and compared the taxonomic and functional diversity of twelve beetle assemblages, and tested their relationships with different environmental gradients (drivers). Beetle diversity has a strong classical (negative) relationship with latitude, and diversity patterns appear to be strongly related to climatic drivers, particularly temperature maxima and minima. Beetle assemblages are therefore likely to respond strongly to climate change.

Chapters 4 and 2 indicate that beetles exhibit clear biodiversity patterns, both temporally at a regional level, and spatially at a continental scale. Beetles are one of the most abundant and functionally diverse groups of terrestrial arthropods found in the north, and are an excellent model for biodiversity studies. However, it was important to determine whether the patterns I discovered among the Coleoptera (including their associations with environmental and climatic gradients) could be generalized for more diverse terrestrial arthropod fauna. In Chapter 5, I expand the scope of my research to include all taxa of ground-dwelling macroarthropods collected from the 12 sites in this study. Additionally, I refine my definition of "functional diversity" and approach the topic using new trait-based methods, whereby a community of organisms is described by the multidimensional distribution of traits related to ecological function. By combining this expanded notion of functional diversity with a thorough examination of taxonomic diversity, I am able to elucidate the causal mechanisms behind large-scale biodiversity patterns, and how these vary along climatic gradients.

Chapter 5: Environmental constraints on taxonomic and functional diversity of terrestrial arthropods across northern Canada

C. M. Ernst and C. M. Buddle

5.1 Abstract

Taxonomic diversity (TD) and functional diversity (FD) are closely related but the mechanisms responsible for shaping and relating these measures of diversity require empirical investigation, as this can provide insight into ecological function and community stability. Patterns of TD and FD were analyzed for 46,000 individuals from 809 taxa of ground-dwelling arthropods collected from 12 communities spanning a large geographic extent and strong climatic gradients in northern Canada. Relationships between TD and FD were tested, as were those between diversity and environmental variables that might be driving the patterns. TD and FD were strongly related, and declined significantly with colder mean annual temperature, the only variable that had a significant effect on community structure. Functional redundancy was high in the high Arctic, despite the paucity of TD. This suggests environmental filtering plays an important role in structuring biodiversity patterns in regions with extreme climates, whereas the more diverse southerly communities may be shaped by niche complementarity. This study advances our understanding of the relationships between TD and FD, and sheds light on how these community attributes might be shaped by different assembly processes along large climatic gradients.

5.2 Introduction

The diversity of life is often studied by measuring the number and relative abundance of species in a community (i.e., taxonomic diversity, TD) and how these metrics change across time and space (Magurran, 2013; Naeem & Wright, 2003). Recently, there has been a paradigm shift in biodiversity science, with greater inclusion of complimentary genetic, morphological and/or functional measures of diversity alongside the traditional taxonomic metrics (Schleuter et al., 2010).

"Functional diversity" (FD) is used to express a component of biodiversity that encompasses the range of things that organisms do. A functional view of diversity and community structure offers some important advantages over more traditional approaches (McGill et al., 2006). It may be a better predictor of ecosystem productivity, processes and functions than TD, and may effectively indicate a community's vulnerabilities to ecological change (Schleuter et al., 2010). Function also influences species diversity patterns, as species richness may be limited by biotic interactions, differences in life history traits, and environmental gradients that influence niche availability (Lamanna et al., 2014).

To understand the dynamics between TD and FD, it is important to determine how environmental variability influences both (Cadotte et al., 2011). TD and FD are likely affected differently by environmental changes or gradients, so FD should be evaluated alongside TD to provide a holistic view about how biodiversity responds to ecological change (Bellard et al., 2012; Schleuter et al., 2010). Including functional diversity in macroecological studies may yield more powerful tests of biodiversity theories (Beck et al., 2012; Lamanna et al., 2014; McGill et al., 2006).

Unlike TD indices, which treat organisms in a community as distinct taxonomic units, FD considers communities as a collection and distribution of functional traits in a multidimensional functional space whose axes represent functional features (McGill et al., 2006; Rosenfeld, 2002). Functional traits are measurable morphological, physiological, reproductive, behavioural, or temporal features (e.g., Bishop, 2012; Bremner et al., 2003; Pedley & Dolman, 2014; Schirmel et al., 2012) that directly determine productivity and fitness, habitat and food requirements, and the nature of interactions (predator-prey, competition, etc.) with other taxa (Cadotte et al., 2011). There are three complementary attributes of functional diversity : (i) functional richness (FRic) measures how much of the total available functional space is occupied by the taxa present, and can indicate the extent of potentially unused niche space; (ii) functional evenness (FEve) describes how regularly taxon abundances are distributed in the functional space, and can indicate under- or over-utilization of resources, as well as vulnerability to environmental change; (iii) functional divergence (FDiv) measures the degree to which the abundance of a community is distributed toward the extremities of occupied trait space, and high FDiv can indicate significant niche differentiation among taxa (Mason et al., 2013; Mouchet et al., 2010; Schleuter et al., 2010; Villéger et al., 2008).

The concept of niche complementarity stems from the competitive exclusion principle (Hardin, 1960) and implies that the functional traits of organisms in a community must differ to avoid resource use overlap. It follows that increased taxonomic richness should be correlated with increased FD (Hooper et al., 2005; Knelman & Nemergut, 2014). Greater functional diversity is typically taken as evidence that niche complementarity plays an important role in community assembly processes, but it may be less important when environmental constraints restrict the composition of communities to taxa with particular traits (Mason & de Bello, 2013).

Thus, when functional diversity is lower, it is taken as evidence for environmental filtering (Mason & de Bello, 2013). Environmental filtering may be more pronounced in stressed communities, such as in regions with extreme climates (i.e., deserts or arctic biomes) (Mason et al., 2013), in which case FD should be lower in environments that impose greater constraints. The processes may thus influence the amount of functional redundancy in a community; redundancy acts as ecological "insurance" in the face of local species extinctions (Elmqvist et al., 2003; Rosenfeld, 2002), since the co-occurrence of taxa with similar functions but different responses to disturbances can mitigate potential negative effects (Pillar et al., 2013).

The expansive arctic and boreal regions of northern Canada represent natural climatic gradients that range from extremely inhospitable to near-temperate conditions (Strong et al., 1989). These regions are well suited for testing, as a large-scale 'natural experiment', the effects of climate on biodiversity and community structure. Macroarthropods are one of the most globally significant contributors to TD and FD, and are ubiquitous in all terrestrial ecosystems, even those with extreme climatic conditions (Danks, 1981). They can be easily collected in high numbers and display strong behavioural, physical and physiological responses to changes in their environment.

The overall objective of this study was to test the significance of environmental filtering and niche complementarity in large-scale community assembly by linking ecological and climatic gradients, taxonomic diversity and functional diversity. Specifically, the objectives were to: 1) to describe large-scale spatial patterns in the TD and FD of terrestrial macroarthropod communities across northern Canada, 2) assess whether environmental filtering has a greater impact on biodiversity in environments subjected to more extreme climates/climate variability. We predict that: i) terrestrial macroarthropod TD and FD are correlated at large spatial scales,

with higher FD in communities with higher TD (support for niche complementarity); ii) patterns of terrestrial macroarthropod TD and FD are associated with climatic gradients, with lower diversity in colder ecoclimatic zones, and iii) environmental filtering will play a more important role in shaping biodiversity in zones with harsher (colder) climates.

5.3 Methods

5.3.1 Study region and sampling locations

In 2010 and 2011, as part of a larger research project (e.g., Ernst & Buddle, 2013; Timms et al., 2013) terrestrial arthropods were collected at twelve locations in the three northernmost ecoclimatic zones of northern Canada (Strong et al., 1989): four locations were in the north boreal zone, four in the subarctic and four in the high arctic (Fig. 5.1). Taken together, these zones represent a significant gradient of climatic severity (Table 5.1). At each location, three replicates were established within about 15 km of each other. Since habitat selection by northern arthropods is highly dependent on moisture and vegetation (Danks, 2004; Kevan & Danks, 1986), each replicate contained two broadly delimited and ecologically distinct habitats (mesic and wet). To ensure consistency of sampling, all replicates were established in open areas with no tree canopy cover; we encountered some dwarf black spruce in some of the more southern sites.

5.3.2 Arthropod sampling and specimen processing

In all replicated habitats at each location, nine pitfall and nine yellow pan traps were set in three transects as a 30 x 75 m grid. A total of 108 traps were deployed per location (1296 traps in the entire sampling design) and they were serviced three times over two weeks (see Table 5.1

for collection dates, and for a complete description of trapping and collection protocols, see Ernst & Buddle, 2013). Specimens were placed in 95% ethanol and returned to the laboratory for sorting. Macroarthropods that were predominantly ground- or surface-dwelling (including those that are largely sessile on host plants) were retained from the samples. Other flying arthropods commonly collected via flight intercept traps or visually attracted to yellow pan traps were excluded (includinig adult flies (Diptera), adult wasps and bees (Hymenoptera), caddisflies (Trichoptera), adult moths and butterflies (Lepidoptera), and dragonflies (Odonata)). Due to the difficultly of accurately extracting very small surface-dwelling microarthropods such as springtails (Collembola) and mites (Acari), these were omitted from the final samples.

Adult beetles and spiders were identified to species or morphospecies. All other adult arthropods and immatures of all types were identified to the highest taxonomic resolution required to generate reasonable trait information (order, family or subfamily). The abundance of each taxon at each site was recorded: samples were pooled for all sampling periods, replicates and habitats. Voucher specimens of all species are now contained in at least one of the following collections: Lyman Entomological Museum (Macdonald Campus of McGill University, Sainte-Anne-de-Bellevue, Québec, Canada), Canadian National Collection of Insects, Arachnids and Nematodes (Ottawa, Ontario, Canada), Canadian Museum of Nature (Ottawa, Ontario, Canada).

5.3.3 Functional traits

Eight functional traits were measured for each arthropod specimen: biomass, dispersal capacity, primary food source, mode of feeding, preferred substrate, vegetation cover preference, humidity preference, temperature range tolerance (Table 5.2). If a trait could not be directly measured/observed or was not common knowledge, it was surmised using information available

from other sources (see Appendix A3-1). Once individuals' traits were scored and coded for a taxon, average trait states were obtained for that taxon and a taxon-trait matrix was constructed (Appendix A3-2).

5.3.4 Environmental variables

The plant community at each site was quantitatively assessed by randomly establishing five 1 m^2 quadrats in and adjacent each trap grid. A percent cover classification system, the Braun-Blanquet scale (Braun-Blanquet, 1964), was used to characterize the vegetation in each quadrat. Plants were assigned to a class (forbs, shrubs, graminoids, mosses, lichens), and given a Braun-Blanquet score of 1 to 6. The mean score for each class was determined for the area around each trap grid. The average maximum height of the vegetation of any class (MaxVegHt) was determined, an average soil depth (i.e., permafrost depth, SoilD) was determined for each trap grid (Table 5.1).

Climate data are available online (Canadian National Climate Data and Information Archive (http://climate.weatheroffice.gc.ca). Climate normals (calculated using at least 15 years of data taken between 1981-2010) recorded at the weather station closest to each site were used to obtain a variety of climate means, and, given their proximity, all replicates at the same site were considered to have the same climate conditions. Since many climate measures are often correlated, these variables were plotted against each other and only weakly or uncorrelated variables were retained as possible explanatory variables: mean total precipitation (TotPrecip), mean annual number of sun hours (SunHrs), mean annual temperature (MeanTemp), and mean annual number of days without frost (Frost) (Table 5.1).

5.3.5 Data analyses

All analyses were conducted using R, version 3.1.1 (R Core Team, 2014). The total abundance of all taxa was described for each location, as were observed species richness, and standard TD metrics of Simpson's diversity, and evenness. Although the sampling methods were standardized, the resulting sample sizes were unequal and there were many uncommon taxa. Therefore, the Chao1 index (Chao, 1984), an asymptotic estimator, was used to generate unbiased estimates of expected taxonomic richness at each location (all performed using the vegan package; Oksanen et al., 2010). Comparisons were made between the mean of each index for sites contained in the same ecoclimatic zone using ANOVA, and if significant differences were indicated, pairwise comparisons were performed using post-hoc Tukey HSD tests.

Redundancy analysis (RDA) was used to visualize similarities in overall taxonomic community structure and to test the relationships between community structure and the environmental drivers. A Hellinger-transformed taxon abundance distance matrix was used, as it is suitable for taxon matrices containing many zeros or rare taxa (Legendre & Gallagher, 2001). The environmental variables were used as constraints. First the colinearity of the environmental variables was examined by calculating their variance inflation factors (VIF); all were well below an acceptable threshold of 10 (Borcard et al., 2011) and so all variables were all retained for the RDA. Because RDA is a constrained procedure, the resulting axes can explain the variation of the dependent matrix (Borcard et al., 2011). Permutation tests were used to test the significance of the environmental constraints.

Differences in the overall trophic structure between sites were visualized by comparing the proportion of the site's total arthropod biomass contained in the four dominant trophic groups (carnivore, herbivore, detritivore and omnivore), and these differences were tested using

MANOVA and post-hoc ANOVA/Tukey HSD if significant differences were identified. The FD package (Laliberté et al., 2014) was used to calculate three multidimensional functional diversity indices based on the trait and taxon abundance matrices: FRic, FEve and FDiv. Because traits were nominal as well as continuous, Gower dissimilarity indices (Gower, 1971) were used to perform the PCoA (principal components analysis). The Gower dissimilarity matrix was square root transformed to achieve Euclidean distances prior to analysis (Laliberté et al., 2014). Due to computational power limitations a reduced number of axes (seven out of 691) were used to perform the analysis, but the reduced-space representation was still of sufficiently high quality: the remaining axes retained 62.4 % of the available trait space information.

FRic was calculated as the volume of the minimum convex hull required to encompass all taxa in one site (Laliberté et al., 2014), and was standardized by the global FRic (i.e., that including all species) to produce an equivalent index bounded between zero and one. The overall or "average" functional identity of the community of arthropods at each site was determined by generating community-weighted means (CWM) of each trait (Laliberté et al., 2014). For continuous traits, the mean trait value of all taxa present in a site is computed and weighted by the relative abundances of each taxon. Nominal traits are returned as the dominant class. While FRic is calculated without consideration of relative abundances, both FEve and FDiv do incorporate relative abundance and are bounded between zero and one. Smaller values represent low richness, evenness and divergence, while values closer to one represent high evenness and divergence.

The relationships between functional diversity and the environmental variables were tested in several ways. First, distance-based RDA (db-RDA) was used to test the relationship between the variables and the overall functional identity of each site (i.e., the CWMs). The db-

RDA is a constrained ordination procedure that first performs a PCoA (principal coordinates analysis) is on the distance matrix (i.e., of the site CWMs), and the resulting eigenvalues of all the principal coordinates are used as the response in the subsequent RDA (Legendre & Legendre, 2012). The distance matrix of the CWMs was generated using the Gower dissimilarity index (Gower, 1971), which is appropriate for calculating (dis)similarities between objects that are ordinal or nominal characters (Borcard et al., 2011). This matrix was non-Euclidean so was square root transformed. A PCoA was performed on this matrix, and a RDA was then performed on the PCoA eigenvalues, using the matrix of explanatory variables as a constraint. Permutation tests were used to test the significance of the constraints (explanatory variables). To examine the relationships between the explanatory variables and different functional diversity indices (FRic, FEve, FDis), we constructed a series of linear models. We used the results from the db-RDA to reduce the number of explanatory variables to find the most parsimonious prediction of the functional diversity indices.

Last, the relationships between taxonomic diversity and functional diversity were examined using a series of simple linear regressions, and functional redundancy was calculated for each site. Functional redundancy (FR) is mathematically defined by de Bello et al. (2007) as the difference between taxonomic diversity and functional diversity, and is calculated by finding the difference between Simpson's diversity and Rao's Q (an alternative measure of functional divergence that incorporates functional evenness, much as Simpson's diversity incorporates taxonomic richness) (Mouchet et al., 2010). FR ranges from zero to one. When all taxa have completely different traits, then FR = 0; when all taxa share identical traits species, the number of taxa is very large, and the taxa are equally abundant, then FR approaches.

5.4 Results

A total of 46,009 arthropods was collected from the twelve sampling locations. Among these, 809 taxa were identified, predominantly spiders (23,015 individuals, 306 taxa) and beetles (9,062 individuals, 464 taxa) (Appendix A3-3). The total abundance at each site ranged from 1603 individuals collected from the high arctic site Iqaluit, NU, to 6254 at the southernmost site in the north boreal zone, Moosonee, ON. Observed taxonomic richness ranged from 15 taxa at the northernmost site, Lake Hazen, NU, to 274 taxa in the boreal site Norman Wells, NWT. The mean observed taxonomic richness was significantly different between all ecoclimatic zones (df = 2, F = 23.56, p = 0.0003), with fewer taxa in the high arctic, and the greatest number in the north boreal zone (Table 5.3). Chao1 estimates of expected taxonomic richness and Simpson's indices supported this, also declining significantly from the high arctic to the north boreal zone zones (Table 5.3). There were no significant differences in evenness among the zones (Table 5.3).

The arrangement of the sites in the RDA ordination indicated that taxonomic assemblages at each location were distinct, and suggest a north-to-south gradient of similarity between ecoclimatic zones (Fig. 5.2). Subarctic sites were generally more similar to north boreal sites than to those in the high arctic. High and subarctic communities were most strongly associated with predatory arthropods, particularly various *Pardosa* sp. (Lycosidae, wolf spiders), juvenile *Linyphiidae* (sheet web spiders), and shore bugs (Saldidae). Spiders were important drivers in the north boreal zone as well, but herbivorous Auchenorrhyncha (plant and leaf hoppers) were also well represented. The total proportion of the variance explained by the six explanatory variables was 63.04% (adjusted R^2 = 0.1868), and the first two axes of the ordination explained 55.74% (37.44 % and 18.29 %, respectively). Only the first axis had a significant relationship with

assemblage structure (F =3.1931, p = 0.01667). This relationship was driven by MeanTemp (F = 2.7494, P= 0 .01); other explanatory variables were not significant.

The stacked bar graphs used to visualize differences in the trophic structure of arthropod communities at each site (Fig. 5.3) showed that carnivores represented the majority of arthropod biomass in all sites, and this was most pronounced in the subarctic. There was a tendency towards greater proportions of omnivore biomass in the high arctic, while herbivores made up a greater proportion of the total biomass in the north boreal sites. The MANOVA indicated that there was a significant difference in overall trophic structure between zones (df = 2, F = 3.017, p = 0.03409). Post-hoc ANOVA and Tukey HSD tests revealed that the average carnivore biomass was significantly higher in the subarctic than in the north boreal zone (p = 0.0255), while the herbivore biomass was significantly higher in the north boreal zone than in the high arctic (p = 0.0104).

The community weighted means (CWM), or functional identity, of each site showed that taxa at all sites were predominantly invertebrate-eating carnivores (Table 5.4). The ground surface (this measure incorporated a variety of soil types) and leaf litter were the most commonly preferred substrates across all sites, though plants emerge as a preferred substrate in one site in each zone. Biomass is generally smaller in the high arctic. Nearly all communities were characterized by taxa with limited or no dispersal availability (i.e., low propensity for ballooning, or aptery/brachyptery), but the high arctic Banks Island (NWT) community primarily contained macropterous taxa. Some interesting differences in habitat use were evident. Communities in the high arctic display preferences for moderate vegetation cover, and wet conditions. These communities also displayed greater tolerance for larger temperature ranges, driven primarily by tolerance for cold temperatures. The communities in the subarctic sites displayed moderately

high temperature ranges, but had an affinity for higher levels of vegetation cover and drier habitats. Further south, north boreal arthropods were more likely to be found in moderately wet habitats with moderate vegetation cover, and these taxa are found in sites that span only a moderate range of temperatures.

The ordination produced by the db-RDA helps to illustrate these site-level similarities and differences (Fig. 5.4). The total proportion of the variance explained by the six explanatory variables was 62.29 % (adjusted $R^2 = 0.1704$), and the first two axes of the ordination explained 40.15 % (24.08 % and 16.07 %, respectively). Only the first axis had a significant relationship with the functional identity of the 12 sites ($F = 3.1931$, $p = 0.01667$). This relationship was driven by MeanTemp ($F = 2.9604$, $p = 0.01$); other explanatory variables were not significant.

The mean functional richness and evenness were highest in the north boreal, and lowest in the high arctic (Table 5.3), while divergence was highest in the high arctic, followed by the north boreal, then the subarctic. ANOVAs indicated that only FRic was significantly different between sites ($df = 2$, $F = 4.919$, $p = 0.036$). Post-hoc Tukey tests show that FRic is significantly higher in the north boreal zone than in the high arctic ($p = 0.045$), and FRic is marginally higher in the subarctic than the high arctic ($p = 0.072$). Since MeanTemp was the only environmental variable that emerged as having a significant effect on the functional identity of the sites (i.e., in the db-RDA), it was selected as the only independent variable for the linear models generated for the three diversity indices. These models indicated that functional richness ($df = 10$, $F = 15.22$, $R^2adj = 0.5638$, $p = 0.003$; Fig. 5.5a) and evenness ($df = 10$, $F = 7.246$, $R^2adj = 0.3622$, $p = 0.023$; Fig. 5.5b) were significantly related to mean annual temperature, but there was no relationship between FDiv and MeanTemp (Fig. 5.5c).

Both observed (Fig. 5.6a) and expected (Fig. 5.6b) taxonomic richness were significantly related to functional richness, once two extreme outliers from the western north boreal region (Norman Wells and Yellowknife, NWT) were removed ($df = 8$, $F = 57.45$, $R^2adj = 0.8625$, $P < 0.0001$; $df = 8$, $F = 58.91$, $R^2adj = 0.8655$, $P < 0.0001$). There was no relationship between FRic and Simpson's diversity or evenness, even with the removal of outliers. Functional redundancy (FR) was generally high across all sites, but it was significantly lower in the high arctic than in the subarctic or north boreal zones (Table 5.3), and there was no difference between the subarctic and north boreal zones. Functional redundancy increased significantly with increased mean annual temperature ($df = 10$, $F = 5.446$, $R^2adj = 0.2879$, $p = 0.0418$; Fig. 5.5d).

5.5 Discussion

This study represents one of the largest efforts – both in taxonomic and spatial scope – to use standardized field sampling to describe the patterns and processes of taxonomic and functional biodiversity and community structure. Across the three northernmost ecoclimatic zones of Canada, arthropod functional diversity is strongly correlated with taxonomic diversity: higher TD is correlated with higher FD across the entire extent of this study, suggesting that niche complementarity plays an important role in shaping arthropod community structure across large spatial scales. However, arthropod biodiversity and community structure is also strongly influenced by one important environmental constraint: mean annual temperature. Lower temperatures correlate with reduced TD and FD; there are far fewer taxa in the high arctic and they occupy significantly less functional trait space than the taxa of warmer ecoclimatic zones. The reduction in TD in the far north is also associated with greater functional redundancy, suggesting that environmental filtering plays a more significant role in shaping community

structure in extreme climates and that TD may be limited by the possession of functional traits that permit persistence in harsh climates (Currie et al., 2004; Grace et al., 2010; Spasojevic et al., 2014). Therefore, there is evidence that the effects of environmental filtering or constraints are not uniform along large climatic gradients: a greater suite of functional traits are acceptable in more clement habitats, permitting greater niche complementarity and greater TD.

Taxonomic diversity and community structure were significantly related to mean annual temperature, with greater observed and expected taxon richness in warmer, more southerly sites. A latitudinal gradient of community similarity was also evident between sites. Although some exceptions exist, including among terrestrial arthropods (e.g., Janzen, 1981), negative relationships between latitude and taxonomic (species) richness are well established in the literature (Pianka, 1966; Turner, 2004; Willig et al., 2003). Latitudinal climatic gradients, especially of temperature, are among the more well-supported proposed mechanisms driving this diversity pattern. Higher temperatures could be linked to increased primary productivity (more food for more organisms; productivity hypothesis), or could create more physiologically favourable environments for a greater number of species (ambient energy hypothesis) (see review in Willig et al., 2003). A number of recent studies suggest that temperature is strongly associated with temporal and spatial changes in arctic arthropod species diversity and assemblage structure at the local or regional scale (Bolduc et al., 2013; Danks, 2004; Ernst & Buddle, 2013; Høye & Forchhammer, 2008; Mjaaseth et al., 2005), and national scale (Chapter 4).

In this study, functional richness was generally low across sites: communities primarily consisted of small, active, non-flying predators, and these trends were more pronounced with colder temperatures. Colder temperatures are associated with reduced primary productivity, and

so also with reduced presence and activity of plant-feeding arthropods. Workers who have observed the spatial distribution of arthropod fauna and evidence of their activities (especially herbivorous feeding) in the field in high arctic sites often mention a perceived paucity of arthropods on, or feeding on, palatable plants (pers. obs., see also Strathdee & Bale, 1998). In a study of high arctic plants and herbivores, Savile (in Strathdee and Bale 1998) found only a single leaf-feeding arthropod species and no stem or root borers, despite the availability of 48 species of potential host plants.

If temperature reduces the range or abundance of herbivorous taxa in very cold regions, then one would expect to find fewer predators these areas (Strathdee & Bale, 1998). However, this is not the case: this study, and earlier work on spatial and temporal changes in the trophic structure of terrestrial beetles in northern Canada (Ernst & Buddle, 2013, and Chapter 4), provide evidence of carnivore-dominant communities in northern regions. All communities examined in this study are strongly shaped by a high abundance and biomass of carnivorous arthropods, especially in the subarctic, and a greater proportion of predators in the high arctic were omnivorous. While herbivores are more specialized, the generalist nature of many arthropod predator diets may allow them to persist more effectively in colder climates where herbivorous prey items are scarcer. Flexible feeding modes and diets that are not strictly reliant on herbivorous prey – including omnivory or intratrophic predation – may therefore be important and common traits among arctic predators. Indeed, in this study omnivory is most prevalent among arthropods in the high arctic, where both plant food and herbivorous prey are less abundant. The relationships between climate and diet, and the tremendous dominance of predatory (carnivorous and omnivorous) taxa, suggests that cold temperatures are limiting the niche breadth of arctic arthropods.

Functional diversity indices can provide different lines of evidence for the over- or underutilization of functional trait space, or potential niches. Low functional richness, evenness and divergence are all signs that available resources, or niches, are not being maximally exploited by members of a community; in other words, that there is low niche complementarity (or, greater overlap of niches/resource use). Functional richness and evenness declined with increasing climatic severity (colder temperatures), and were lowest in the high arctic, providing evidence that potential niches are being underutilized. Functional divergence was highest in the high arctic, which could be interpreted as contradictory evidence, but there were no clear patterns in FDiv between climatic zones or along temperature gradients; this may reflect that the taxa present in the high arctic were obligated to occupy more extreme regions of trait space in order to persist in the extreme environmental conditions present.

Arthropod TD and FD are both mediated primarily by temperature, and the significant relationships found between TD and FD may likewise be mediated by the environment. Among arctic and alpine plant communities, temperature has long been recognized as an important limiting factor for the expression of functional traits, and of TD (Smith et al., 1997). A recent study of plant taxa along climate and moisture gradients found that more benign locations (warmer with better water availability) had higher TD, which structural equation models indicated were explained by reduced environmental constraints on functional trait diversity (Spasojevic et al., 2014). In regions of extreme cold, it is common to find functionally similar taxa co-occurring in well-blended assemblages in the same microhabitats, suggesting that limitations imposed by the physical environment essentially override competition, rendering it to a status of "minor importance" among community assembly processes (Savile, 1960). These, and

the present study, support the hypothesis that environmental constraints on the diversity of functional traits are more pronounced in more extreme climates (Currie et al., 2004).

When trait diversity is constrained by climate, a community will exhibit reduced functional redundancy. Functional redundancy is considered important for the maintenance of ecosystem processes and the stability and resilience of systems in the face of change (Pillar et al., 2013; Rosenfeld, 2002). A community with diverse taxa that have a range of functional responses is more likely to stabilize with minimal effects on ecosystem processes following a disturbance (Hooper et al., 2005). The fact that functional redundancy is lowest in the high arctic suggests that species extinctions could pose a greater risk of loss of whole functional groups, and thus disruptions to ecological processes (Fonseca & Ganade, 2001). If climatic conditions were to change (e.g., via climate warming), then functional redundancy may increase as the pressure of environmental filtering is lessened, and a greater range of traits becomes "acceptable".

The current biodiversity and structure of arthropod communities is likely to change, given their close associations with temperature. Future climate warming is expected to alter vegetation enough to cause geographic shifts of biomes: tree lines are predicted to shift upwards at the expense of subarctic and high arctic tundra (Alo and Wang 2008). This so-called "greening of the arctic" has already begun (Gensuo et al. 2003), and as much as 10% or 2.5 million km2 of high arctic tundra may be lost by 2100; wooded or subarctic tundra may decline by 25% in the same time scale (Sala et al. 2005). Arthropods will have to respond to these significant changes if they are to persist. Responses may include tracking and following suitable habitats in space, undertaking physiological/physical changes that permit them to cope with different climatic conditions, or modifying behaviours related to feeding and activity (Bellard et al., 2012).

Functional traits will strongly influence these responses. For example, arthropods whose

physiological traits permit them to tolerate a greater range of temperatures or habitats with moderate amounts of moisture (rather than extreme lows or highs) may be better able to cope with the direct effects of changing climates. Alate insects or spiders capable of ballooning should be able to disperse to favourable locations; it is noteworthy that the CWMs indicate that northern communities primarily consist of taxa without wings or ballooning capabilities. Body size may be important: depending on the severity and rapidity of environmental change, very small or very large body sizes may be disadvantageous (Johst & Roland, 1997). The high arctic taxa in this study are predominantly small linyphiid spiders and pterosticine beetles; this trend is reflected in the smaller biomass CWMs in the sites studied here, and has generally been observed in the arctic (Danks, 1981). Predators may be more susceptible to negative effects because they are subject to the same environmental constraints as taxa at lower trophic levels, in addition to experiencing bottom-up effects of disturbed lower trophic groups (i.e., their prey items) (Kotze & O'Hara, 2003; Voigt et al., 2007). Carnivore-dominant communities, such as those found in the far north, may therefore be more sensitive to climate change than those that are more functionally diverse.

Although increased temperatures could have a negative effect on existing northern arthropod communities, climate warming could alternatively have a positive or neutral effect on high arctic biodiversity. Warmer temperatures might increase the survival of the existing high arctic taxa (Bellard et al., 2012) and permit an influx of taxa with more diverse functional traits, or there may be no loss or net change in diversity associated with climate change over time (Timms et al., 2013). Higher precipitation and increased carbon dioxide will likely lead to increased plant biomass, diversity and productivity (Bellard et al., 2012; Dormann & Woodin, 2002; Walker et al., 2006), which may favour increased diversity and abundance of herbivores

rather than carnivores, resulting in a shift in overall trophic structure. In addition to increasing the community's TD and FD, any incoming taxa could become important new sources of prey items for the existing predatory taxa. Given the complex trophic dynamics between different taxa, and the great variation in their functional traits and how these may prohibit or facilitate their movement or persistence, it is difficult to predict exactly how climate change will affect TD/FD and community structure in these northern regions, but it is clear that significant changes will occur.

5.6 Conclusion

This study has provided unique evidence for the patterns and processes underlying taxonomic and functional diversity. Using a trait-based functional approach, in addition to traditional taxonomic metrics, over 46,000 terrestrial arthropod specimens representing over 800 taxa and a huge range of functional traits, this research demonstrates important relationships between TD, FD, and environmental constraints. Temperature-driven environmental filtering of functional traits is most pronounced in the climatically extreme high arctic regions, and niche complementarity plays a more important role in diversity and community structure in warmer ecoclimatic zones to the south. Previous studies have demonstrated relationships between TD and temperature; the trait-based approach used here provides novel ways to explore mechanistic hypotheses.

To our knowledge, no other study has presented a field-based, quantitative examination of these relationships at such an extensive spatial scale. While it is clear that temperature is an important filter and driver of biodiversity in the far north, the impacts of warmer temperatures associated with climate change remain to be determined. Effort is required to determine species-

level trait-based responses to environmental change, and also to elucidate how inter-species relationships might mediate or alter these responses. Since climate change is predicted to occur more rapidly and more extensively at high latitudes than anywhere else on the planet (IPCC, 2013, 2014), the urgent need for this research is clear.

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Table 5.1 Sampling locations, dates, and means of six variables considered as possible environmental constraints/drivers of biodiversity in these locations: mean annual temperature (MeanTemp), mean annual precipitation (TotPrecip), mean annual number of frost-free days (Frost), mean annual number of sun hours (SunHrs), mean soil/permafrost depth (SoilD) and mean maximum height of vegetation (MaxVgHt).

Sampling Location		Latitude, Longitude	Sampling Periods 1	2	3	Sampling Year	Mean Temp	Tot Precip	Frost	SoilD	Max VgHt	Sun Hrs
High Arctic	Lake Hazen, NU	81.82975, -71.32244	19-23.vii	23-28.vii	-	2010	-17.7	158.3	5.0	24.9	18.0	1901.6
	Banks Island, NT	73.22412, -119.55255	7-11.vii	11-15.vii	15-19.vii	2011	-12.8	151.5	57.0	45.6	9.5	1641.9
	Cambridge Bay, NU	69.12177, -105.41688	7-11.vii	11-15.vii	15-19.vii	2011	-13.9	141.7	66.0	31.7	16.4	1729.7
	Iqaluit, NU	63.76144, -68.57352	17-21.vii	21-25.vii	25-29.vii	2010	-9.3	403.7	74.0	21.9	22.4	1476.8
Subarctic	Kugluktuk, NU	67.78157, -115.27824	22-26.vi	26-29.vi	29.vi-2.vii	2011	-10.3	247.2	64.0	19.3	35.0	1821.7
	Tombstone Mtns., YT	64.60629, -138.35637	21-24.vi	24-27.vi	27.vi-01.vii	2011	-4.1	324.4	70.0	22.6	29.2	1827.0
	Churchill, MB	58.73573, -93.79789	1-5.vii	5-9.vii	9-13.vii	2010	-6.5	452.7	87.0	60.8	16.5	1799.5
	Schefferville, QC	54.75970, -66.71120	30.vi-3.vii	3-6.vii	6-9.vii	2010	-5.3	792.1	84.0	36.5	50.3	1566.6
North Boreal	Norman Wells, NT	65.29112, -126.62262	7-11.vi	11-14.vi	14-17.vi	2011	-5.1	294.4	106.0	11.0	47.1	1852.0
	Yellowknife, NT	62.52110, -113.38174	7-11.vi	11-15.vi	15-18.vi	2011	-4.3	288.6	115.0	23.4	48.3	2256.5
	Goose Bay, NL	53.21199, -60.45062	15-18.vi	18-21.vi	21-24.vi	2010	0.0	940.4	110.0	55.5	38.4	1644.7
	Moosonee, ON	51.28034, -80.64252	15-19.vi	19-23.vi	23-25.vi	2010	-0.5	703.6	58.0	100.0	62.1	1810.7

Table 5.2 Functional traits included in the estimation of functional diversity indices, including rationale, trait states and notes on trait determination. In all cases, unless the traits were directly observed, they were surmised using information available from other sources (a list of sources is available in Appendix A3-1, and traits for each taxon are provided in A3-2). Average trait states for each taxon were generated from the scores/traits obtained from all specimens of that taxon.

Trait	Rationale	Trait states (and codes)	Notes on trait determination
Biomass (Biomass)	Related to energy and nutrient capture and transfer through trophic levels (Saint-Germain et al. 2007). Adult body sizes are known to be influenced by temperature during juvenile development, and body size can reflects potential fecundity.	Average taxon biomass in mg	Calculated as mg dry mass using body length:dry mass regressions established in the literature. Measured body lengths (from distal end of abdomen or elytra to distal end of head, excluding mouthparts, antennae, flight wings, ovipositors, cerci, etc.) were obtained to the nearest 0.1 mm with digital calipers (large insects) or a microscope and ocular micrometer (most insects). If direct measurements were not made, then median body length recorded in various sources was used as a proxy (most spiders spiders).
Dispersal Capacity (Dispersal)	Development of membranous hind wings, or use of silk for "ballooning", reflects extent of ability to disperse long distances by flight to colonize new areas and exploit food sources and/or suitable habitats available elsewhere. In wings are frequently reduced or lost in habitats that are stable, or where flight is too energetically costly.	Macropterous (Ma), Brachypterous (Br), Polymorphic (Po), None (No), Ballooning (Ba)	Determined for insects and non-spiders via direct observation of morphology, or from sources if not apparent without compromising the physical integrity of valuable dried specimens. Although all spiders have the capacity to balloon, it is more common in individuals with body length of less than 2.5 mm (e.g., see LarrivÉE and Buddle 2011); this was used as a cut-off point for assigning spiders as being capable of "ballooning" or not.
Primary food source (Food)	Reflects specific food/energy resource usage, trophic position, and the nature of interactions with other taxa.	Invertebrates (In), Leaves (Le), Pollen or Nectar (Pn), Plant Sap (Ps), Plants (not specified) (Pl), Wood (Wo), Detritus (De), Moss (Mo), Fungi (Fu), Carrion (C)	Determined using available sources.
Feeding mode (Mode)	Reflects how arthropod moves in its environment, exploits the structure of the habitat, and interacts with other	Active hunter/forager (Ac), Passive (feeds primarily where deposited by adult, largely sessile) (Pa), Orb web	Determined using available sources.

	taxa.	weaver (Or), Sheet web weaver (Sw), Space web weaver (Sp), Ambush hunter (Am)	
Preferred substrate (Substrate)	Represents a measure of microhabitat use, degree of habitat specialization, vertical stratification of habitat use, in some cases interactions with other taxa.	Bark (B); Carrion (C); Detritus (D); Dead wood (Dw); Flowers (F); Ground, general (G); Leaf litter (L); Live wood (Lw); Moss (M); Plants, including shrubs and trees (P); Under rocks (R); In soil (S); Human or natural structures/crevases (St); In or on water (W)	Up to five substrates on which the taxon is typically found were included. Determined using available sources and field observations.
Vegetation cover preference (Cover)	Represents a measure of microhabitat use, degree of habitat specialization. May reflect need for shade/sun conditions, desiccation tolerance/intolerance, or relationships with food sources or food of prey items.	Average total cover (0-30)	Taken from field collected data. Five classes of vegetation were given cover class scores of 1-6 using the Braun-Blanquet (1964) scale. The sum of the five scores was used as a measure of overall vegetation cover.
Humidity preference (Humidity)	Moisture can be a limiting factor for arthropods' habitat use. Suggests degree of habitat specialization, sensitivity to changes in climate, desiccation tolerance/intolerance.	Proportion (0-1)	Calculated using the proportion of specimens of the same taxon found in Wet habitats.
Temperature range (Temp)	Temperature is closely linked to arthropod activity, morphology and distribution. A taxon found in locations spanning a greater range of temperatures suggests that it may not be as strongly affected by climate change or variability, or has a greater capacity for plasticity.	Temperature in °C	Determined using the difference between the maximum and minimum temperatures (15-year means of warmest and coldest months, respectively) across all sites in which the taxon was found.

Table 5.3 Differences in mean taxonomic and functional diversity indices for sites in the three ecolclimatic zones. Bold P values denote statistically significant differences between sites, and different superscript numbers next to means denote sites that are significantly different from each other.

	High Arctic		**Subarctic**		**North Boreal**			
Diversity indices	**Mean**	**Stdev**	**Mean**	**Stdev**	**Mean**	**Stdev**	**F**	**Pr(>F)**
Taxonomic								
Observed Richness	33.000[1]	14.445	138.000[2]	39.556	225.500[3]	54.397	23.560	**<0.001**
Expected Richness (Chao1)	28.584[1]	10.070	108.312[2]	31.931	160.747[3]	30.107	26.210	**<0.001**
Simpson's Diversity	0.484[1]	0.039	0.901[2]	0.061	0.925[2]	0.039	10.11	**0.005**
Evenness	1.444	0.477	3.138	2.611	3.163	1.953	1.072	0.382
Functional								
Richness (FRic)	0.021[1]	0.014	0.187[12]	0.061	0.206[2]	0.146	4.919	**0.036**
Evenness (FEve)	0.420	0.121	0.508	0.054	0.508	0.028	1.691	0.238
Divergence (FDiv)	0.887	0.047	0.802	0.076	0.857	0.038	2.348	0.151
Functional Redundancy	0.756[1]	0.074	0.824[2]	0.064	0.827[2]	0.050	9.613	**0.006**

Table 5.4 Functional identity of each site, represented by multi-trait community-weighted means (CWM); these represent the coordinates (centroid) of the trait distribution in multi-dimensional trait space, or the most commonly expressed variation of a nominal trait. Refer to Table 2 for a description of traits and associated codes.

Zone	Site	Biomass	Temp	Humidity	VegCover	Disp	Food	Mode	Subst
High Arctic	HAZ	1.810928	47.5216	0.6038792	9.816082	No	In	Sw	LP
	BAN	4.02113	47.1509	0.7337587	7.347101	Ma	In	Ac	G
	CAM	9.684376	47.6606	0.6333733	8.53717	No	In	Ac	GL
	IQA	5.5015	47.6776	0.5519174	9.919413	No	In	Ac	GL
Subarctic	KUG	6.879917	45.44095	0.5054823	10.895223	No	In	Ac	GL
	TOM	5.256122	44.98968	0.4546358	10.463744	No	In	Ac	GL
	CHU	7.501368	44.83804	0.4611083	10.869062	No	In	Ac	GL
	SCH	4.306203	43.52638	0.523576	8.84319	No	In	Ac	LP
North Boreal	NOR	7.293458	44.214	0.5311321	8.217744	No	In	Ac	GL
	YEL	3.516783	43.92022	0.5092327	8.177658	No	In	Ac	GL
	GOB	5.369433	42.66353	0.4291882	8.002638	No	In	Ac	GL
	MOO	7.01886	43.51989	0.5272037	8.714452	No	In	Ac	P

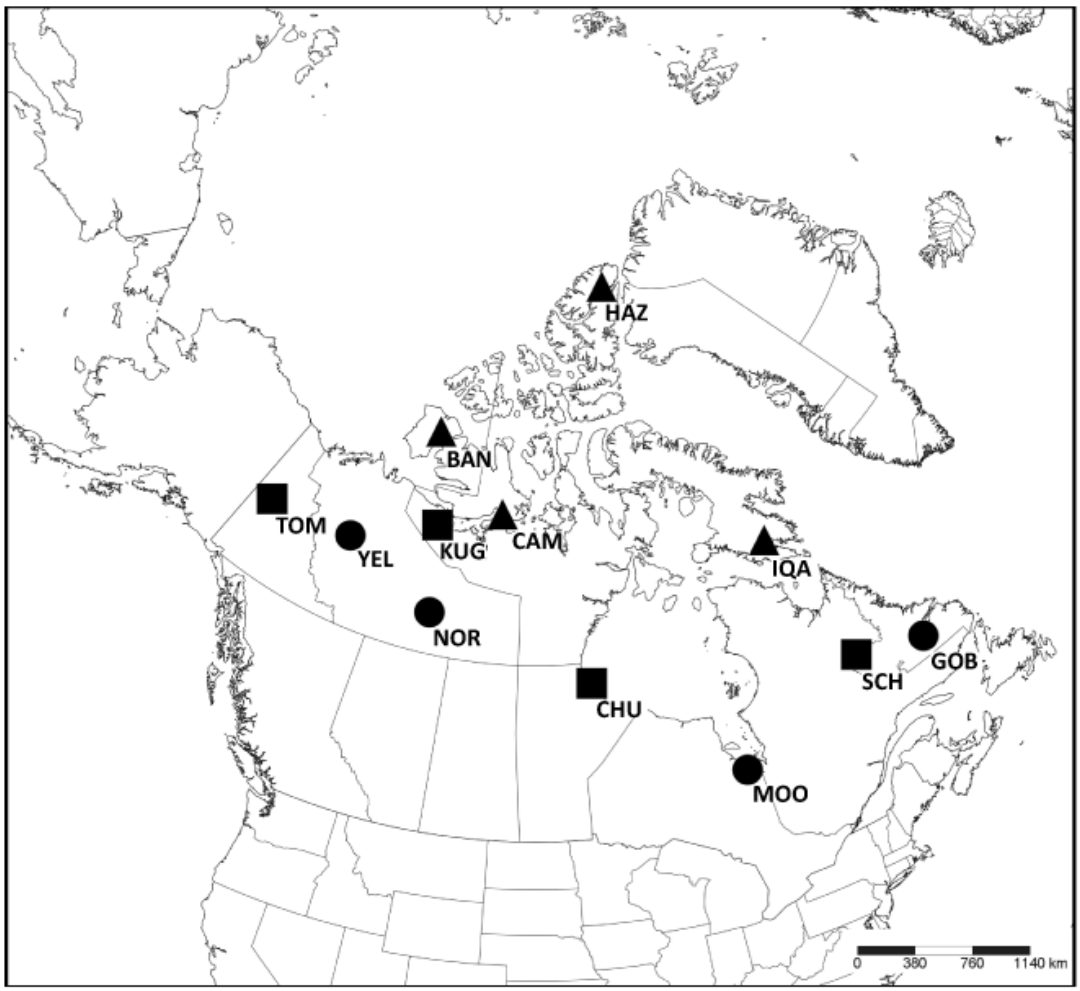

Figure 5.1 Map of the 12 study locations (North Pole Azimuthal projection). Triangles: High Arctic locations; squares: Subarctic; circles: North Boreal. (HAZ: Lake Hazen, NU; BAN: Banks Island, NWT; CAM: Cambridge Bay, NU; IQA: Iqaluit, NU; KUG: Kugluktuk, NU; TOM: Tombstone Mountains., YT; CHU: Churchill, MB; SCH: Schefferville, QC; NOR: Norman Wells, NWT; YEL: Yellowknife, NWT; GOB: Goose Bay, NFLD; MOO: Moosonee, ON).

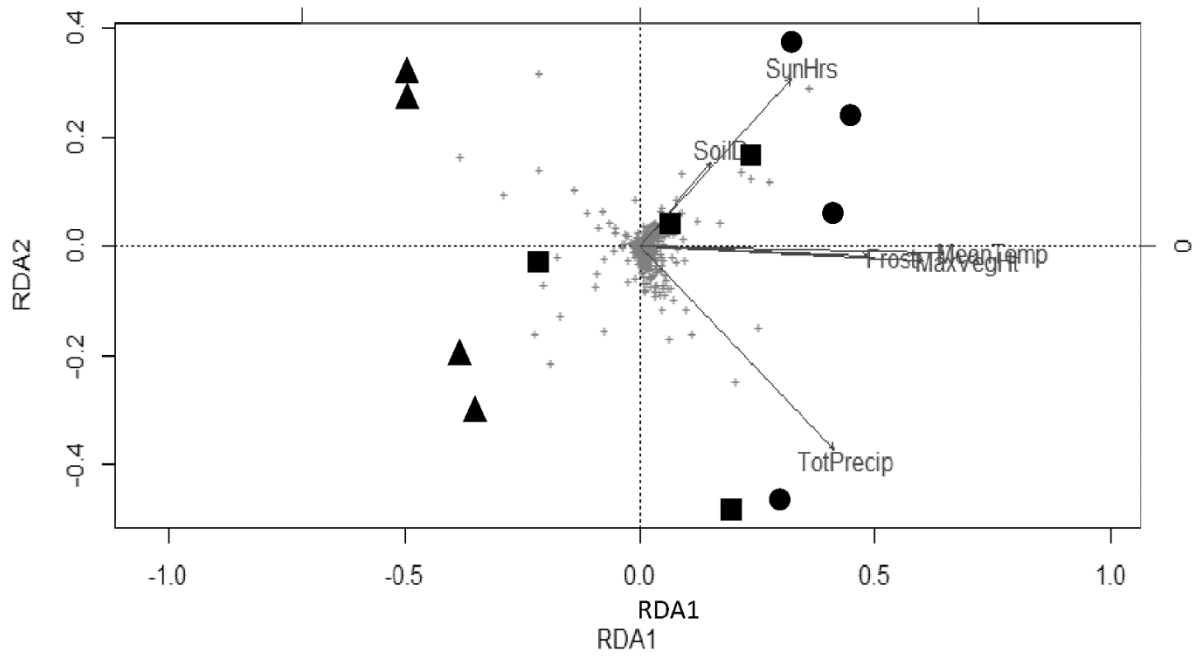

Figure 5.2 Redundancy analysis of taxonomic abundance data. Triangles are high arctic sites, squares are subarctic sites and circles are north boreal sites. Taxa are denoted by "+" symbols. Arrows represent the vectors of the six variables that explain the taxonomic community structure.

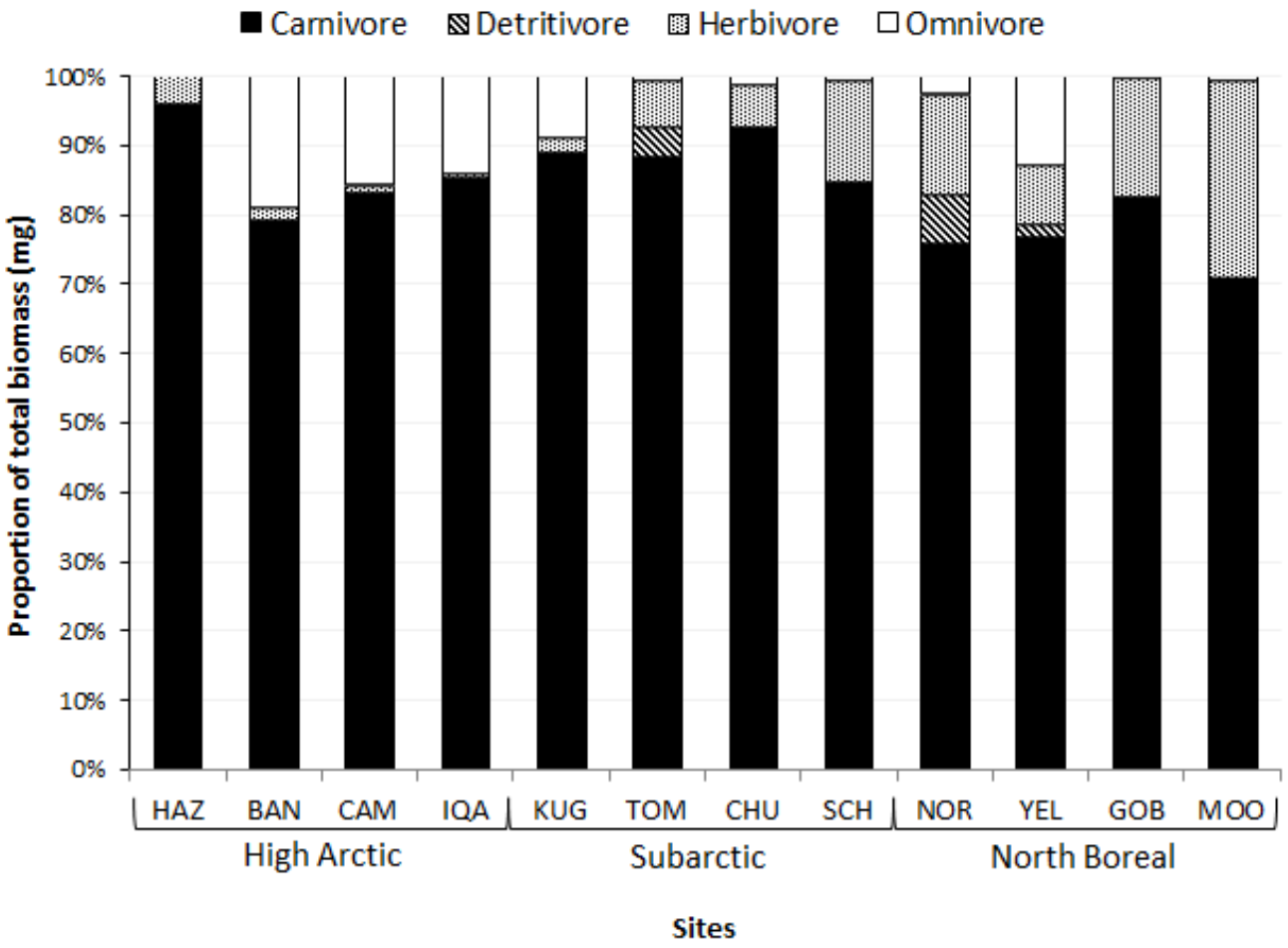

Figure 5.3 Stacked bar graph showing overall trophic structure of the assemblages found at each of the 12 sites as the proportion of the total biomass of arthropods in each trophic level. Sites are grouped by ecoclimatic zone.

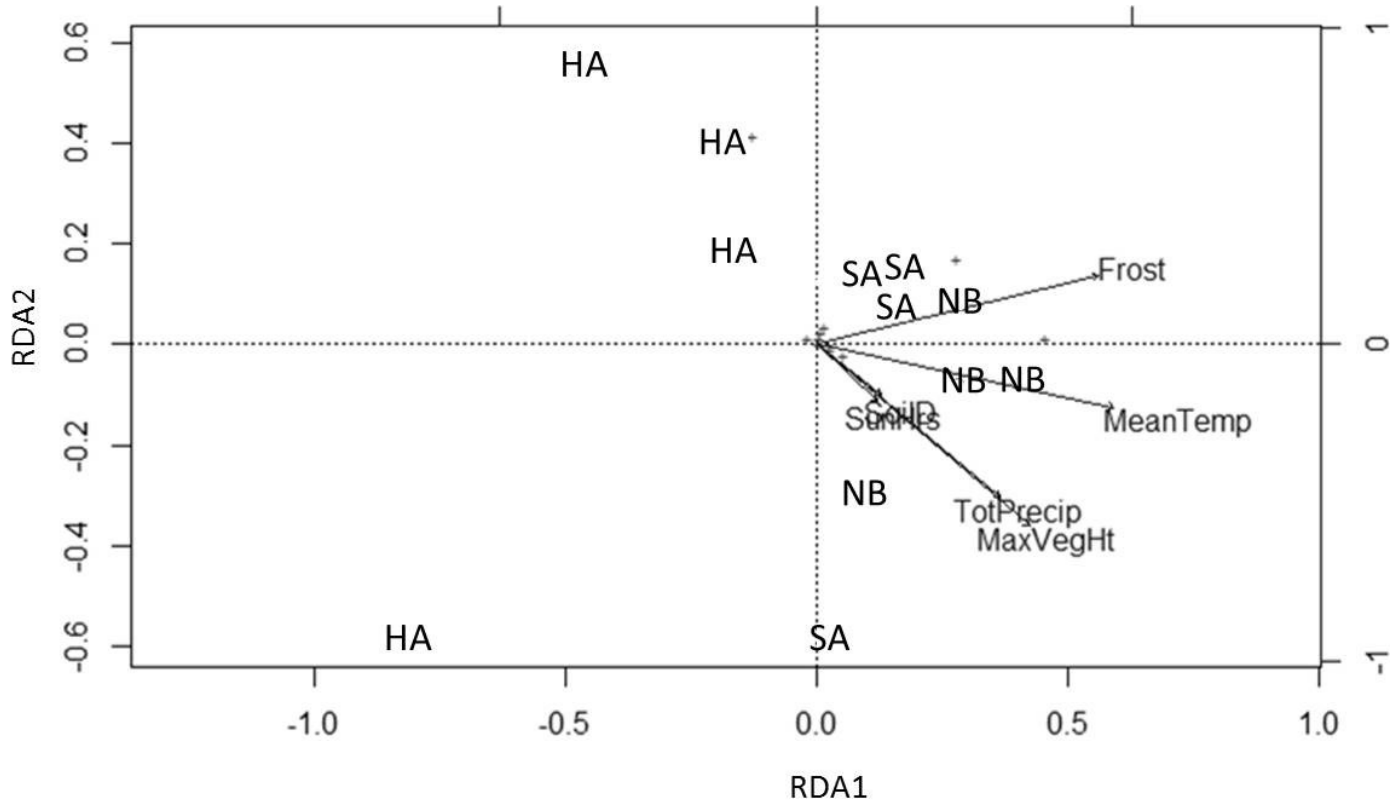

Figure 5.4 Redundancy analysis of the functional identity of sites in this study (i.e., community weighted means (CWMs)), in three ecoclimatic zones: high arctic (HA), subarctic (SA), north boreal (NB). Principal components generated from the PCoA of the CWM distance matrix are shown as "+" symbols, and the arrows represent the vectors of the six variables that explain site-level functional identity.

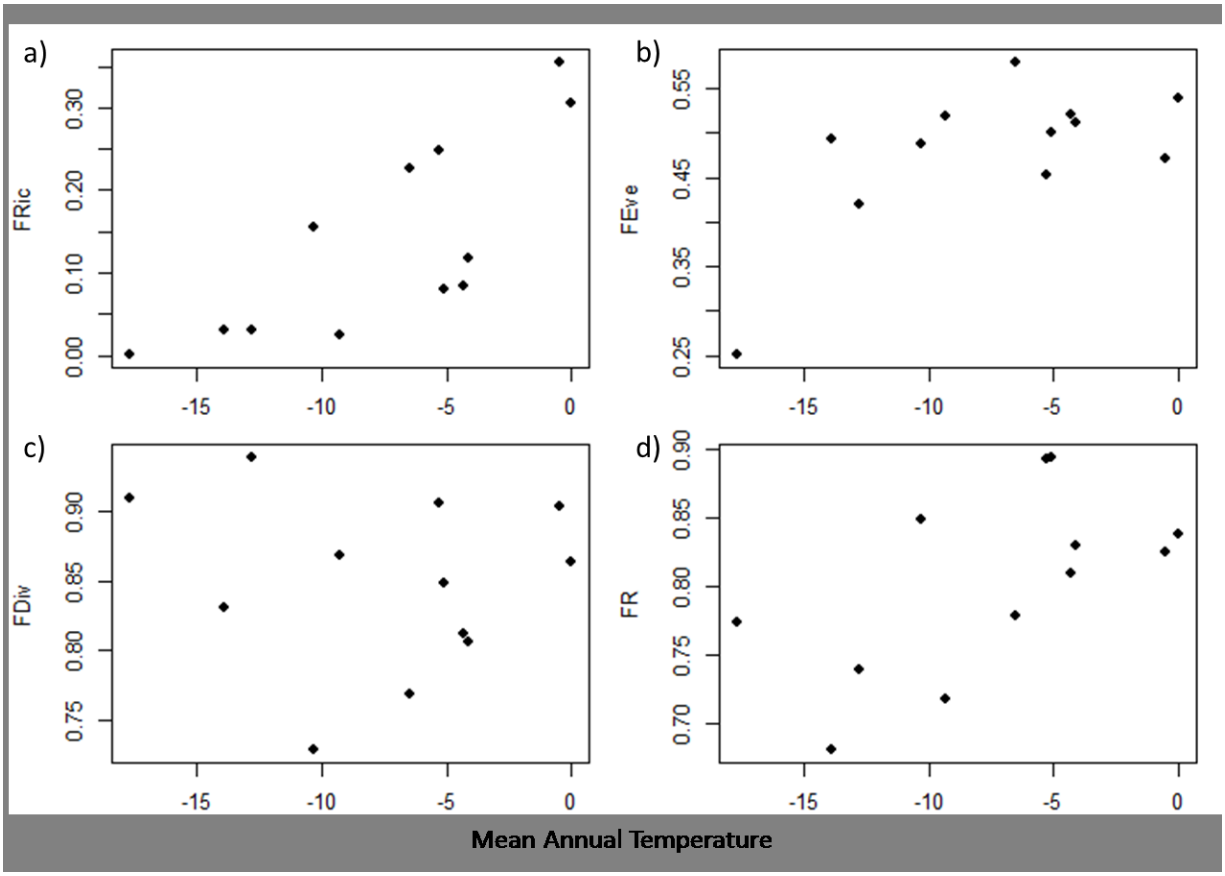

Figure 5.5 Scatterplots of the relationships between four functional diversity indices and mean annual temperature at each site: a) functional richness, b) functional evenness, c) functional divergence, d) functional redundancy.

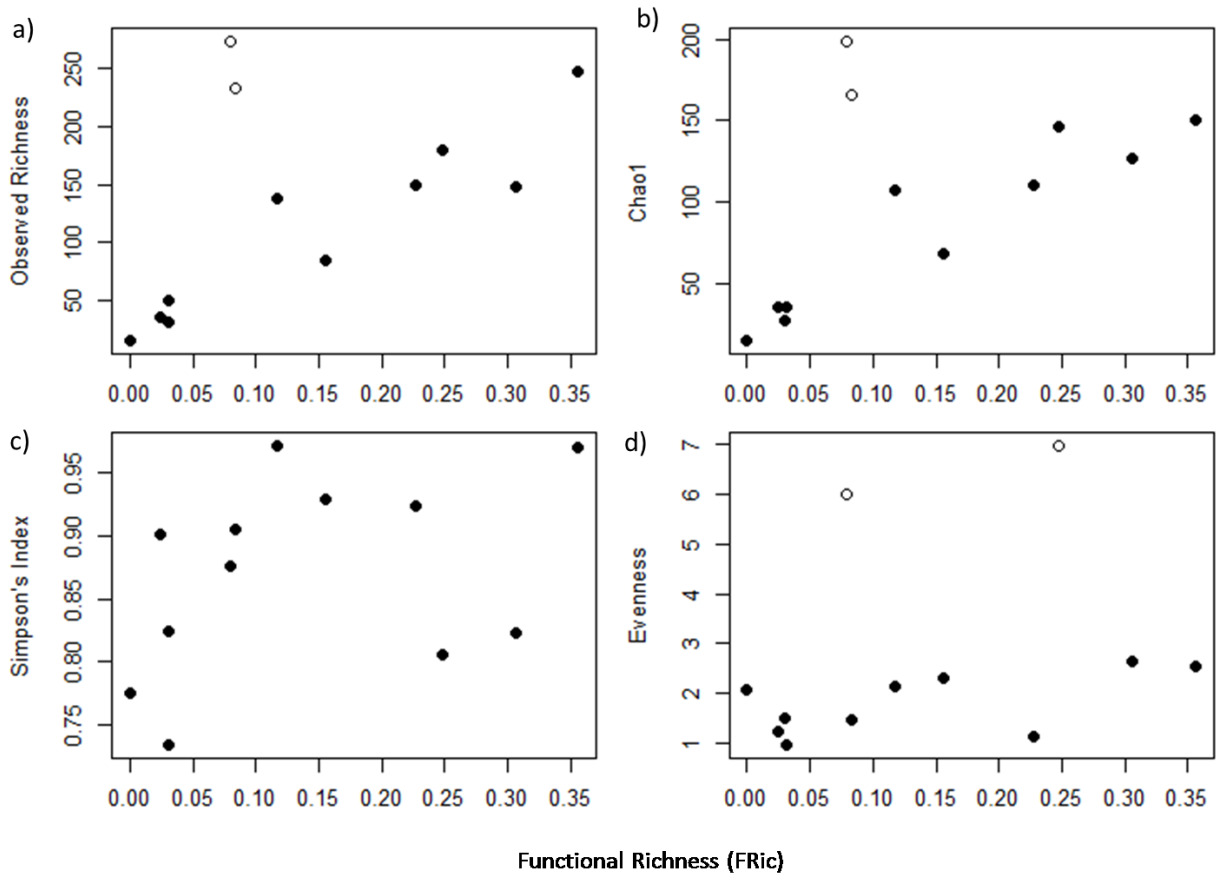

Figure 5.6 Scatterplots of the relationships between four taxonomic diversity indices and functional richness at each site: a) observed taxonomic richness, b) estimated richness (Chao1), c) Simpson's diversity, and d) evenness. Extreme outliers not included in the analyses are denoted by open circles.

Chapter 6: Summary and future directions

6.1 Introduction

The science of community ecology is evolving, and we are rapidly gaining new perspectives about the ways – and reasons – that species assemble in time and space. As we search for patterns and processes, and ways to test developing theories and approaches, there is an increasing need for novel and robust community-level datasets. Arthropods are hyperdiverse and are an important part of all terrestrial ecosystems, and they have clear links to ecological function and stability. Their global ubiquity and ecological relevance make them very attractive, and arguably ideal, targets for community ecology research.

Arthropods may be particularly useful models in northern systems. Animal fauna in boreal and arctic biomes are typically not speciose, and they can be difficult to locate and monitor, making studies of biodiversity and community structure challenging in these vast and important regions. Arthropods offer a solution to this problem: they are abundant, diverse and simple to collect, and, as this thesis has demonstrated, they have tremendous potential to reveal important information about how and why species assemble in the far north and elsewhere.

6.2 Summary of research

6.2.1 Temporal changes in beetle biodiversity and assemblage structure in the subarctic

The objective of this study was to uncover temporal changes in the biodiversity and assemblage structure of beetles in two important habitats that are ubiquitous in northern ecosystems. Additionally, I wanted to test the influence of different environmental variables on

these patterns. Over a period of eight weeks, which represented the majority of the short active season in the subarctic, I collected 2638 beetles in two habitats (wet and mesic) in Kugluktuk, Nunavut. I identified the specimens to species, finding 50 species in 11 families, the vast majority of which were Carabidae. I assigned the beetles to one of seven functional groups, and used biomass as an appropriate metric to represent the relative contributions of each group to the assemblages.

The taxonomic and functional composition of wet and mesic habitat assemblages were markedly different; many species displayed a strong preference for one habitat type or another. However, both assemblages had similar species richness and both exhibited rapid turnover in species and functional group diversity between sampling periods (most noticeably in the mesic habitat). While some functional groups were apparent only for brief periods of time during the study (e.g., pollinators), the functional group containing entomophagous predators hugely dominated the total assemblage biomass in both habitats throughout the entire active season, creating assemblages with an apparent "inverted" trophic structure.

I tested a number of environmental, climatic and spatial variables to see if they were related with assemblage structure. Changes in the structure of assemblages, whether defined taxonomically or functionally, are significantly related to variations in mean daily temperature. This relationship indicates that short-term changes in weather (or, by proxy, long-term changes in climate) can affect the diversity and ecological function of insects in northern systems.

6.2.2 Intertrophic relationships: novel high arctic host-parasite interactions and their implications for arthropod trophic structure

The objective of this study was to conduct a thorough examination of the natural history of newly discovered relationships between carabid beetles and nematomorph parasites in arctic and subarctic regions of Canada. Hairworm-infested beetles were discovered on three high arctic islands, and at one terrestrial location. Community ecology is a rapidly-evolving science that benefits from novel field-based observations that provide insight into the complex interactions that shape biodiversity and the structure of communities.

Beetles from Banks Island, NWT, were infested in particularly high numbers: up to 19% of the total catch was infested at each sampling period. Beetles appeared to be infected haphazardly: there was no significant relationship between infection status and species, body size or sex. Beetles collected in wet habitats were more likely to be infected, which indicates that the paratenic hosts do not disperse very far from the original body of water containing the parasites. Six new host records were recorded, and all hosts were omnivorous or carnivorous species: predation on a paratenic insect host is a prerequisite for infection.

The hairworms collected from all locations appear to represent a single, new species of in the genus *Gordionus* (Nematomorpha: Gordiida). The morphological description provided in this study will soon be supported with molecular data. Given the life cycle of the parasite, which consists of both aquatic and terrestrial stages, this novel study provided significant indirect evidence that omnivorous and predatory terrestrial beetles are widely using flying insects as an important nutrient subsidy. This could explain, at least in part, how the inverted trophic structure of terrestrial arthropods is maintained despite an apparent paucity of terrestrial prey items.

6.2.3 Large-scale latitudinal gradients and drivers of beetle diversity

The objectives of this study were to describe large-scale latitudinal patterns of taxonomic diversity, functional diversity, and assemblage structure across northern Canada, and to determine the climatic and environmental mechanisms driving these patterns. I collected over 9,000 terrestrial beetles at 12 locations in the three northernmost ecoclimatic zones in North America. I identified the beetles morphologically, finding 464 species and 18 functional groups.

I used linear regressions to assess whether latitudinal patterns existed for multiple taxonomic diversity indices as well as functional group richness, and visualized spatial patterns of assemblage structure using ordinations. Species and functional diversity had significant negative relationships with latitude. Taxonomic and functional assemblages within the same ecoclimatic zone were similar, and there was a significant relationship between assemblage structure and latitude.

I used path analysis used to test causal hypotheses for species and functional group richness, and used a permutational approach to assess relationships between assemblage structure and 20 possible climatic and environmental mechanisms. I found that taxonomic and functional assemblage structure were significantly correlated with many of the same climatic factors, particularly factors related to temperature. I determined that, across this large spatial extent, strong latitudinal gradients of diversity and assemblage structure are the result of the mediating effects of climate, particularly temperature.

6.2.4 Terrestrial macroarthropod biodiversity and large-scale mechanisms of community assembly

The objective of this study was to determine the significance of environmental filtering and niche complementarity in large-scale arthropod diversity and community assembly, by linking ecological and climatic gradients, taxonomic diversity, and trait-based functional diversity. Recent developments in methods for calculating indices of functional diversity permit refined examinations of FD that are complementary to traditional TD approaches. Together, they can reveal patterns of biodiversity and help uncover mechanisms responsible for community assembly and ecological function. I examined 46,000 macroarthropods collected from 12 communities that span a large geographic extent and strong climatic gradients in northern Canada. The specimens were identified at least to family but most often to genus, and yielded 809 taxa, primarily beetles and spiders. I also described each individual in terms of eight functional traits that encompassed different aspects of morphology, behaviour and physiology, and average characters were determined for each taxon so that multidimensional trait-based metrics of FD could be calculated. I calculated TD (richness, evenness, expected richness, Simpson's index) and FD (richness, evenness, divergence) indices, as well as functional redundancy.

When I tested the relationships between TD and FD in the 12 communities, I found that they were highly correlated. Also, it was clear both aspects of biodiversity decline significantly with colder mean annual temperatures. Variability in overall community structure (taxonomic and functional; the former determined using relative abundances of species and the latter determined using community-weighted means of functional traits) was best explained by mean annual temperature. Functional redundancy, a metric that considers TD and FD, was especially

high in the far north, despite the fact that there were few species. This suggested that environmental filtering plays a more important role in biodiversity patterns in regions with extreme climates, whereas the diversity and community assembly of the more southerly communities are more likely structured by niche complementarity.

This study advances our understanding of the relationships between TD and FD, and of how they are mitigated by different processes along large climatic gradients. It also highlights the unique nature and vulnerability of arthropod communities – and thus of ecological function – in the far north.

6.3 Synthesis of recommendations for future work

The biodiversity (TD and FD) and structure of terrestrial macroarthropod communities in northern Canada have several consistent patterns, the most striking of which are: (1) large-scale inverse relationships between biodiversity/assemblage structure and latitude; (2) strong correlations between TD and FD; and (3) the dominance of active predatory taxa. Another important finding of this study is that climate (temperature) gradients provide the best explanation for the variability observed in arthropod biodiversity and assemblage structure over time and across space. Lastly, the effects of climate on biodiversity and community assembly seem to be more pronounced in the high arctic than in the south. This study advances our understanding of the relationships between TD and FD, and of how they are mitigated by different processes in time and along large spatial gradients. Given the rapid and significant rise in temperature projected for northern biomes and the fact that predatory taxa are often more sensitive to environmental variability (Kotze and O'Hara 2003, Voigt et al. 2007)., major changes to arthropod diversity are expected in the north, with vast implications for the function

and stability of northern ecosystems. Northern arthropod assemblages present significant opportunities for biodiversity research and conservation efforts, and their sensitivity to climate make them ideal targets for long-term terrestrial diversity monitoring.

To date, general mechanisms underlying biodiversity and species assembly have proven elusive, which suggests that gaps in the data could be hindering our ability to better understand the processes behind these patterns. The recent inclusion of complimentary genetic, morphological and functional measures of diversity alongside the taxonomic metrics has begun to bridge these gaps (Magurran 2004). While it is clear that temperature is an important driver of biodiversity in the far north, the ecological effects of future climate warming remain to be determined. More effort must be made to identify trait-based responses to environmental change and their ecological ramifications, and also to elucidate how inter-species relationships might mediate or alter these responses. As shown here, functional diversity may provide new insight into how environmental gradients or changes influence biodiversity at different scales.

In addition to expanding the lens through which we examine diversity patterns to one greater than one solely consisting of taxonomy, we can also begin to address other limitations inherent to most large-scale biodiversity studies and theories (see Chapter 4). While certain limitations are understandable, they have created a situation where we lack sufficient information to make many generalizable statements about large-scale patterns and processes of diversity (Stevens et al., 2003; Safi et al., 2011). Greater effort must be made to generate standardized, quantitative datasets about species abundances/densities and functional traits for different communities, at large scales, and in understudied yet ecologically important biomes. This will require carefully designed field-based studies, which can be logistically and financially challenging. The establishment of multi-institutional and collaborative projects whereby

resources and methods are shared across large extents (such as the NBP) will be a key step forward, while simultaneously filling knowledge gaps and helping prevent unnecessary duplication of effort.

The rising popularity and increasingly obvious utility of trait-based approaches to biodiversity research raise an important issue. In order to accurately assign or quantify the traits of individual organisms or even of individual species, researchers will need specimens-in-hand and accurate life history information. This points to a need for observational, field-based, fundamental research: in other words, natural history. Although natural history has, over recent decades, become increasingly viewed as an unfashionable "soft science" (or worse, as a pastime), there is arguably a greater need than ever to enhance (or at the very least protect) existing museum collections and to spend more time studying organisms in their natural environments (Tewksbury et al. 2014). If ecologists are going to ask and answer questions about large-scale biodiversity patterns and processes, we must generate more information about species: their distributions, their traits, their interactions, and their responses to the environment. Empirical evidence drawn from natural settings will likely yield not only new, but also novel, information that will help advance the field of community ecology in a meaningful way:

> *"…the better approach to [studying] any complex system is the stepwise buildup of knowledge by natural history, scientific in nature but only tentatively guided by preexisting broad theoretical concepts. The most enduring knowledge, of both fact and theory, is thereby bottom up and evidence based, with models built piece by piece from well-documented phenomena and cause-and-effect explanations, tested and linked together to generate increasingly broad principles and, eventually, overarching theories"* (Tschinkel and Wilson 2014)

The studies presented in this thesis, which were conducted with standardized samples of diverse arthropods from widespread northern biomes, are a major step towards beginning to address these knowledge gaps. This thesis contains one of the most comprehensive field-based community-level datasets of animal distributions, biodiversity and community structure in the current literature. The data, and the curated arthropod specimens, will have continued use in future diversity assessments, meta-analyses and comprehensive reviews; hopefully this work is only one of many future field-based contributions to the ongoing evolution of the science of community ecology.

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Appendix 1: Supplementary materials for Chapter 2

Appendix A1-1 Summary of the beetle species collected in this study. Species' taxonomic identities, functional group assignments, and abundance in each habitat are shown.

Family	Subfamily	Species	Functional Group	Mesic (#)	Wet (#)
		Carnivores			
Carabidae	Carabinae	*Carabus chamissonis* Fischer von Waldheim	Entomophage	41	28
Carabidae	Carabinae	*Carabus vietinghoffii* Adams	Entomophage	12	34
Carabidae	Elaphrinae	*Blethisa catenaria* Brown	Entomophage	0	32
Carabidae	Elaphrinae	*Elaphrus lapponicus* Gyllenhal*	Entomophage	4	5
Carabidae	Harpalinae	*Cymindis unicolor* Kirby	Entomophage	26	1
Carabidae	Harpalinae	*Pterosticus barryorum* Ball	Entomophage	13	0
Carabidae	Harpalinae	*Pterostichus brevicornis* (Kirby)	Entomophage	680	254
Carabidae	Harpalinae	*Pterostichus caribou* Ball	Entomophage	571	253
Carabidae	Harpalinae	*Pterostichus hudsonicus* LeConte	Entomophage	5	0
Carabidae	Harpalinae	*Pterostichus vermiculosus* (Ménétries)	Entomophage	16	155
Carabidae	Harpalinae	*Stereocerus haematopus* (Dejean)	Entomophage	52	1
Carabidae	Nebriinae	*Notiophilus borealis* Harris*	Entomophage	23	0
Carabidae	Scaritinae	*Dyschirius melanocholicus* Putzeys*	Entomophage	5	4
Carabidae	Trechinae	*Bembidion* Latreille species 1	Entomophage	0	2
Coccinellidae	Scymninae	species 1	Entomophage	8	0
Staphylinidae	Aleocharinae	species 1 (Tribe Tachyusini)	Entomophage	0	1
Staphylinidae	Aleocharinae	*Acrotona* Thomson species 1	Entomophage	1	0
Staphylinidae	Aleocharinae	*Atheta borealis* Klimaszewski and Langor*	Entomophage	0	2
Staphylinidae	Aleocharinae	*Atheta* species 1	Entomophage	0	1
Staphylinidae	Aleocharinae	*Boreophilia hyperborea* (Brundin)*	Entomophage	0	1
Staphylinidae	Aleocharinae	*Gymnusa konopackii* Klimaszewski*	Saprophage	0	2
Staphylinidae	Aleocharinae	*Liogluta nigropolita* (Bernhauer)*	Entomophage	0	1
Staphylinidae	Aleocharinae	*Mocyta fungi* (Gravenhorst)*	Entomophage	1	0
Staphylinidae	Omaliinae	*Holoboreaphilus nordenskioeldi* (Mäklin)	Entomophage	0	1
Staphylinidae	Omaliinae	*Acidota quadrata* (Zettersted)t*	Entomophage	1	0
Staphylinidae	Omaliinae	*Olophrum latum* Mäklin	Entomophage	0	4
Staphylinidae	Omaliinae	*Olophrum rotundicolle* (Sahlberg)*	Entomophage	0	1
Staphylinidae	Staphylininae	*Philonthus* Stephens species 1*†	Saprophage	0	2
Staphylinidae	Staphylininae	*Quedius fellmani* (Zetterstedt)	Entomophage	13	0
Staphylinidae	Steninae	*Pycnoglypta heydeni* Eppelsheim	Entomophage	0	5
Staphylinidae	Steninae	*Stenus fasciculatus* Sahlberg	Entomophage	0	7
Staphylinidae	Steninae	*Stenus immarginatus* Mäklin	Entomophage	0	2

Staphylinidae	Steninae	*Stenus melanarius* Stephens*	Entomophage	0	2
Staphylinidae	Steninae	*Stenus* near *noctivagus* Casey*	Entomophage	0	2
Staphylinidae	Steninae	*Stenus* Latreille species 1	Entomophage	0	3
Staphylinidae	Steninae	*Stenus* Latreille species 2	Entomophage	0	5
Staphylinidae	Steninae	*Stenus* Latreille species 3*†	Entomophage	0	2
		Herbivores			
Anobiidae	Dorcatominae	species 1	Mycophage	0	1
Carabidae	Harpalinae	*Amara alpina* (Paykull)	Granivore	132	56
Carabidae	Harpalinae	*Amara pseudobrunnea* Lindroth*	Granivore	5	0
Byrrhidae	Byrrhinae	*Byrrhus eximius* LeConte*	Bryophage	13	4
Cantharidae	Cantharinae	*Podabrus piniphilus* (Eschscholtz)	Florivorae	17	30
Curculionidae	Molytinae	*Lepyrus nordenskioeldi* Faust	Folivore	7	2
Curculionidae	Molytinae	*Lepyrus gemellus* Kirby	Folivore	1	0
Elateridae	Negastriinae	*Berninelsonius hyperboreus* (Gyllenhal)	Folivore	15	0
Latridiidae	Corticariinae	species 1	Mycophage	0	1
Leiodidae	Leiodinae	*Leiodes* Latreille species 1	Mycophage	7	0
Leiodidae	Leiodinae	*Agathidium* Panzer species 1	Mycophage	7	0
Leiodidae	Leiodinae	*Liocyrtusa nigriclavis* Hlisnikovsky*	Mycophage	3	0
		Saprophages			
Silphidae		*Thanatophilus lapponicus* (Herbst)	Necrophage	1	3

* new species record for the territory of Nunavut, † undescribed species

Appendix A1-2 Changes in the total biomass (g) of beetles in seven functional groups over eight sampling periods in a) mesic and b) wet habitats.

a)

Sampling Period	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Entomophages	2878.1	1326.1	3332.4	2316.1	894.1	613.9	806.9	1008.1
Bryophages	90.7	46.6	53.1	0.0	0.0	16.0	0.0	0.0
Florivores	3.5	23.3	24.1	30.4	0.0	0.0	0.0	0.0
Folivores	106.3	58.1	218.2	0.0	0.0	43.6	7.3	86.2
Granivores	232.5	179.4	722.2	305.9	118.8	11.2	58.4	83.9
Mycophages	0.8	5.9	2.4	0.0	1.3	0.0	3.5	1.2
Necrophages	0.0	0.0	34.8	0.0	0.0	0.0	0.0	0.0

b)

Sampling Period	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Entomophages	4212.6	2494.8	3252.3	2043.0	997.3	456.6	522.0	715.4
Bryophages	24.8	0.0	38.9	0.0	0.0	0.0	0.0	0.0
Florivores	0.0	26.5	77.9	20.9	3.5	0.0	0.0	0.0
Folivores	29.7	0.0	0.0	34.5	0.0	0.0	0.0	0.0
Granivores	203.2	357.0	210.9	135.0	104.8	0.0	14.7	0.0
Mycophages	0.0	0.6	0.5	0.0	0.0	0.0	0.0	0.0
Necrophages	0.0	0.0	0.0	0.0	25.3	0.0	0.0	87.9

Appendix A1-3 Email received from Kevin Floate, Editor-in-Chief of *The Canadian Entomologist,* authorizing publication of the manuscript (Chapter 2) in this thesis

Floate, Kevin [Kevin.Floate@AGR.GC.CA]

December 8, 2014 11:16 AM

Hi Crystal:

Excellent.

There is no issue regarding using your own data (text, figures, tables) reformatted for a thesis. There is perhaps some concern if you were to take the journal formatted reprint and stuck it in the thesis.

Happy holidays!

Dr. Kevin Floate, Editor-in-Chief

The Canadian Entomologist

Kevin Floate, Research Scientist

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Appendix 2: Supplementary materials for Chapter 4

Appendix A2-1 Names and abundances of beetle taxa collected from 12 sites. Asterics (*) denote new territorial records.

		High Arctic				Subarctic				North Boreal			
Family **Subfamily**	**Species**	**HAZ**	**BAN**	**CAM**	**IQU**	**KUG**	**TOM**	**CHU**	**SCH**	**NOR**	**YEL**	**GOB**	**MOO**
Anthicidae													
Anthicinae													
	Anthicus sp.1									16			
Buprestidae													
	Buprestinae												
	Anthaxia (*Melanthaxia*) *inornata*									90	16		7
Byrrhidae													
Byrrhinae													
	Byrrhus sp.							1					
	Byrrhus sp. 2										3		
	Byrrhus sp. 3								3				
	Byrrhus sp. 4					3							
	Byrrhus sp. 5									1			
	Byrrhus sp. 6						19						
	Byrrhus sp. 7												37
	Byrrhus sp. 8						2						
	Cytilus sp.									4	3		13

	Simplocara sp.							1					
Syncalyptinae													
	Curimopsis setulosa										1		
	Curimopsis sp.								1				
	Curimopsis sp. 2						3						
Cantharidae													
Cantharinae													
	Dichelotarsus laevicollis								1				
	Dichelotarsus puberulus								6				1
	Dichelotarsus sp.							29					
	Rhagonycha fraxini											28*	1
	Rhagonycha mandibularis							87					
	Rhagonycha sp.					2							
Carabidae													
Carabinae													
	Carabus chamissonis					1		48		42			
	Carabus granulatus												174
	Carabus maeander									30			6
	Carabus serratus											27*	
	Carabus taedatus							24					
	Carabus truncaticollis						100						
	Carabus vietinghoffii					6				8			
	Scaphinotus bilobus												1
	Sphaeroderus stenostomus												5
Cicindelinae													
	Cicindela limbalis									2			
	Cicindela longilabris longilabris									2			

Elaphrinae													
	Blethisa catenaria					9							
	Blethisa quadricollis												2
	Diacheila arctica									1			
	Diacheila polita						16						
	Elaphrus clairvillei							6		4			4
	Elaphrus fuliginosus										1*		
	Elaphrus lapponicus						27	16		9	4		
	Elaphrus lecontei												1
Harpalinae													
	Agonum affine							9		11			7
	Agonum consimile									1			
	Agonum exaratum			2									
	Agonum gratiosum							3		29	100	1	23
	Agonum metallescens												8
	Agonum mutatum											2	
	Agonum quinquepunctatum							6		6			
	Agonum superioris												2
	Agonum thoreyi												1
	Amara alpina		303	804	111	213		28	3				
	Amara erratica									1			
	Amara hyperborea								83	4	6		
	Amara laevipennis							1			4	21*	
	Amara littoralis												1
	Amara pseudobrunnea						1		10	1*	2	1	
	Amara torrida									1			1
	Badister obtusus									1	2		1

Bradycellus neglectus										2*		
Bradycellus nigrinus												4
Calathus ingratus								2	9	10	9	3
Chlaenius alternatus									38	2		
Chlaenius lithophilus												1
Chlaenius niger												1
Cymindis unicolor					2	1	1					
Dicheirotrichus cognatus												5
Harpalus solitaris									1	1		
Harpalus nigritarsis						6			9	3		
Harpalus pleuritieus									1			
Platynus decentis												1
Platynus mannerheimii								1				2
Poecilus lucublandis												6
Pterostichus adstrictus									20	4		15
Pterostichus arcticola						18	1	2				
Pterostichus barryorum					10							
Pterostichus brevicornis			2		392	64	80	3				
Pterostichus caribou		154	846		325		69					
Pterostichus haematopus				306	106	6	54	110	3	1		
Pterostichus hudsonicus					4							
Pterostichus melanarius												204
Pterostichus parasimilis						244						
Pterostichus patruelis									6*	2*	1	9
Pterostichus pensylvanicus									19		6*	
Pterostichus pinguedineus								1				
Pterostichus punctatissimus							71		18	22		

	Pterostichus tareumiut		197										
	Pterostichus tenuis												4
	Pterostichus vermiculosus			1		42							
	Syntomus americanus										2	1	
	Synuchus impunctatus												1
Loricerinae													
	Loricera pilicornis							1					
Nebriinae													
	Nebria gyllenhali								3				
	Notiophilus aquaticus								1				
	Notiophilus borealis					22	5	9	3				
	Notiophilus intermedius									1*	1*		
	Notiophilus semistriatus										2*	1	
Patrobinae													
	Patrobus foveocollis								3		1		
	Patrobus longicornis												5
	Patrobus septentrionis								3	10			
	Patrobus stygicus									3			
Scaritinae													
	Clivina fossor												5
	Dyschirius frigidus						1						
	Dyschirius globulosus										1*		
	Dyschirius hiemalis							13	1	3	15		
	Dyschirius integer												18
	Dyschirius melanocholicus					2	16						
	Dyschirius nigricornis							6					
	Dyschirius subarcticus						1						

Trechinae													
	Bembidion bimaculatum												2
	Bembidion dilaticolle												1
	Bembidion diligens									2*			
	Bembidion forestriatum										1		
	Bembidion fortestriatum												8
	Bembidion grapei								1				
	Bembidion morulum							1		38	17		
	Bembidion quadratulum											1*	
	Bembidion transparens									1			21
	Bembidion versicolor												15
	Syntomus americanus									3			
	Trechus crassiscapus								1				
Cerambycidae													
Lepturinae													
	Pidonia scripta										1*		
	Rhagium inquisitor											6	
Chrysomelidae													
Galerucinae													
	Altica sp. 1									1			
	Altica sp. 2												13
	Altica sp. 3										1		
	Altica sp. 4								1				
	Altica sp. 5											2	
	Alticine sp.							1					
	Alticine sp.2												1
	Alticine sp. 3												1

	Alticine sp. 4								20				
	Chaetocnema sp.												1
	Chaetocnema sp.2									2			
	Crepidodera sp.												8
	Glyptina sp.									1			
	Mantura sp.									1			
	Neogalerucella pusilla							1					4
	Tricholochmaea sp.									3			6
	Tricholochmaea vaccinii								2			3*	
Cleridae													
Clerinae													
	Trichodes ornatus									40			
Coccinellidae													
Coccinellinae													
	Anisosticta bitriangularis									1			8
	Ceratomegilla ulkei						5	2					
	Coccinella hieroglyphica									1			
	Hippodamia sp.								2				
	Hippodamia sp. 2										1		
	Coccinellid sp.									1	1		
	Coccinellid sp. 2											4	
	Coccinellid sp. 3									2			
	Coccinellid sp. 4									1			
	Coccinellid sp. 5					5							
	Coccinellid sp. 6									4			
	Coccinellid sp. 7									1			
	Coccinellid sp. 8										18		

	Coccinellid sp. 9										2		
	Coccinellid sp. 10						1						
	Coccinellid sp. 11							6					
Corylophidae													
	Corylophid sp.										19		6
	Corylophid sp. 2										1		1
	Corylophid sp. 3										1		1
	Corylophid sp. 4										1		1
Cryptophagidae													
Atomariinae													
	Atomaria sp.												3
	Atomaria sp. 2										1		18
	Atomaria sp. 3												75
	Atomaria sp. 4						1						
	Atomaria sp. 5										1		
	Tisactia sp.									1			
Cryptophaginae													
	Cryptophagus sp.							4					
	Cryptophagus sp. 2									55			
	Cryptophagus sp. 3						2						
	Cryptophagus sp. 4										31		
	Cryptophagus sp. 5									1			
	Cryptophagus sp. 6											45	
	Cryptophagus sp. 7								9				
Curculionidae													
Cossoninae													
	Rhyncolus brunneus										2		

Curculioninae													
	Anthonomus nigrinus									1			
	Ellescus ephippiatus							1					
	Isochnus arcticus		24	1									
Cyclominae													
	Listronotus humilis							1*				1*	
Dryophthorinae													
	Sphenophorus costipennis												1
Entiminae													
	Lepidophorus lineatocollis						1			27			
	Otiorhynchus ovatus											2	
	Sciaphilus asperatus												1
	Sitona lineellus									1			
Erirhininae													
	Grypus equiseti												32
	Notaris aethiops						1	2		3	6		
	Procas lecontei										1		
Molytinae													
	Hylobius congener											63	
	Hypera diversipunctata					1*	1						
	Hypera sp.*C*			1									
	Hypera sp.*T*						1						
	Lepyrus gemellus					1							
	Lepyrus nordenskioeldi					8							
	Lepyrus nordenskioeldi			2									
	Lepyrus sp.*C*			10									
	Lepyrus sp.*H*							21					

	Lepyrus sp.*N*									4			
	Lepyrus sp.*T*						1						
	Pissodes nemorensis											5*	
Scolytinae													
	Pityokteines sp.1										1		
	Scolytine sp.											1	
	Scolytine sp. 2										1		
Elateridae													
Elaterinae													
	Agriotes limosus									2		5	
	Ampedus nigrinus									5			
	Ampedus pullus									9			
	Dalopius pallidus												21
	Sericus incongruus									2	5	4	
Negastriinae													
	Negastrius arnetti												1
	Neohypdonus gentilis												4*
Prosterinae													
	Ascoliocerus sanborni						16						
	Beckerus appressus								3				
	Eanus decoratus						2	5	1			1	
	Eanus maculipennis								1			3	
	Hypnoidus abbreviatus												5
	Hypnoidus bicolor						4		28	1	5	1	1
	Hypnoidus rivularius						1			1			
	Limonius aeger											3	
	Pseudanostirus ochreipennis										2		

	Pseudanostirus triundulatus										1	5	1
	Selatosomus aeripennis										15		
	Setasomus aratus										1		
	Sylvanelater mendax									1			
Eucinetidae													
	Eucinetus haemorrhoidalis									6			
Histeridae													
	Histeridae sp.											1	
Hydraenidae													
	Hydraena sp.							1					
Hydrophilidae													
Sphaeridiinae													
	Cercyon sp.									1			
	Cercyon sp. 2											73	
	Cercyon sp. 3												1
	Megasternum sp.												1
	Phaenonotum sp.									1			
	Phaenonotum sp.2								1				
Lampyridae									1				4
	Lampyrid sp.												1
	Lampyrid sp. 2								1				
	Lampyrid sp. 3												3
Latridiidae													
Corticariinae													
	Corticaria sp.											4	
	Corticaria sp. 2					1							
	Corticaria sp.3						20						

	Corticaria sp. 4						2						
	Corticaria sp. 4						2						
	Corticaria sp. 5									18			
	Corticarina sp.									8			
	Melanophthalma sp.									9			
	Melanophthalma sp. 2										26		
	Melanophthalma sp. 3											1	
	Melanophthalma sp. 4												7
Latridiinae													
	Enicmus sp.		21										
	Enicmus sp. 2											7	
	Latridius sp. 3			3									
	Latridius sp. 4									1			
Leiodidae													
Coloninae													
	Catops sp.								1				
	Colon asperatum												26
	Colon bidentatum												1
	Colon dentatum												4
	Colon magnicolle												1
	Colon oblongum									7*	27*		26
	Colon politum												7*
Leiodinae													
	Agathidium sp.									1			
	Agathidium sp. 2							2					
	Agathidium sp. 3									1			
	Agathidium sp. 4						6						

	Agathidium sp. 5						2						
	Agathidium sp. 6									5			
	Anisotoma sp. 7									2			
	Hydnobius sp.												12
	Leiodes assimilis												7
	Leiodes neglecta												23
	Leiodes punctostriata									2	24		2
	Leiodes sp.												2
	Leiodes sp. 2												32
	Leiodes sp. 3									1			
Lucanidae													
Lucaninae													
	Platycerus sp.										1		
Mordellidae													
	Mordellochroa scapularis									1*			
Nitidulidae													
Carpophilinae													
	Epuraea sp.											1	
	Epuraea sp. 2							10					
	Epuraea sp. 3												1
	Epuraea sp. 4									35			
	Epuraea sp. 5								2				
	Epuraea sp. 6						2						
	Epuraea sp. 7										83		
Cryptarchinae													
	Glischrochilus siepmanni										2*		
Phalacridae													

	Stilbus sp.												2
Ptiliidae													
	Ptiliid sp.												9
	Ptiliid sp. 2										1		
Ptinidae													
Dorcatominae													
	Caenocara sp.							5					
	Caenocara sp. 2						1						
	Caenocara sp. 3										3		
Pythidae												1	
	Priognathus monilicornis											1*	
Scarabaeidae													
Aphodiinae													
	Aegialia lacustris							1					1
Scirtidae													
	Cyphon sp.											1	
	Cyphon sp. 2												3
	Cyphon sp. 3									7			
Scydmaenidae													
Scydmaeninae													
	Scydmaenid sp.										1		
Silphidae													
	Nicrophorus defodiens									2	1		
	Thanatophilus lapponicus						4						
	Thanatophilus sagax						19			64	2		
Staphylinidae													
Aleocharinae													

Aleochara assiniboin										1*		
Aleocharine sp. 1		2										
Aleocharine sp. 2											16	
Aleocharine sp. 3											2	
Aleocharine sp. 4										3		
Aleocharine sp. 5												8
Aleocharine sp. 6									3			
Aleocharine sp. 7									1			
Aleocharine sp. 8							2					
Aleocharine sp. 9					1							
Aleocharine sp. 10												4
Aleocharine sp. 11									29			
Aleocharine sp. 12								4				
Aleocharine sp. 13						1						
Aleocharine sp. 14										34		
Aleocharine sp. 15							1					
Aleocharine sp. 16				1								
Aleocharine sp. 17					1							
Aleocharine sp. 18												20
Aleocharine sp. 19									4			
Aleocharine sp. 20						1						
Aleocharine sp. 21										4		
Aleocharine sp. 22							2					
Aleocharine sp. 23					1							
Aleocharine sp. 24												1
Aleocharine sp. 25									5			
Aleocharine sp. 26								5				

Aleocharine sp. 27						1						
Aleocharine sp. 28										6		
Aleocharine sp. 29					1							
Aleocharine sp. 30												1
Aleocharine sp. 31									12			
Aleocharine sp. 32								1				
Aleocharine sp. 33						4						
Aleocharine sp. 34										1		
Aleocharine sp. 35					1							
Aleocharine sp. 36												5
Aleocharine sp. 37									4			
Aleocharine sp. 38								3				
Aleocharine sp. 39										9		
Aleocharine sp. 40					1							
Aleocharine sp. 41												3
Aleocharine sp. 42									1			
Aleocharine sp. 43								29				
Aleocharine sp. 44										2		
Aleocharine sp. 45												4
Aleocharine sp. 46								1				
Aleocharine sp. 47												7
Aleocharine sp. 48									19			
Aleocharine sp. 49										7		
Aleocharine sp. 50												1
Aleocharine sp. 51									4			
Aleocharine sp. 52										7		
Gnypeta ashei	14											

Liogluta nigropolita				1								
Euaesthetinae												
Euaesthetus sp.												13
Omaliinae												
Acidota quadrata			12									
Eusphalerum sp.										1		
Eusphalerum sp. 2						34						
Olophrum latum			7									
Omaliine sp. 1						1						
Omaliine sp. 2											1	
Omaliine sp. 3							5					
Omaliine sp. 4					3							
Omaliine sp. 5												3
Omaliine sp. 6									1			
Omaliine sp. 7								10				
Omaliine sp. 8						1						
Omaliine sp. 9										3		
Omaliine sp. 10							1					
Omaliine sp. 11												2
Omaliine sp. 12									1			
Omaliine sp. 13								3				
Omaliine sp. 14						1						
Omaliine sp. 15										1		
Omaliine sp. 16							3					
Omaliine sp. 17									3			
Omaliine sp. 18								1				
Omaliine sp. 19						1						

	Omaliine sp. 20								2				
	Omaliine sp. 21						3						
	Omaliine sp. 22						3						
	Omaliine sp. 23						1						
	Omaliine sp. 24										2		
	Omaliine sp. 25										1		
Oxyporinae													
	Oxyporus sp.										1		
	Oxyporus sp. 2												8
Paederinae													
	Paederine sp.									34			
	Paederine sp. 2										42		
Piestinae													
	Piestine sp.											1	
Proteininae													
	Proteinine sp.									1			
	Proteinus sp. 2								3				
Pselaphinae													
	Pselaphine sp.											1	
	Pselaphine sp. 2												1
	Pselaphine sp. 3									2			
	Reichenbachia sp.												1
Scaphidiinae													
	Baeocera sp.											6	
Scydmaeninae													
	Brachycepsis sp.							2					
	Scydmaenid sp.								6				

Staphylininae												
Quedius fellmanii					2							
Staphylinine sp.												1
Staphylinine sp. 2							4					
Staphylinine sp. 3									8			
Staphylinine sp. 4						1						
Staphylinine sp. 5										5		
Staphylinine sp. 6							2					
Staphylinine sp. 7									4			
Staphylinine sp. 8						1						
Staphylinine sp. 9										9		
Staphylinine sp. 10												2
Staphylinine sp. 11									9			
Staphylinine sp. 12						4						
Staphylinine sp. 13										1		
Staphylinine sp. 14												4
Staphylinine sp. 15									4			
Staphylinine sp. 16						6						
Staphylinine sp. 17												2
Staphylinine sp. 18						7						
Staphylinine sp. 19												7
Staphylinine sp. 20												2
Staphylinine sp. 21												5
Staphylinine sp. 22												1
Tympanophorus puncticollis												1
Steninae												
Stenus sp.		1										

Stenus sp. 2			3									
Stenus sp. 3											2	
Stenus sp. 4							1					
Stenus sp. 5					4							
Stenus sp. 6												16
Stenus sp. 7									21			
Stenus sp. 8								2				
Stenus sp. 9						1						
Stenus sp. 10										6		
Stenus frigidus			1									
Tachyporinae												
Bryophacis arcticus					7		11					
Bryophacis smetanai										1		
Ischnosoma longicorne										3		
Ischnosoma pictum							1				10	
Ischnosoma splendidum										3		
Lordithon fungicola										3		
Mycetophorus nigrans					3*		5			1		
Mycetoporus smetanai										1		
Tachinus basalis						1						
Tachinus elongatus						3	3			6		
Tachyporus borealis										7		
Tachyporus nimbicola							1*					
Tachyporus nitidulus										3		
Tachyporus rulomus										5		
Tachyporine sp.				1								
Tachyporine sp. 2												4

Tachyporine sp. 3									3			
Tachyporine sp. 4								23				
Tachyporine sp. 5												6
Tachyporine sp. 6									7			
Tachyporine sp. 7								1				
Tachyporine sp. 8										1		
Tachyporine sp. 9												9
Tachyporine sp. 10									8			
Tachyporine sp. 11								1				
Tachyporine sp. 12							1					
Tachyporine sp. 13												1
Tachyporine sp. 14									3			
Tachyporine sp. 15								3				
Tachyporine sp. 16												3
Tachyporine sp. 17									12			
Tachyporine sp. 18								10				
Tachyporine sp. 19										1		
Tachyporine sp. 20									1			
Tachyporine sp. 21										1		
Tachyporine sp. 22								1				
Tachyporine sp. 23										10		
Tenebrionidae												
Stenochiinae												
Upis ceramboides										2		
Grand Total	14	702	1696	420	1180	701	674	423	998	714	381	1159

Appendix A2-2 Email received from Katie Galvin, Editorial Office staff of PLoS ONE, authorizing publication of the manusceipt (Chapter 4) in this thesis

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Actions
To:
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Dear Dr. Ernst,

Thank you for your email.

Congratulations on your recent acceptance. It is perfectly fine to include extracts of the manuscript in your thesis.

Please do let me know if you have any further questions, I'd be happy to help.

Kind regards,

Katie

Katie Galvin
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Hello,

thank you for this great news. I have contacted the press team regarding a planned press release.There is one other thing:

I have just completed my PhD and this paper represents a chapter of my thesis. I am in the process of finalizing my thesis for deposition, and would like to ask permission to include the text and figures of PONE-D-14-47392R2 in the thesis, but reformatted as a thesis chapter.

Thank you for considering this request.

_____
Crystal Ernst
Department of Natural Resource Sciences
McGill University, Macdonald Campus

Appendix 3: Supplementary materials for Chapter 5

Appendix A3-1 List of references used to generate functional trait matrix

Print references

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Encyclopaedia of Life http://eol.org/

World Spider Catalogue http://www.wsc.nmbe.ch/

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Experts consulted

R. Anderson (Canadian Museum of Nature; CNC), Y. Bousquet (Canadian National Collection of Insects, Arachnids and Nematodes; CNC), C. Buddle (McGill), A. Davies (CNC), H. Douglas (CNC), H. Goulet (CNC), J. Klimaszewski (Natural Resources Canada), L. Lesage (CNC), T. MacRae, S. Peck (CMN), and A. Smetana (CNC)

Appendix A3-2 Trait measures and codes for all taxa

Taxon	Biomass	Temp	Humidity	VegCover	Disp	Food	Mode	Subst
Acidota sp.	0.399	41.400	0.833	8.815	Br	In	Ac	LM
Aculepeira packardi	20.471	33.100	1.000	7.372	No	In	Or	PSt
Aegialia lacustris	10.384	41.800	0.000	10.740	Ma	Om	Ac	Dw
Agathidium sp. 1H	0.333	38.700	0.000	12.480	Ma	Fu	Ac	LP
Agathidium sp. 1N	0.333	43.200	0.000	7.250	Ma	Fu	Ac	LP
Agathidium sp. 1T	0.333	41.700	0.167	11.183	Ma	Fu	Ac	LP
Agathidium sp. 2T	0.333	41.700	0.000	11.167	Ma	Fu	Ac	LP
Agathidium sp. 3	0.333	43.200	0.167	7.265	Ma	Fu	Ac	LP
Agonum affine	8.172	43.200	1.000	9.507	Ma	In	Ac	GP
Agonum consimile	4.287	43.200	1.000	7.340	Ma	In	Ac	G
Agonum exaratum	3.320	41.400	1.000	9.035	Ma	In	Ac	G
Agonum gratiosum	6.819	43.200	0.910	7.982	Br	In	Ac	GP
Agonum metallescens	8.042	35.800	1.000	8.675	Ma	In	Ac	GP
Agonum mutatum	7.415	33.100	1.000	7.545	Po	In	Ac	GMP
Agonum quinquepunctatum	6.819	43.200	0.500	10.052	Po	In	Ac	G
Agonum superioris	4.829	35.800	1.000	8.606	Su	In	Ac	G
Agonum thoreyi	5.412	35.800	1.000	8.728	Ma	Om	Ac	GMP
Agriotes limosus	13.551	43.200	0.000	7.325	Ma	Pl	Ac	FP
Agyneta allosubtilis	0.171	43.200	0.333	9.441	Ba	In	Sw	LP
Agyneta olivacea	0.245	49.600	0.655	7.981	Ba	In	Sw	LP
Agyneta sp.1	0.245	44.700	0.574	11.931	Ba	In	Sw	LP
Aleochara assiniboin	0.233	42.600	1.000	7.782	Ma	In	Ac	DLM
Aleocharine sp. 10M	0.233	35.800	0.125	8.911	Ma	In	Ac	DLM
Aleocharine sp. 10N	0.233	43.200	1.000	7.711	Ma	In	Ac	DLM
Aleocharine sp. 10Y	0.233	42.600	0.000	7.472	Ma	In	Ac	DLM
Aleocharine sp. 11N	0.233	43.200	1.000	7.897	Ma	In	Ac	DLM
Aleocharine sp. 1B	0.233	34.900	0.500	5.624	Ma	In	Ac	DLM
Aleocharine sp. 1G	0.233	33.100	0.875	7.461	Ma	In	Ac	DLM
Aleocharine sp. 1H	0.233	38.700	1.000	12.108	Ma	In	Ac	DLM
Aleocharine sp. 1K	0.233	38.600	1.000	13.500	Ma	In	Ac	DLM
Aleocharine sp. 1M	0.233	35.800	0.000	8.740	Ma	In	Ac	DLM
Aleocharine sp. 1N	0.233	43.200	0.414	7.535	Ma	In	Ac	DLM
Aleocharine sp. 1S	0.233	36.700	0.500	8.399	Ma	In	Ac	DLM
Aleocharine sp. 1T	0.233	41.700	1.000	11.344	Ma	In	Ac	DLM
Aleocharine sp. 1Y	0.233	42.600	1.000	7.744	Ma	In	Ac	DLM
Aleocharine sp. 2H	0.233	38.700	0.000	12.480	Ma	In	Ac	DLM
Aleocharine sp. 2I	0.233	35.700	1.000	12.000	Ma	In	Ac	DLM
Aleocharine sp. 2K	0.233	38.600	1.000	12.000	Ma	In	Ac	DLM
Aleocharine sp. 2M	0.233	35.800	0.150	8.887	Ma	In	Ac	DLM
Aleocharine sp. 2N	0.233	43.200	0.000	7.250	Ma	In	Ac	DLM

Aleocharine sp. 2T	0.233	41.700	1.000	11.344	Ma	In	Ac	DLM
Aleocharine sp. 2Y	0.233	42.600	1.000	7.735	Ma	In	Ac	DLM
Aleocharine sp. 3H	0.233	38.700	0.500	12.426	Ma	In	Ac	DLM
Aleocharine sp. 3K	0.233	38.600	0.000	9.667	Ma	In	Ac	DLM
Aleocharine sp. 3M	0.233	35.800	0.000	9.000	Ma	In	Ac	DLM
Aleocharine sp. 3N	0.233	43.200	0.800	7.541	Ma	In	Ac	DLM
Aleocharine sp. 3S	0.233	36.700	1.000	8.401	Ma	In	Ac	DLM
Aleocharine sp. 3T	0.233	41.700	0.000	11.167	Ma	In	Ac	DLM
Aleocharine sp. 3Y	0.233	42.600	1.000	7.738	Ma	In	Ac	DLM
Aleocharine sp. 4G	0.233	33.100	0.500	7.491	Ma	In	Ac	DLM
Aleocharine sp. 4K	0.233	38.600	0.000	9.333	Ma	In	Ac	DLM
Aleocharine sp. 4M	0.233	35.800	0.000	9.000	Ma	In	Ac	DLM
Aleocharine sp. 4N	0.233	43.200	0.083	7.325	Ma	In	Ac	DLM
Aleocharine sp. 4S	0.233	36.700	1.000	8.384	Ma	In	Ac	DLM
Aleocharine sp. 4T	0.233	41.700	0.500	11.208	Ma	In	Ac	DLM
Aleocharine sp. 4Y	0.233	42.600	1.000	7.745	Ma	In	Ac	DLM
Aleocharine sp. 5K	0.233	38.600	0.000	9.667	Ma	In	Ac	DLM
Aleocharine sp. 5M	0.233	35.800	0.400	8.840	Ma	In	Ac	DLM
Aleocharine sp. 5N	0.233	43.200	0.750	7.727	Ma	In	Ac	DLM
Aleocharine sp. 5S	0.233	36.700	1.000	8.384	Ma	In	Ac	DLM
Aleocharine sp. 5Y	0.233	42.600	0.889	7.705	Ma	In	Ac	DLM
Aleocharine sp. 6K	0.233	38.600	0.000	9.667	Ma	In	Ac	DLM
Aleocharine sp. 6M	0.233	35.800	0.333	8.776	Ma	In	Ac	DLM
Aleocharine sp. 6N	0.233	43.200	0.000	7.250	Ma	In	Ac	DLM
Aleocharine sp. 6S	0.233	36.700	0.897	8.432	Ma	In	Ac	DLM
Aleocharine sp. 6Y	0.233	42.600	1.000	7.763	Ma	In	Ac	DLM
Aleocharine sp. 7M	0.233	35.800	0.000	8.840	Ma	In	Ac	DLM
Aleocharine sp. 7S	0.233	36.700	1.000	8.320	Ma	In	Ac	DLM
Aleocharine sp. 8M	0.233	35.800	0.143	8.681	Ma	In	Ac	DLM
Aleocharine sp. 8N	0.233	43.200	0.947	7.844	Ma	In	Ac	DLM
Aleocharine sp. 8Y	0.233	42.600	0.143	7.757	Ma	In	Ac	DLM
Aleocharine sp. 9M	0.233	35.800	1.000	8.606	Ma	In	Ac	DLM
Aleocharine sp. 9N	0.233	43.200	1.000	7.754	Ma	In	Ac	DLM
Aleocharine sp. 9Y	0.233	42.600	1.000	7.782	Ma	In	Ac	DLM
Alopecosa aculeata	12.192	43.200	0.352	7.616	No	In	Ac	GL
Alopecosa exasp.erans	11.812	41.400	0.429	6.475	No	In	Ac	GL
Alopecosa hirtipes	23.178	45.200	0.035	8.416	No	In	Ac	GL
Alopecosa pictilis	17.853	39.900	0.254	10.663	No	In	Ac	GL
Altica sp. 1	2.174	43.200	1.000	7.880	Ma	Le	Ac	P
Altica sp. 2	1.120	35.800	0.692	8.737	Ma	Le	Ac	P
Altica sp. 3	1.120	42.600	0.000	7.384	Ma	Le	Ac	P
Altica sp. 4	1.120	36.700	1.000	8.320	Ma	Le	Ac	P

Altica sp. 5	1.593	33.100	1.000	7.409	Ma	Le	Ac	P
Alticine sp. 1H	1.593	38.700	1.000	12.415	Ma	Le	Ac	P
Alticine sp. 1M	1.593	35.800	1.000	8.672	Ma	Le	Ac	P
Alticine sp. 2M	1.593	35.800	0.000	8.560	Ma	Le	Ac	P
Alticine sp. S	0.745	36.700	0.950	8.349	Ma	Le	Ac	P
Amara alpina	11.190	45.200	0.198	8.549	Po	Om	Ac	G
Amara erratica	6.476	43.200	1.000	7.880	Ma	Om	Ac	G
Amara hyperborea	17.182	43.200	0.022	8.284	Ma	Se	Ac	G
Amara laevipennis	4.115	43.000	0.000	7.682	Ma	Se	Ac	G
Amara littoralis	6.936	35.800	0.000	9.000	Ma	Om	Ac	G
Amara pseudobrunnea	2.759	43.200	0.200	8.442	Ma	Om	Ac	G
Amara torrida	13.717	43.200	0.500	8.440	Ma	Om	Ac	G
Amaurobiidae IM	0.102	40.300	0.444	7.765	Ba	In	Sw	DwLR
Ampedus nigrinus	11.653	43.200	0.000	7.500	Ma	Pl	Ac	FP
Ampedus pullus	3.873	43.200	0.000	7.500	Ma	Pl	Ac	FP
Anisosticta bitriangularis	0.745	43.200	0.889	8.544	Ma	In	Ac	GP
Anisotoma sp. 2	0.461	43.200	0.000	7.250	Ma	Fu	Ac	LP
Anthaxia inornata	2.871	43.200	0.655	7.695	Ma	Pn	Ac	F
Anthicus sp. 1	1.593	43.200	1.000	7.375	Ma	Om	Ac	F
Anthonomus nigrinus	2.157	43.200	0.000	7.250	Ma	Le	Ac	P
Antistea brunnea	1.147	35.800	0.167	8.699	No	In	Sw	L
Aphid	0.193	49.500	0.231	8.188	N	Sa	Pa	P
Aphileta misera	0.229	35.800	1.000	8.639	Ba	In	Sw	LP
Araneidae Immature	0.182	43.200	0.500	8.296	Ba	In	Or	PSt
Araneus groenlandicola	20.471	38.700	0.000	12.480	No	In	Or	PSt
Arctachaea sp.1	0.581	43.200	1.000	7.897	No	In	Sp	P
Arctella lapponica	0.296	43.400	0.571	10.696	Ba	In	Sp	LP
Arcterigone pilifrons	0.135	36.500	0.750	7.301	Ba	In	Sw	LP
Arctosa alpigena	6.855	44.800	0.411	8.227	No	In	Ac	GL
Arctosa emertoni	14.209	35.800	0.000	8.800	No	In	Ac	GL
Arctosa insignita	10.025	44.800	0.878	12.046	No	In	Ac	GL
Arctosa raptor	29.414	43.200	0.835	9.382	No	In	Ac	GL
Arctosa rubicunda	14.636	43.200	0.714	7.973	No	In	Ac	GL
Argenna obesa	0.465	43.200	0.904	7.856	No	In	Sp	LP
Ascoliocerus sanborni	4.646	41.700	0.688	11.280	Br	Pl	Ac	FP
Atomaria sp. 1M	0.461	35.800	0.000	8.853	Ma	Fu	Ac	GLPW
Atomaria sp. 2M	0.461	42.600	0.000	8.892	Ma	Fu	Ac	GLPW
Atomaria sp. M	0.461	35.800	0.000	8.989	Ma	Fu	Ac	GLPW
Atomaria sp. T	0.461	41.700	0.000	11.199	Ma	Fu	Ac	GLPW
Atomaria sp. Y	0.461	42.600	1.000	7.782	Ma	Fu	Ac	GLPW
Auchenorrhyncha Nymph	0.727	44.800	0.326	9.168	Br	Sa	Pa	P
Badister obtusus	3.031	43.200	0.250	7.934	Ma	In	Ac	L

Baeocera sp.	0.023	33.100	0.667	7.409	Ma	Fu	Ac	DL
Baryphyma groenlandicum	0.279	43.400	0.996	12.169	Ba	In	Sw	LP
Baryphyma kulczynskii	0.114	49.600	0.814	9.128	Ba	In	Sw	LP
Baryphyma trifonsaffine	0.171	36.700	1.000	8.434	Ba	In	Sw	LP
Bathyphantes brevipes	0.609	35.800	1.000	8.728	No	In	Sw	LP
Bathyphantes brevis	0.279	35.800	1.000	8.669	Ba	In	Sw	LP
Bathyphantes canadensis	0.147	35.800	1.000	8.669	Ba	In	Sw	LP
Bathyphantes gracilis	0.229	42.600	1.000	7.782	Ba	In	Sw	LP
Bathyphantes pallidus	0.316	43.200	0.950	8.437	Ba	In	Sw	LP
Bathyphantes simillimus	0.229	43.200	0.792	8.942	Ba	In	Sw	LP
Beckerus appressus	52.199	36.700	1.000	8.384	Ma	Pl	Ac	FP
Bembidion bimaculatum	3.948	35.800	0.000	9.000	Ma	In	Ac	G
Bembidion dilaticolle	3.948	35.800	0.000	9.000	Ma	In	Ac	G
Bembidion diligens	0.363	43.200	1.000	7.880	Ma	In	Ac	G
Bembidion forestriatum	0.688	42.600	0.778	8.613	Ma	In	Ac	GL
Bembidion grapei	1.531	36.700	0.000	8.200	Po	In	Ac	G
Bembidion morulum	0.557	43.200	0.982	7.882	Po	In	Ac	G
Bembidion quadratulum	0.902	33.100	1.000	7.372	Ma	In	Ac	G
Bembidion transparens	0.869	43.200	0.773	8.687	Po	In	Ac	GM
Bembidion versicolor	0.661	35.800	1.000	8.644	Ma	In	Ac	GP
Blethisa catenaria	14.408	38.600	0.889	12.815	Ma	In	Ac	G
Blethisa quadricollis	52.118	35.800	1.000	8.700	Ma	In	Ac	G
Brachycepsis sp.	0.029	38.700	0.000	12.480	Ma	In	Ac	DLM
Bradycellus neglectus	0.775	42.600	0.000	7.428	Ma	In	Ac	GP
Bradycellus nigrinus	2.502	35.800	1.000	8.714	Ma	In	Ac	GP
Bryophacis arcticus	0.233	40.400	0.167	11.539	Ma	In	Ac	DLM
Bryophacis smetanai	0.233	42.600	0.000	7.833	Ma	In	Ac	DLM
Byrrhus sp. 1	3.471	42.600	0.000	7.384	Ma	Mo	Ac	M
Byrrhus sp. 1S	8.374	36.700	0.000	8.389	Ma	Mo	Ac	M
Byrrhus sp. 2	3.471	42.600	1.000	7.782	Ma	Mo	Ac	M
Byrrhus sp. 2H	11.653	38.700	0.000	12.480	Ma	Mo	Ac	M
Byrrhus sp. 2K	11.653	38.600	0.667	11.500	Ma	Mo	Ac	M
Byrrhus sp. 2N	11.653	43.200	1.000	7.340	Ma	Mo	Ac	M
Byrrhus sp. 2T	11.653	41.700	0.789	11.288	Ma	Mo	Ac	M
Byrrhus sp. 3	3.471	42.600	1.000	7.782	Ma	Mo	Ac	M
Byrrhus sp. 3M	20.357	35.800	0.027	8.794	Ma	Mo	Ac	M
Byrrhus sp. 3T	20.357	41.700	1.000	11.344	Ma	Mo	Ac	M
Caelifera sp.	44.871	44.800	0.882	8.179	Ma	Le	Ac	P
Caelifera IM	12.413	43.200	0.450	8.511	Br	Le	Ac	P
Caenocara sp. 1H	0.041	38.700	0.000	12.547	Ma	Fu	Ac	DL
Caenocara sp. 1T	0.041	41.700	1.000	11.438	Ma	Fu	Ac	DL
Caenocara sp. 1Y	0.041	42.600	0.333	7.696	Ma	Fu	Ac	DL

Calathus ingratus	8.974	43.200	0.152	7.761	Po	In	Ac	GLP
Callilepis pluto	3.045	42.600	0.000	7.646	No	In	Ac	DwLR
Carabus chamissonis	34.210	44.800	0.099	10.070	Br	In	Ac	GL
Carabus granulatus	83.219	35.800	0.138	8.761	Br	In	Ac	GP
Carabus maeander	75.234	43.200	0.861	7.915	Po	In	Ac	GP
Carabus serratus	83.219	33.100	0.000	7.421	Po	In	Ac	G
Carabus taedatus	94.653	38.700	0.000	12.501	Br	In	Ac	GL
Carabus truncaticollis	45.426	41.700	0.390	11.227	Br	In	Ac	G
Carabus vietinghoffii	113.554	44.800	0.786	8.998	Br	In	Ac	G
Carorita limnaea	0.046	43.200	0.250	7.676	Ba	In	Sw	LP
Catops sp.	2.871	36.700	1.000	8.320	Ma	Ca	Ac	DL
Centromerus longibulbus	0.199	40.300	0.930	7.945	Ba	In	Sw	LP
Ceraticelus bulbosus	0.071	43.200	0.927	8.375	Ba	In	Sw	LP
Ceraticelus crassiceps	0.171	43.000	0.308	9.245	Ba	In	Sw	LP
Ceraticelus emertoni	0.079	35.800	0.000	8.560	Ba	In	Sw	LP
Ceraticelus laetabilis	0.095	35.800	1.000	8.728	Ba	In	Sw	LP
Ceraticelus laetus	0.378	35.800	1.000	8.728	No	In	Sw	LP
Ceraticelus rowensis	0.199	42.600	1.000	7.782	Ba	In	Sw	LP
Ceraticelus silus	0.105	36.700	0.667	8.436	Ba	In	Sw	LP
Ceraticelus similis	0.071	35.800	0.333	8.738	Ba	In	Sw	LP
Ceraticelus sp.1	0.087	42.600	0.500	7.627	Ba	In	Sw	LP
Ceratinella brunnea	0.135	43.200	0.519	8.402	Ba	In	Sw	LP
Ceratinella buna	0.087	36.700	0.000	8.440	Ba	In	Sw	LP
Ceratinella ornatula	0.199	40.300	0.429	8.480	Ba	In	Sw	LP
Ceratinella parvula	0.051	43.200	0.857	8.376	Ba	In	Sw	LP
Ceratinops latus	0.114	43.200	0.500	7.580	Ba	In	Sw	LP
Ceratinopsis labradorensis	0.199	43.200	0.936	8.275	Ba	In	Sw	LP
Ceratomegilla ulkei	5.174	41.700	0.143	11.622	Br	In	Ac	GP
Cercopidae	1.545	44.800	0.583	11.032	Ma	Sa	Ac	P
Cercyon sp. 1N	0.120	43.200	1.000	7.340	Ma	De	Ac	D
Cercyon sp. G	0.120	33.100	0.000	7.429	Ma	De	Ac	D
Cercyon sp. M	0.120	35.800	1.000	8.728	Ma	De	Ac	D
Chaetocnema sp. 1	0.461	43.200	1.000	7.340	Ma	Le	Ac	P
Chaetocnema sp. 2	0.461	35.800	0.000	8.800	Ma	Le	Ac	P
Chalcoscirtus alpicola	0.365	42.600	0.000	7.384	No	In	Ac	LP
Cheniseo hagnicultor	0.071	33.100	1.000	7.372	Ba	In	Sw	LP
Chlaenius alternatus	22.826	43.200	1.000	7.719	Ma	In	Ac	G
Chlaenius lithophilus	9.393	35.800	1.000	8.672	Ma	In	Ac	G
Chlaenius niger	26.701	35.800	1.000	8.606	Ma	In	Ac	GLW
Cicadellidae	1.194	49.600	0.339	8.982	Ma	Sa	Ac	P
Cicindela limbalis	32.468	43.200	1.000	7.880	Ma	In	Ac	G
Cicindela longilabris longilabris	32.468	43.200	0.000	7.250	Ma	In	Ac	G

Cicurina brevis	0.958	35.800	0.000	8.560	No	In	Sp	LP
Clivina fossor	3.471	35.800	0.000	8.752	Po	Om	Ac	GPS
Clubiona bryantae	0.050	43.200	0.750	8.129	Ba	In	Ac	LPR
Clubiona furcata	1.251	40.300	1.000	8.556	No	In	Ac	LPR
Clubiona kulczynskii	7.128	35.800	0.500	8.803	No	In	Ac	LPR
Clubiona norvegica	5.499	43.200	0.500	8.448	No	In	Ac	LPR
Clubiona opeongo	5.499	33.100	1.000	7.446	No	In	Ac	LPR
Clubiona praematura	1.050	38.700	0.500	12.386	No	In	Ac	LPR
Clubiona riparia	1.477	35.800	0.000	8.800	No	In	Ac	LPR
Clubiona trivialis	1.477	36.700	1.000	8.434	No	In	Ac	LPR
Clubionidae Immature	0.028	43.200	0.317	10.778	Ba	In	Ac	LPR
Cnephalocotes obscurus	0.124	43.200	0.227	7.737	Ba	In	Sw	LP
Coccinella hieroglyphica	1.120	43.200	1.000	7.897	Ma	In	Ac	GP
Coccinellid sp. 1	0.256	43.200	1.000	7.820	Ma	In	Ac	GP
Coccinellid sp. 10	0.256	33.100	0.000	7.404	Ma	In	Ac	GP
Coccinellid sp. 11	0.228	38.600	0.800	12.833	Ma	In	Ac	GP
Coccinellid sp. 2	0.188	43.200	0.500	7.573	Ma	In	Ac	GP
Coccinellid sp. 3	0.120	43.200	1.000	7.340	Ma	In	Ac	GP
Coccinellid sp. 4	0.256	43.200	0.500	7.565	Ma	In	Ac	GP
Coccinellid sp. 5	0.256	43.200	1.000	7.340	Ma	In	Ac	GP
Coccinellid sp. 6	0.256	42.600	0.000	7.563	Ma	In	Ac	GP
Coccinellid sp. 7	0.256	42.600	0.000	7.472	Ma	In	Ac	GP
Coccinellid sp. 8	0.256	41.700	0.000	11.028	Ma	In	Ac	GP
Coccinellid sp. 9	0.256	38.700	0.333	12.438	Ma	In	Ac	GP
Coccoidea	0.687	43.000	0.500	8.339	Ma	Sa	Pa	P
Coleoptera Larva	3.725	49.600	0.439	9.206	No	In	Ac	G
Collinsia plumosa	0.124	35.800	0.762	8.737	Ba	In	Sw	LP
Colon asperatum	0.256	35.800	0.269	8.616	Ma	Fu	Ac	L
Colon bidentatum	0.370	35.800	0.000	8.800	Ma	Fu	Ac	L
Colon dentatum	0.100	35.800	0.000	8.680	Ma	Fu	Ac	L
Colon oblongum	0.370	43.200	0.508	8.159	Ma	Fu	Ac	L
Colon politum	0.461	35.800	0.000	8.874	Ma	Fu	Ac	L
Coreidae	0.299	41.700	0.000	11.199	Ma	Sa	Ac	P
Corticaria sp.	0.120	43.200	0.389	7.501	Ma	Fu	Ac	LP
Corticaria sp. 1G	0.120	33.100	0.250	7.397	Ma	Fu	Ac	LP
Corticaria sp. 1K	0.120	38.600	0.000	9.333	Ma	Fu	Ac	LP
Corticaria sp. 1T	0.120	41.700	0.250	11.218	Ma	Fu	Ac	LP
Corticaria sp. 2T	0.120	41.700	0.000	11.199	Ma	Fu	Ac	LP
Corticaria sp. 3T	0.120	41.700	0.000	11.199	Ma	Fu	Ac	LP
Corticarina sp. 1	0.120	43.200	0.375	7.383	Ma	Fu	Ac	LP
Corylophid sp. 1	0.120	42.600	0.800	7.983	Ma	Fu	Ac	GLPW
Corylophid sp. 2	0.120	42.600	1.000	8.194	Ma	Fu	Ac	GLPW

Corylophid sp. 3	0.120	42.600	1.000	8.194	Ma	Fu	Ac	GLPW
Corylophid sp. 4	0.120	42.600	1.000	8.194	Ma	Fu	Ac	GLPW
Crepidodera sp.	0.745	35.800	0.250	8.780	Ma	Le	Ac	P
Cryptophagus sp. 1H	0.461	38.700	0.500	12.285	Ma	Fu	Ac	GLPW
Cryptophagus sp. 1N	0.461	43.200	0.164	7.392	Ma	Fu	Ac	GLPW
Cryptophagus sp. 1T	0.461	41.700	0.500	11.199	Ma	Fu	Ac	GLPW
Cryptophagus sp. 1Y	0.461	42.600	0.194	7.691	Ma	Fu	Ac	GLPW
Cryptophagus sp. 2N	0.461	43.200	0.000	7.250	Ma	Fu	Ac	GLPW
Cryptophagus sp. G	0.461	33.100	0.311	7.411	Ma	Fu	Ac	GLPW
Cryptophagus sp. S	0.461	36.700	0.778	8.420	Ma	Fu	Ac	GLPW
Curimopsis setulosa	0.745	42.600	0.000	7.384	Ma	Mo	Ac	M
Curimopsis sp. S	0.745	36.700	0.000	8.528	Ma	Mo	Ac	M
Curimopsis sp. T	0.745	41.700	0.333	11.133	Ma	Mo	Ac	M
Cybaeopsis euopla	0.581	43.200	0.500	8.176	No	In	Sw	DwLR
Cymindis unicolor	7.660	43.400	0.250	10.551	Br	In	Ac	G
Cyphon sp. 1G	2.871	33.100	1.000	7.446	Ma	De	Ac	DL
Cyphon sp. 1M	0.745	35.800	1.000	8.687	Ma	Om	Ac	DLP
Cyphon sp. 1N	0.745	43.200	1.000	7.885	Ma	Om	Ac	DLP
Cytilus alternatus	2.871	43.200	0.950	8.347	Ma	Mo	Ac	M
Dalopius pallidus	6.980	35.800	0.000	8.804	Ma	Pl	Ac	FP
Delphacidae	1.151	44.800	0.727	8.572	Br	Sa	Ac	P
Diacheila arctica	7.415	43.200	1.000	7.340	Ma	In	Ac	GM
Diacheila polita	6.936	41.700	0.563	11.274	Br	In	Ac	G
Dicheirotrichus cognatus	1.040	35.800	0.000	8.800	Ma	Om	Ac	GP
Dichelotarsus laevicollis	4.646	36.700	1.000	8.434	Ma	Pn	Ac	F
Dichelotarsus puberulus	4.646	40.300	0.857	8.382	Ma	Pn	Ac	F
Dichelotarsus sp. 1	4.646	38.700	0.483	12.256	Ma	Pn	Ac	F
Dictyna arundinacea	0.581	33.100	1.000	7.462	No	In	Sp	LP
Dictyna brevitarsus	0.753	43.200	1.000	7.672	No	In	Sp	LP
Dictyna major	0.581	35.800	0.000	9.000	No	In	Sp	LP
Dictynidae Immature	0.082	50.300	0.333	9.749	Ba	In	Sp	LP
Dicymbium elongatum	0.135	43.200	1.000	7.897	Ba	In	Sw	LP
Diplocentria bidentata	0.114	44.600	0.387	8.353	Ba	In	Sw	LP
Diplocentria perplexa	0.124	36.700	0.000	8.200	Ba	In	Sw	LP
Diplocentria rectangulata	0.051	40.000	0.000	8.368	Ba	In	Sw	LP
Diplocephalus barbiger	0.199	44.100	0.267	8.468	Ba	In	Sw	LP
Diplocephalus cristatus	0.245	35.800	1.000	8.606	Ba	In	Sw	LP
Diplopoda	1.333	48.300	0.000	8.500	No	De	Ac	L
Dipoena nigra	0.753	33.100	0.000	7.400	No	In	Sp	P
Dismodicus decemoculatus	0.171	35.800	1.000	8.606	Ba	In	Sw	LP
Dolomedes striatus	54.886	35.800	1.000	7.762	No	In	Ac	PRW
Dolomedes triton	79.934	35.800	1.000	8.728	No	In	Ac	PRW

Drassodes mirus	12.345	43.000	1.000	9.136	No	In	Ac	DwLR
Drassodes neglectus	12.607	43.200	0.167	7.426	No	In	Ac	DwLR
Dyschirius frigidus	0.869	41.700	0.000	11.028	Ma	Om	Ac	GMS
Dyschirius globulosus	0.557	42.600	0.000	7.833	Po	Om	Ac	GS
Dyschirius hiemalis	0.869	43.200	0.875	9.632	Ma	Om	Ac	GS
Dyschirius integer	0.869	35.800	1.000	8.652	Ma	Om	Ac	GS
Dyschirius melanocholicus	0.406	43.400	1.000	11.391	Br	Om	Ac	GMS
Dyschirius nigricornis	0.464	38.700	0.167	12.518	Br	Om	Ac	GS
Dyschirius subarcticus	0.775	41.700	1.000	11.438	Ma	Om	Ac	GS
Eanus decoratus	8.374	41.700	0.778	11.151	Ma	Pl	Ac	FP
Eanus maculipennis	3.693	40.000	1.000	7.665	Ma	Pl	Ac	FP
Elaphrus clairvillei	9.970	43.200	1.000	9.925	Ma	In	Ac	GP
Elaphrus fuliginosus	13.012	42.600	1.000	7.782	Ma	In	Ac	G
Elaphrus lapponicus	7.588	43.200	0.946	10.777	Ma	In	Ac	GM
Elaphrus lecontei	8.701	35.800	1.000	8.606	Ma	In	Ac	G
Ellescus ephippiatus	1.010	38.700	1.000	12.371	Ma	Le	Ac	P
Emblyna annulipes	0.958	44.600	0.833	8.367	No	In	Sp	LP
Emblyna borealis	0.438	44.100	0.059	8.685	No	In	Sp	LP
Emblyna phylax	0.581	33.100	1.000	7.643	No	In	Sp	LP
Enicmus sp. 1B	0.120	34.900	0.524	6.010	Ma	Fu	Ac	LP
Enicmus sp. 1G	0.120	33.100	0.000	7.383	Ma	Fu	Ac	LP
Enoplognatha caricis	0.872	42.600	0.750	7.998	No	In	Sp	P
Entelecara sombra	0.114	43.200	0.000	7.250	Ba	In	Sw	LP
Epuraea sp. 1G	1.593	33.100	0.000	7.280	Ma	Pn	Ac	FP
Epuraea sp. 1H	0.461	38.700	0.100	12.457	Ma	Sa	Ac	DLP
Epuraea sp. 1M	0.461	35.800	1.000	8.606	Ma	Sa	Ac	DLP
Epuraea sp. 1N	0.461	43.200	1.000	7.531	Ma	Sa	Ac	DLP
Epuraea sp. 1S	0.461	36.700	1.000	8.320	Ma	Sa	Ac	DLP
Epuraea sp. 1T	0.461	41.700	0.000	11.183	Ma	Sa	Ac	DLP
Epuraea sp. 1Y	0.461	42.600	0.964	7.729	Ma	Sa	Ac	DLP
Erigone arctica	0.497	41.400	0.639	7.268	No	In	Sw	LP
Erigone arctophylacis	0.378	35.800	1.000	8.666	No	In	Sw	LP
Erigone atra	0.356	43.200	1.000	8.653	No	In	Sw	LP
Erigone dentigera	0.297	43.200	0.915	8.762	Ba	In	Sw	LP
Erigone psychrophila	0.400	44.100	0.890	8.455	No	In	Sw	LP
Erigone sp.1	0.378	35.700	1.000	12.400	No	In	Sw	LP
Erigone tirolensis	0.356	35.700	1.000	10.960	No	In	Sw	LP
Estrandia grandaeva	0.423	38.700	1.000	10.140	No	In	Sw	LP
Euaesthetus sp. 1	0.023	35.800	1.000	8.690	Ma	In	Ac	DLM
Eucinetus haemorrhoidalis	1.120	43.200	0.333	7.405	Ma	Fu	Ac	BGL
Euryopis argentea	0.613	43.200	0.339	7.598	No	In	Sp	P
Eusphalerum sp. 1	0.049	42.600	1.000	7.782	Ma	Pn	Ac	F

Eusphalerum sp. T	0.049	41.700	0.706	11.291	Ma	Pn	Ac	F
Evarcha proszynskii	3.045	43.200	0.143	7.556	No	In	Ac	LP
Flatidae	3.570	43.200	0.000	7.500	Ma	Sa	Ac	P
Floricomus rostratus	0.124	38.700	1.000	8.827	Ba	In	Sw	LP
Formicidae	2.073	43.200	0.124	7.586	No	Om	Ac	G
Glischrochilus siepmanni	1.027	42.600	0.500	7.609	Ma	Sa	Ac	DLP
Glyphesis idahoanus	0.079	35.800	1.000	8.728	Ba	In	Sw	LP
Glyphesis scopulifer	0.057	43.200	0.800	8.233	Ba	In	Sw	LP
Glyptina sp.	0.745	43.200	1.000	7.897	Ma	Le	Ac	P
Gnaphosa borea	9.930	44.800	0.469	10.112	No	In	Ac	DwLR
Gnaphosa brumalis	15.745	44.800	0.079	8.704	No	In	Ac	DwLR
Gnaphosa microps	6.778	43.200	0.369	10.263	No	In	Ac	DwLR
Gnaphosa muscorum	23.979	43.200	0.029	7.894	No	In	Ac	DwLR
Gnaphosa orites	6.778	43.400	0.045	12.425	No	In	Ac	DwLR
Gnaphosa parvula	10.853	43.200	0.619	8.408	No	In	Ac	DwLR
Gnaphosidae Immature	0.716	44.800	0.381	9.224	No	In	Ac	DwLR
Gnypeta ashei	0.023	36.600	0.571	10.337	Ma	In	Ac	DL
Gonatium crassipalpum	0.279	43.200	0.471	10.211	Ba	In	Sw	LP
Grammonota angusta	0.702	43.200	0.000	7.325	No	In	Sw	LP
Grammonota gigas	0.356	40.300	0.791	8.431	No	In	Sw	LP
Grammonota maritima	0.996	43.000	0.889	11.360	No	In	Sw	LP
Grammonota sp.1	0.702	42.600	0.000	7.609	No	In	Sw	LP
Grypus equiseti	7.269	35.800	0.000	8.919	Ma	Le	Ac	P
Habronattus borealis	4.790	43.200	0.000	7.250	No	In	Ac	LP
Hahnia cinerea	0.369	42.600	0.000	7.685	Ba	In	Sw	L
Hahnia glacialis	0.453	43.200	0.000	8.211	No	In	Sw	L
Hahnia ononidum	0.319	43.200	0.000	7.358	Ba	In	Sw	L
Hahniidae Immature	0.102	43.200	0.060	8.511	Ba	In	Sw	L
Haplodrassus eunis	2.947	43.200	0.000	7.404	No	In	Ac	DwLR
Haplodrassus hiemalis	6.608	44.800	0.679	10.127	No	In	Ac	DwLR
Haplodrassus signifer	9.275	43.200	0.079	8.055	No	In	Ac	DwLR
Harpalus nigritarsis	7.902	43.200	1.000	9.015	Ma	Om	Ac	G
Harpalus pleuritieus	9.824	43.200	1.000	7.880	Ma	In	Ac	GP
Harpalus solitaris	6.254	43.200	0.500	7.676	Ma	In	Ac	G
Heteroptera Nymph	0.255	49.600	0.294	8.983	Br	Sa	Ac	P
Hilaira canaliculata	0.639	43.200	1.000	9.397	No	In	Sw	LP
Hilaira herniosa	0.497	43.200	0.375	9.370	No	In	Sw	LP
Hilaira proletaria	0.996	41.400	1.000	8.431	No	In	Sw	LP
Hilaira vexatrix	0.702	42.100	0.696	9.260	No	In	Sw	LP
Hippodamia sp. 1	1.593	36.700	0.000	8.320	Ma	In	Ac	GP
Hippodamia sp. 2	3.693	42.600	1.000	7.745	Ma	In	Ac	GP
Histeridae sp. 1	6.980	33.100	1.000	7.643	Ma	In	Ac	GL

Hogna frondicola	24.950	40.000	0.000	7.536	No	In	Ac	GL
Horcotes quadricristatus	0.095	43.400	0.032	8.984	Ba	In	Sw	LP
Hybauchenidium aquilonare	0.199	43.400	0.887	6.691	Ba	In	Sw	LP
Hybauchenidium gibbosum	0.497	36.700	0.035	8.366	No	In	Sw	LP
Hydnobius sp.	0.256	35.800	0.000	8.800	Ma	Fu	Ac	LS
Hydraena sp. 1	2.871	38.700	1.000	12.415	Ma	Om	Ac	DGLM
Hylesinine sp.	0.965	42.600	0.000	7.384	Ma	Lw	Ac	BP
Hylobius congener	13.903	33.100	0.000	7.395	Ma	Le	Ac	P
Hypera diversipunctata	8.115	43.400	0.000	10.266	Br	Le	Ac	P
Hypera sp. C	4.820	41.400	0.000	8.319	Br	Le	Ac	P
Hypera sp. T	5.975	41.700	1.000	11.232	Br	Le	Ac	P
Hypnoidus abbreviatus	4.646	35.800	0.000	8.704	Ma	Pl	Ac	FP
Hypnoidus bicolor	2.871	43.200	0.350	8.606	Ma	Pl	Ac	FP
Hypnoidus rivularius	3.025	43.200	1.000	9.286	Ma	Pl	Ac	FP
Hypomma subarcticum	0.199	42.600	1.000	7.745	Ba	In	Sw	LP
Hypselistes florens	0.447	43.200	1.000	7.880	No	In	Sw	LP
Hypselistes semiflavus	0.199	43.200	1.000	7.340	Ba	In	Sw	LP
Hypsosinga groenlandica	1.147	43.200	0.450	10.854	No	In	Or	PSt
Hypsosinga pygmaea	0.581	43.200	1.000	8.150	No	In	Or	PSt
Hypsosinga rubens	0.521	43.200	0.357	7.451	No	In	Or	PSt
Improphantes complicatus	8.269	43.000	0.111	9.551	No	In	Sw	LP
Incestophantes washingtoni	8.269	43.000	0.500	8.710	No	In	Sw	LP
Ischnosoma pictum	0.233	41.500	0.182	7.917	Ma	In	Ac	DL
Ischnosoma splendidum	0.233	42.600	1.000	7.782	Ma	In	Ac	DL
Ischnosoma timbriatum	0.233	42.600	1.000	7.770	Ma	In	Ac	DL
Islandiana falsifica	0.229	43.200	0.600	9.567	Ba	In	Sw	LP
Islandiana longisetosa	0.105	35.800	0.353	8.803	Ba	In	Sw	LP
Islandiana princeps	0.105	38.700	1.000	12.415	Ba	In	Sw	LP
Isochnus arcticus	0.611	41.400	0.120	6.186	Br	Le	Ac	P
Ivielum sibiricum	0.135	41.700	0.000	11.071	Ba	In	Sw	LP
Kaestneria pullata	0.199	43.200	0.444	8.682	Ba	In	Sw	LP
Kaestneria rufula	0.199	43.200	1.000	8.147	Ba	In	Sw	LP
Lampyrid sp. 1M	9.930	35.800	0.000	8.800	Ma	Nf	Nf	P
Lampyrid sp. 1S	6.980	36.700	1.000	8.320	Ma	Nf	Nf	P
Lampyrid sp. 2	4.646	35.800	0.000	8.800	Ma	Nf	Nf	P
Larinioides cornutus	9.063	35.800	0.500	8.186	No	In	Or	PSt
Lathys pallida	0.102	42.600	0.000	7.472	Ba	In	Sp	LP
Latridius sp. 1C	0.120	41.400	0.000	8.500	Ma	Fu	Ac	LP
Latridius sp. 1N	0.120	43.200	0.000	7.500	Ma	Fu	Ac	LP
Leiodes assimilis	1.120	35.800	0.000	8.560	Ma	Fu	Ac	LS
Leiodes neglecta	1.120	35.800	0.000	8.609	Ma	Fu	Ac	LS
Leiodes punctostriata	1.120	43.200	0.786	7.761	Ma	Fu	Ac	LS

Leiodes sp. 1M	1.120	35.800	0.000	8.560	Ma	Fu	Ac	LS
Leiodes sp. 1M F	1.120	35.800	0.000	8.661	Ma	Fu	Ac	LS
Leiodes sp. 1N	1.120	43.200	0.000	7.250	Ma	Fu	Ac	LS
Lepidophorus lineatocollis	3.801	43.200	0.000	7.390	Br	Le	Ac	P
Lepidoptera Larva	7.657	49.600	0.446	9.772	No	Le	Ac	P
Lepthyphantes alpinus	0.229	43.200	0.571	9.093	Ba	In	Sw	LP
Lepthyphantes zebra	0.199	38.700	1.000	12.415	Ba	In	Sw	LP
Lepyrus gemellus	60.844	38.600	1.000	12.000	Br	Le	Ac	P
Lepyrus nordenskioeldi	29.622	43.400	0.100	10.803	Br	Le	Ac	P
Lepyrus sp. C	29.622	41.400	0.200	8.417	Br	Le	Ac	P
Lepyrus sp. H	29.622	38.700	0.333	12.378	Br	Le	Ac	P
Lepyrus sp. N	29.622	43.200	0.500	7.565	Br	Le	Ac	P
Lepyrus sp. T	29.622	41.700	0.000	11.167	Br	Le	Ac	P
Limonius aeger	4.646	33.100	0.000	7.400	Ma	Pl	Ac	FP
Linyphiidae Immature	0.038	50.300	0.692	9.063	Ba	In	Sw	LP
Liogluta nigropolita	0.233	35.700	1.000	12.000	Ma	In	Ac	DL
Listronotus humilis	2.596	41.500	1.000	9.930	Br	Le	Ac	P
Lithobiidae Immature	3.687	41.700	0.595	11.232	No	In	Ac	Litter
Lordithon fungicola	0.233	42.600	0.333	7.790	Ma	In	Ac	DL
Loricera pilicornis	6.819	38.700	1.000	12.371	Ma	In	Ac	GP
Lycosidae Immature	1.050	50.300	0.530	9.703	No	In	Ac	GL
Lygaeidae Immature	1.077	43.200	0.182	7.469	Ma	Se	Ac	P
Mantura sp.	1.593	43.200	1.000	7.340	Ma	Le	Ac	P
Masikia indistincta	0.159	41.400	0.957	6.569	Ba	In	Sw	LP
Mecynargus borealis	0.071	40.400	0.417	12.029	Ba	In	Sw	LP
Mecynargus monticola	0.124	38.600	0.800	12.233	Ba	In	Sw	LP
Mecynargus paetulus	0.124	45.400	0.750	7.626	Ba	In	Sw	LP
Mecynargus sphagnicola	0.159	43.400	1.000	10.753	Ba	In	Sw	LP
Mecynargus tungusicus	0.105	41.700	0.000	11.167	Ba	In	Sw	LP
Megasternum sp.	0.120	35.800	1.000	8.672	Ma	De	Ac	D
Meioneta amersaxatilis	0.297	49.600	0.750	9.241	Ba	In	Sw	LP
Meioneta fabra	0.245	38.700	0.333	12.680	Ba	In	Sw	LP
Meioneta jacksoni	0.199	43.000	0.218	9.115	Ba	In	Sw	LP
Meioneta maritima	0.105	48.200	0.211	7.815	Ba	In	Sw	LP
Meioneta nigripes	0.171	36.500	0.000	9.152	Ba	In	Sw	LP
Meioneta simplex	0.135	44.800	0.605	7.879	Ba	In	Sw	LP
Melanophthalma sp. 1N	0.120	43.200	0.333	7.464	Ma	Fu	Ac	LP
Melanophthalma sp. 1Y	0.120	42.600	0.538	7.710	Ma	Fu	Ac	LP
Melanophthalma sp. G	0.120	33.100	0.000	7.400	Ma	Fu	Ac	LP
Melanophthalma sp. M	0.120	35.800	0.286	8.745	Ma	Fu	Ac	LP
Melanthaxia inornata	2.648	43.200	1.000	7.897	Ma	Le	Ac	P
Mermessus entomologicus	0.027	40.000	0.941	7.578	Ba	In	Sw	LP

Mermessus tridentata	0.297	40.000	0.750	8.181	Ba	In	Sw	LP
Mermessus undulatus	0.147	43.200	0.800	9.093	Ba	In	Sw	LP
Metopobactrus prominulus	0.124	44.800	0.718	12.129	Ba	In	Sw	LP
Micaria aenea	1.147	43.200	0.125	7.408	No	In	Ac	DwLR
Micaria alpina	0.958	43.200	0.606	11.655	No	In	Ac	DwLR
Micaria constricta	2.324	38.700	0.200	12.550	No	In	Ac	DwLR
Micaria pulicaria	0.958	43.200	0.879	8.678	No	In	Ac	DwLR
Micaria rossica	2.324	43.200	0.767	7.661	No	In	Ac	DwLR
Microlinyphia dana	0.159	42.600	1.000	7.724	Ba	In	Sw	LP
Microlinyphia mandibulata	1.463	35.800	1.000	8.672	No	In	Sw	LP
Microlinyphia pusilla	1.742	35.800	1.000	8.672	No	In	Sw	LP
Microneta viaria	0.279	43.200	0.500	7.348	Ba	In	Sw	LP
Miridae	0.663	44.600	0.250	10.375	Ma	Sa	Ac	P
Misumena vatia	4.147	43.200	0.500	7.311	No	In	Am	FP
Mordellochroa scapularis	1.120	43.200	0.000	7.250	Ma	Pl	Ac	DwLP
Muscidae Larva	1.715	43.300	0.000	9.745	No	De	Ac	Litter
Mycetoporus nigrans	0.491	44.700	0.333	11.324	Ma	In	Ac	DL
Mycetoporus smetanai	0.491	42.600	1.000	7.782	Ma	In	Ac	DL
Nabidae	3.591	35.800	0.000	8.680	Ma	In	Am	P
Nebria gyllenhali	14.445	36.700	0.000	8.469	Ma	In	Ac	G
Negastrius arnetti	0.745	35.800	0.000	8.560	Ma	Pl	Ac	FP
Neoantistea agilis	0.550	33.100	0.000	7.327	No	In	Sw	L
Neoantistea magna	1.147	35.800	0.000	8.875	No	In	Sw	L
Neogalerucella pusilla	1.593	41.800	0.800	9.531	Ma	Le	Ac	P
Neohypdonus gentilis	0.813	35.800	0.000	9.000	Ma	Pl	Ac	FP
Neriene clathrata	1.570	42.600	1.000	7.745	No	In	Sw	LP
Nicrophorus defodiens	48.428	43.200	1.000	7.832	Ma	In	Ac	DL
Notaris aethiops	8.115	43.200	0.917	8.776	Ma	Le	Ac	P
Notiophilus aquaticus	3.102	36.700	0.000	8.200	Po	In	Ac	G
Notiophilus borealis	2.045	43.400	0.154	10.362	Po	In	Ac	GM
Notiophilus intermedius	1.771	43.200	0.000	7.361	Br	In	Ac	G
Notiophilus semistriatus	2.202	42.600	0.000	7.614	Po	In	Ac	GMP
Oedothorax trilobatus	0.316	43.200	0.931	8.097	Ba	In	Sw	LP
Olophrum latum	0.372	41.400	0.571	8.770	Br	In	Ac	DL
Omaliine sp. 1G	0.049	33.100	1.000	7.643	Br	In	Ac	DL
Omaliine sp. 1H	0.049	38.700	1.000	12.406	Br	In	Ac	DL
Omaliine sp. 1K	0.049	38.600	1.000	13.500	Br	In	Ac	DL
Omaliine sp. 1M	0.049	35.800	0.000	8.720	Br	In	Ac	DL
Omaliine sp. 1N	0.049	43.200	0.000	7.250	Br	In	Ac	DL
Omaliine sp. 1S	0.049	36.700	0.100	8.398	Br	In	Ac	DL
Omaliine sp. 1T	0.049	41.700	1.000	11.232	Br	In	Ac	DL
Omaliine sp. 1Y	0.049	42.600	1.000	7.782	Br	In	Ac	DL

Omaliine sp. 2H	0.049	38.700	0.000	12.400	Br	In	Ac	DL
Omaliine sp. 2M	0.049	35.800	0.000	8.900	Br	In	Ac	DL
Omaliine sp. 2N	0.049	43.200	0.000	7.250	Br	In	Ac	DL
Omaliine sp. 2S	0.049	36.700	1.000	8.434	Br	In	Ac	DL
Omaliine sp. 2T	0.049	41.700	0.000	11.199	Br	In	Ac	DL
Omaliine sp. 2Y	0.049	42.600	0.000	7.384	Br	In	Ac	DL
Omaliine sp. 3H	0.049	38.700	1.000	12.386	Br	In	Ac	DL
Omaliine sp. 3N	0.049	43.200	1.000	7.891	Br	In	Ac	DL
Omaliine sp. 3S	0.049	36.700	1.000	8.434	Br	In	Ac	DL
Omaliine sp. 3T	0.049	41.700	0.000	11.167	Br	In	Ac	DL
Omaliine sp. 4S	0.049	36.700	0.000	8.484	Br	In	Ac	DL
Omaliine sp. 4T	0.049	41.700	0.333	11.257	Br	In	Ac	DL
Omaliine sp. 5T	0.049	41.700	1.000	11.316	Br	In	Ac	DL
Omaliine sp. 6T	0.049	41.700	1.000	11.438	Br	In	Ac	DL
Omalline sp. 3Y	0.049	42.600	0.000	7.472	Br	In	Ac	DL
Opiliones	1.457	35.800	1.000	8.606	No	De	Ac	Litter
Oreoneta beringiana	1.360	35.700	1.000	10.960	No	In	Sw	LP
OReoneta brunnea	0.804	40.400	0.429	11.168	No	In	Sw	LP
Oreoneta sp.1	0.996	35.700	1.000	12.000	No	In	Sw	LP
Oreonetides flavescens	0.171	33.100	0.667	7.522	Ba	In	Sw	LP
Oreonetides rectangulatus	0.261	43.200	0.400	8.533	Ba	In	Sw	LP
Oreonetides vaginatus	0.916	43.200	0.300	7.897	No	In	Sw	LP
Oreophantes recurvatus	0.804	35.800	1.000	8.672	No	In	Sw	LP
Otiorhynchus ovatus	1.304	33.100	0.000	7.468	Br	Le	Ac	P
Oxyporus occipitalis	3.477	42.600	0.000	7.833	Ma	Fu	Ac	DL
Oxyporus sp. 1M	3.477	35.800	1.000	8.728	Ma	Fu	Ac	DL
Ozyptila arctica	0.958	43.400	0.571	11.453	No	In	Am	LR
Ozyptila curvata	0.958	35.800	1.000	8.672	No	In	Am	LR
Ozyptila gertschi	1.198	43.200	0.333	8.511	No	In	Am	LR
Ozyptila praticola	0.958	38.700	0.000	12.400	No	In	Am	LR
Ozyptila sinceracanadensis	0.438	43.200	0.555	7.677	No	In	Am	LR
Pachygnatha clerckii	3.566	49.600	0.923	8.425	No	In	Or	LPR
Paederine sp. 1N	0.901	43.200	1.000	7.839	Ma	In	Ac	DLM
Paederine sp. 1Y	0.901	42.600	1.000	7.773	Ma	In	Ac	DLM
Pardosa albomaculata	17.369	36.700	0.000	8.440	No	In	Ac	GL
Pardosa algens	10.542	49.500	0.949	8.432	No	In	Ac	GL
Pardosa concinna	5.722	44.800	0.387	11.677	No	In	Ac	GL
Pardosa furcifera	9.525	43.000	0.598	10.832	No	In	Ac	GL
Pardosa fuscula	9.041	43.200	0.940	8.679	No	In	Ac	GL
Pardosa glacialis	6.722	45.900	0.563	11.676	No	In	Ac	GL
Pardosa groenlandica	14.852	42.600	0.000	7.472	No	In	Ac	GL
Pardosa hyperborea	2.824	43.200	0.557	7.991	No	In	Ac	GL

Pardosa labradorensis	5.841	41.700	0.111	8.650	No	In	Ac	GL
Pardosa mackenziana	5.488	43.200	0.083	7.431	No	In	Ac	GL
Pardosa modica	3.220	43.200	1.000	7.340	No	In	Ac	GL
Pardosa moesta	3.220	43.200	0.684	8.165	No	In	Ac	GL
Pardosa podhorskii	10.196	43.400	0.990	13.136	No	In	Ac	GL
Pardosa rubicunda	14.636	35.800	0.000	8.560	No	In	Ac	GL
Pardosa sodalis	8.269	43.400	0.903	11.829	No	In	Ac	GL
Pardosa uintana	4.716	43.200	0.523	8.073	No	In	Ac	GL
Pardosa xerampelina	5.841	43.200	0.487	8.155	No	In	Ac	GL
Patrobus foveocollis	12.668	42.600	0.250	8.196	Po	In	Ac	GLS
Patrobus longicornis	26.701	35.800	0.000	9.000	Po	Om	Ac	G
Patrobus septentrionis	13.361	43.200	0.692	7.965	Ma	In	Ac	G
Patrobus stygicus	13.897	43.200	1.000	7.891	Ma	In	Ac	GM
Pelecopsis mengei	0.147	43.200	1.000	7.805	Ba	In	Sw	LP
Pelegrina montana	4.397	35.800	0.667	8.711	No	In	Ac	LP
Pellenes montanus	3.247	43.200	0.000	7.250	No	In	Ac	LP
Pentatomidae	2.908	43.200	0.176	7.551	Ma	In	Ac	PG
Perregrinus deformis	0.105	42.600	1.000	7.830	Ba	In	Sw	LP
Phaenonotum sp. 1N	2.871	43.200	1.000	7.880	Ma	De	Ac	D
Phaenonotum sp. 1S	2.871	36.700	1.000	8.384	Ma	De	Ac	D
Phidippus whitmani	26.536	43.200	0.000	7.340	No	In	Ac	LP
Philodromidae Immature	1.477	44.800	0.385	11.756	No	In	Ac	P
Philodromus alascensis	3.458	36.700	0.000	8.440	No	In	Ac	P
Philodromus cesp.itum	2.758	42.600	1.000	7.782	No	In	Ac	P
Phlattothrata parva	0.057	43.200	1.000	7.897	Ba	In	Sw	LP
Pidonia scripta	9.930	42.600	0.000	7.472	Ma	Pn	Ac	F
Pirata bryantae	1.714	43.200	0.909	8.226	No	In	Ac	GL
Pirata canadensis	0.930	35.800	0.000	8.857	No	In	Ac	GL
Pirata cantralli	2.675	43.200	0.732	8.424	No	In	Ac	GL
Pirata piraticus	4.112	43.200	0.869	8.791	No	In	Ac	GL
Pissodes nemorensis	7.269	33.100	0.000	7.328	Ma	Lw	Ac	P
Pityohyphantes subarcticus	3.659	35.800	1.000	8.606	No	In	Sw	LP
Pityokteines sp. 1	1.524	42.600	0.000	7.472	Ma	Lw	Ac	BP
Platycerus sp. 1	1.120	42.600	0.000	7.384	Ma	Fu	Ac	LS
Platynus decentis	21.617	35.800	1.000	8.728	Su	In	Ac	GLPS
Platynus mannerheimii	8.974	40.300	1.000	8.595	Su	In	Ac	GMP
Pocadicnemis americana	0.171	43.200	0.200	7.757	Ba	In	Sw	LP
Poeciloneta vakkhanka	0.378	41.700	0.000	11.199	No	In	Sw	LP
Poeciloneta variegata	0.378	38.700	1.000	12.415	No	In	Sw	LP
Poecilus lucublandis	19.321	35.800	0.000	9.000	Su	In	Ac	GPS
Priognathus monilicornis	0.041	33.100	1.000	7.643	Ma	Fu	Ac	DL
Procas lecontei	7.269	42.600	0.000	7.833	Ma	Le	Ac	P

Proteinine sp. 1N	0.023	43.200	0.000	7.500	Ma	De	Ac	DL
Proteinus sp. 1S	0.023	36.700	0.000	8.389	Ma	De	Ac	DL
Pselaphine sp. 1G	0.023	33.100	1.000	7.372	Ma	In	Ac	DLM
Pselaphine sp. 1M	0.009	35.800	1.000	8.606	Ma	In	Ac	DLM
Pselaphine sp. 1N	0.009	43.200	1.000	7.619	Ma	In	Ac	DLM
Pseudanostirus ochreipennis	6.466	42.600	0.000	7.833	Ma	Pl	Ac	FP
Pseudanostirus triundulatus	25.884	42.600	0.143	7.604	Ma	Pl	Ac	FP
Pseudoscorpionida	0.343	35.800	0.000	8.560	No	In	Ac	Litter
Psyllidae	0.582	49.600	0.111	8.854	Ma	Sa	Ac	P
Pterostichus adstrictus	14.261	43.200	0.128	7.936	Ma	In	Ac	GLP
Pterostichus arcticola	3.865	41.700	0.762	11.108	Ma	In	Ac	GLP
Pterostichus barryorum	5.352	38.600	0.000	9.333	Br	In	Ac	G
Pterostichus brevicornis	3.217	48.200	0.255	11.280	Br	In	Ac	GL
Pterostichus caribou	7.687	45.200	0.371	9.076	Br	In	Ac	G
Pterostichus haematopus	15.389	44.800	0.442	10.802	Po	In	Ac	G
Pterostichus hudsonicus	7.366	38.600	0.000	9.333	Br	In	Ac	G
Pterostichus melanarius	42.472	35.800	0.123	8.864	Po	In	Ac	GP
Pterostichus parasimilis	3.085	41.700	0.500	11.253	Br	In	Ac	G
Pterostichus patruelis	5.213	43.200	1.000	8.237	Po	In	Ac	GLMPW
Pterostichus pensylvanicus	14.261	43.200	0.640	7.688	Ma	In	Ac	GLP
Pterostichus pinguedineus	6.036	36.700	0.000	8.200	Br	In	Ac	G
Pterostichus punctatissimus	50.090	43.200	0.856	10.668	Br	In	Ac	GLP
Pterostichus tareumiut	4.287	34.900	0.365	5.957	Br	In	Ac	G
Pterostichus tenuis	13.361	35.800	1.000	8.700	Ma	In	Ac	GM
Pterostichus vermiculosus	26.864	43.400	1.000	13.115	Br	In	Ac	G
Ptiliid sp. 1M	0.119	35.800	0.000	8.667	Ma	Fu	Ac	DL
Ptiliid sp. 1Y	0.041	42.600	0.000	7.472	Ma	Fu	Ac	DL
Quedius fellmanii	1.894	38.600	0.000	9.333	Ma	In	Ac	DLM
Reduviidae	2.814	43.200	0.692	7.902	Ma	In	Am	P
Reichenbachia sp.	0.009	35.800	1.000	8.672	Ma	In	Ac	DLM
Rhagium inquisitor	61.896	33.100	0.000	7.468	Ma	Pl	Ac	GP
Rhagonycha fraxini	2.871	35.800	1.000	7.544	Ma	Pn	Ac	F
Rhagonycha mandibularis	2.871	38.700	0.333	12.365	Ma	Pn	Ac	F
Rhagonycha sp. 1K	2.871	38.600	1.000	12.750	Ma	Pn	Ac	F
Rhyncolus brunneus	1.524	42.600	0.000	7.833	Ma	Lw	Ac	BP
Robertus borealis	0.389	35.800	0.800	8.172	No	In	Sp	LP
Robertus fuscus	0.613	43.200	0.692	7.665	No	In	Sp	LP
Rugathodes aurantius	0.254	35.800	1.000	8.728	Ba	In	Sp	L
Saldidae	2.119	49.600	0.900	6.422	Ma	In	Ac	G
Saldidae Nymph	0.876	48.300	1.000	8.089	Br	In	Ac	G
Salticidae Immature	0.182	43.200	0.514	9.168	Ba	In	Ac	LP
Satilatlas carens	0.229	38.600	0.833	12.056	Ba	In	Sw	LP

Satilatlas gertschi	0.124	42.600	1.000	7.703	Ba	In	Sw	LP
Satilatlas marxii	0.213	38.700	0.500	12.163	Ba	In	Sw	LP
Scaphinotus bilobus	26.701	35.800	0.000	8.800	Br	In	Ac	GLMPS
Sciaphilus asperatus	5.975	35.800	0.000	9.000	Ma	Le	Ac	P
Sciastes dubius	0.472	36.700	0.000	8.440	No	In	Sw	LP
Sciastes mentasta	0.378	43.200	1.000	7.340	No	In	Sw	LP
Sciastes truncatus	0.199	43.200	0.368	7.539	Ba	In	Sw	LP
Scironis tarsalis	0.114	43.200	1.000	7.892	Ba	In	Sw	LP
Scolytine sp. 1	1.524	33.100	0.000	7.400	Ma	Lw	Ac	BP
Scotinotylus pallidus	0.071	33.100	1.000	7.372	Ba	In	Sw	LP
Scotinotylus sacer	0.124	43.200	0.200	7.826	Ba	In	Sw	LP
Scydmaenid sp.	0.114	42.600	0.857	8.251	Ma	In	Ac	DLM
Scyletria inflata	0.124	35.800	0.893	8.684	Ba	In	Sw	LP
Selatosomus aeripennis	21.397	42.600	0.000	7.426	Ma	Pl	Ac	FP
Semljicola beringianus	0.159	48.200	0.996	6.314	Ba	In	Sw	LP
Semljicola obtusus	0.087	38.700	0.286	9.024	Ba	In	Sw	LP
Sergiolus montanus	6.115	35.800	1.000	8.672	No	In	Ac	DwLR
Sericus incongruus	8.374	43.200	0.727	7.652	Ma	Pl	Ac	FP
Setasomus aratus	8.374	42.600	0.000	7.833	Ma	Pl	Ac	FP
Siagonium punctatum	0.491	33.100	0.000	7.400	Ma	Fu	Ac	DLM
Silometopoides pampia	0.229	50.200	0.368	10.288	Ba	In	Sw	LP
Simplocara sp. 1	0.461	38.700	0.000	12.400	Ma	Mo	Ac	M
Sisicottus montanus	0.124	36.700	0.133	8.369	Ba	In	Sw	LP
Sisicottus quoylei	0.124	36.700	0.000	8.528	Ba	In	Sw	LP
Sisicus penifusifer	0.027	33.100	0.000	7.280	Ba	In	Sw	LP
Sisis rotundus	0.199	43.200	0.143	8.054	Ba	In	Sw	LP
Sitona lineellus	3.431	43.200	1.000	7.880	Br	Le	Ac	P
Sitticus cutleri	3.247	43.200	1.000	7.340	No	In	Ac	LP
Sitticus floricolapalustris	3.566	36.700	1.000	8.320	No	In	Ac	LP
Sitticus ranieri	3.908	43.200	0.143	8.153	No	In	Ac	LP
Sitticus striatus	1.418	43.200	1.000	10.122	No	In	Ac	LP
Sphaeroderus stenostomus	32.468	35.800	0.000	8.704	Br	In	Ac	GLP
Sphenophorus costipennis	34.676	35.800	1.000	8.672	Br	Le	Ac	P
Staphylinine sp. 1H	1.894	38.700	0.000	12.688	Ma	In	Ac	DLM
Staphylinine sp. 1M	1.894	35.800	0.000	9.000	Ma	In	Ac	DLM
Staphylinine sp. 1N	1.894	43.200	0.250	7.467	Ma	In	Ac	DLM
Staphylinine sp. 1T	1.894	41.700	0.000	11.028	Ma	In	Ac	DLM
Staphylinine sp. 1Y	1.894	42.600	0.600	7.625	Ma	In	Ac	DLM
Staphylinine sp. 2H	1.894	38.700	0.500	12.426	Ma	In	Ac	DLM
Staphylinine sp. 2N	1.894	43.200	0.250	7.470	Ma	In	Ac	DLM
Staphylinine sp. 2T	1.894	41.700	0.000	11.028	Ma	In	Ac	DLM
Staphylinine sp. 2Y	1.894	42.600	0.556	7.652	Ma	In	Ac	DLM

Staphylinine sp. 3M	1.894	35.800	0.000	8.560	Ma	In	Ac	DLM
Staphylinine sp. 3N	1.894	43.200	1.000	7.771	Ma	In	Ac	DLM
Staphylinine sp. 3T	1.894	41.700	0.250	11.156	Ma	In	Ac	DLM
Staphylinine sp. 3Y	1.894	42.600	0.000	7.384	Ma	In	Ac	DLM
Staphylinine sp. 4M	1.894	35.800	0.750	8.595	Ma	In	Ac	DLM
Staphylinine sp. 4N	1.894	43.200	1.000	7.893	Ma	In	Ac	DLM
Staphylinine sp. 4T	1.894	41.700	0.333	11.143	Ma	In	Ac	DLM
Staphylinine sp. 5M	1.894	35.800	1.000	8.672	Ma	In	Ac	DLM
Staphylinine sp. 5T	1.894	41.700	0.571	11.241	Ma	In	Ac	DLM
Staphylinine sp. 6M	1.894	35.800	1.000	8.658	Ma	In	Ac	DLM
Staphylinine sp. 7M	1.894	35.800	1.000	8.639	Ma	In	Ac	DLM
Staphylinine sp. 8M	1.894	35.800	1.000	8.703	Ma	In	Ac	DLM
Staphylinine sp. 9M	1.894	35.800	0.000	9.000	Ma	In	Ac	DLM
Stemonyphantes blauveltae	2.781	42.600	1.000	7.753	No	In	Sw	LP
Stenus frigidus	0.491	41.400	1.000	8.704	Ma	In	Ac	DLW
Stenus sp. 1B	0.491	34.900	1.000	5.922	Ma	In	Ac	DLW
Stenus sp. 1C	0.491	41.400	0.667	8.797	Ma	In	Ac	DLW
Stenus sp. 1G	0.491	33.100	0.500	7.522	Ma	In	Ac	DLW
Stenus sp. 1H	0.491	38.700	0.500	12.674	Ma	In	Ac	DLW
Stenus sp. 1K	0.491	38.600	1.000	12.667	Ma	In	Ac	DLW
Stenus sp. 1M	0.491	35.800	0.875	8.688	Ma	In	Ac	DLW
Stenus sp. 1N	0.491	43.200	0.952	7.635	Ma	In	Ac	DLW
Stenus sp. 1S	0.491	36.700	1.000	8.352	Ma	In	Ac	DLW
Stenus sp. 1T	0.491	41.700	1.000	11.344	Ma	In	Ac	DLW
Stenus sp. 1Y	0.491	42.600	0.833	7.698	Ma	In	Ac	DLW
Steotoda albomaculata	4.790	42.600	0.000	7.472	No	In	Sp	GL
Stilbus sp.	1.169	35.800	0.000	9.000	Ma	Sa	Ac	DLP
Stratiomyidae Larva	0.892	43.000	0.250	8.692	No	Om	Ac	DG
Styloctetor stativus	0.297	43.200	0.136	7.448	Ba	In	Sw	LP
Sylvanelater mendax	11.653	43.200	0.000	7.250	Ma	Pl	Ac	FP
Symphyta Larva	6.137	45.400	0.560	8.062	No	Le	Ac	P
Syntomus americanus	0.837	43.200	0.167	7.408	Po	In	Ac	GP
Synuchus impunctatus	13.361	35.800	0.000	8.560	Po	Om	Ac	GLP
Tachinus basalis	0.901	41.700	1.000	11.438	Ma	In	Ac	DLM
Tachinus elongatus	0.901	43.000	0.583	9.767	Ma	In	Ac	DLM
Tachyporine sp. 1M	0.149	35.800	0.000	8.730	Ma	In	Ac	DLM
Tachyporine sp. 1N	0.149	43.200	0.333	7.466	Ma	In	Ac	DLM
Tachyporine sp. 1S	0.149	36.700	0.000	8.366	Ma	In	Ac	DLM
Tachyporine sp. 2M	0.149	35.800	0.667	8.733	Ma	In	Ac	DLM
Tachyporine sp. 2N	0.149	43.200	0.571	7.535	Ma	In	Ac	DLM
Tachyporine sp. 2S	0.149	36.700	0.000	8.528	Ma	In	Ac	DLM
Tachyporine sp. 2Y	0.149	42.600	0.000	7.472	Ma	In	Ac	DLM

Tachyporine sp. 3M	0.149	35.800	1.000	8.633	Ma	In	Ac	DLM
Tachyporine sp. 3N	0.149	43.200	0.500	7.573	Ma	In	Ac	DLM
Tachyporine sp. 3S	0.149	36.700	1.000	8.434	Ma	In	Ac	DLM
Tachyporine sp. 4H	0.149	38.700	0.000	12.400	Ma	In	Ac	DLM
Tachyporine sp. 4M	0.149	35.800	1.000	8.606	Ma	In	Ac	DLM
Tachyporine sp. 4N	0.149	43.200	0.333	7.543	Ma	In	Ac	DLM
Tachyporine sp. 4S	0.149	36.700	0.333	8.438	Ma	In	Ac	DLM
Tachyporine sp. 5M	0.149	35.800	1.000	8.647	Ma	In	Ac	DLM
Tachyporine sp. 5N	0.149	43.200	0.833	7.532	Ma	In	Ac	DLM
Tachyporine sp. 5S	0.149	36.700	0.000	8.458	Ma	In	Ac	DLM
Tachyporine sp. 5Y	0.149	42.600	1.000	7.782	Ma	In	Ac	DLM
Tachyporine sp. 6N	0.149	43.200	1.000	7.880	Ma	In	Ac	DLM
Tachyporine sp. 6Y	0.149	42.600	0.000	7.833	Ma	In	Ac	DLM
Tachyporine sp. 7S	0.149	36.700	0.000	8.200	Ma	In	Ac	DLM
Tachyporine sp. 7Y	0.149	42.600	0.900	7.735	Ma	In	Ac	DLM
Tachyporus borealis	0.149	42.600	0.429	7.685	Ma	In	Ac	DLM
Tachyporus nimbicola	0.149	38.700	1.000	12.371	Ma	In	Ac	DLM
Tachyporus nitidulus	0.211	42.600	0.333	7.575	Ma	Fu	Ac	LP
Tachyporus rulomus	0.149	42.600	1.000	7.753	Ma	In	Ac	DLM
Talavera minuta	0.424	43.200	0.500	7.605	Ba	In	Ac	LP
Tapinocyba bicarinata	0.036	43.200	0.600	8.085	Ba	In	Sw	LP
Tapinocyba minuta	0.027	43.200	0.155	7.946	Ba	In	Sw	LP
Tapinocyba simplex	0.087	43.200	0.833	7.728	Ba	In	Sw	LP
Tapinocyba sp.1	0.042	36.700	0.000	8.440	Ba	In	Sw	LP
Tarsiphantes latithorax	0.135	44.100	0.206	8.676	Ba	In	Sw	LP
Tennesseellum formicum	0.245	42.600	0.000	7.414	Ba	In	Sw	LP
Tetragnatha caudata	17.666	35.800	0.571	8.808	No	In	Or	P
Tetragnatha extansa	7.307	36.700	1.000	8.384	No	In	Or	P
Tetragnatha versicolor	12.872	33.100	1.000	7.372	No	In	Or	P
Tetragnathidae Immature	0.716	49.600	1.000	9.015	No	In	Or	LPR
Thanatophilus lapponicus	39.548	41.700	0.250	11.207	Ma	Ca	Ac	D
Thanatophilus sagax	28.760	43.200	0.988	8.287	Ma	Ca	Ac	D
Thanatus arcticus	19.743	44.800	0.533	11.365	No	In	Ac	P
Thanatus formicinus	9.063	36.700	0.000	8.200	No	In	Ac	P
Thanatus striatus	1.477	43.200	1.000	7.743	No	In	Ac	P
Theonoe stridula	0.017	42.600	0.667	7.530	Ba	In	Sp	P
Theridiidae Immature	0.102	43.000	0.833	8.394	Ba	In	Sp	P
Theridion differens	0.322	43.200	1.000	7.897	No	In	Sp	P
Thomisidae Immature	0.396	50.300	0.373	10.169	Ba	In	Am	LR
Thripidae	0.443	43.200	0.328	7.446	Ma	Pl	Ac	P
Thymoites minnesota	0.484	35.800	0.000	8.900	No	In	Sp	P
Tibellus maritimus	9.063	43.200	0.706	7.908	No	In	Ac	P

Tibellus oblongus	11.335	43.200	0.000	7.250	No	In	Ac	P
Tingidae	0.100	43.500	0.344	11.020	Ma	Le	Pa	P
Tipulidae Larva	18.162	49.500	0.400	10.497	No	In	Ac	DG
Tisactia sp.	0.461	43.200	1.000	7.897	Ma	Fu	Ac	GLPW
Tiso aestivus	0.124	43.200	0.667	7.310	Ba	In	Sw	LP
Tmeticus ornatus	1.215	35.800	0.000	8.800	No	In	Sw	LP
Trebacosa marxi	7.827	35.800	1.000	8.606	No	In	Ac	GL
Trechus crassiscapus	1.531	36.700	1.000	8.434	Br	In	Ac	GLM
Trichodes ornatus	13.551	43.200	0.675	7.676	Ma	Pn	Ac	FP
Tricholochmaea ribicola	2.871	43.200	0.778	8.345	Ma	Le	Ac	P
Tricholochmaea vaccinii	2.871	40.000	1.000	7.871	Ma	Le	Ac	P
trochosa terricola	15.071	35.800	0.136	7.951	No	In	Ac	GL
tunagyna debilis	0.185	40.300	0.800	8.200	Ba	In	Sw	LP
Tympanophorus puncticollis	0.491	35.800	0.000	8.800	Ma	In	Ac	DLM
Upis ceramboides	72.639	42.600	0.000	7.609	Ma	De	Ac	DwGP
Vermontia thoracica	0.095	43.200	0.818	8.799	Ba	In	Sw	LP
Wabasso cacuminatus	0.079	42.600	0.951	7.915	Ba	In	Sw	LP
Wabasso quaestio	0.087	43.200	0.880	9.899	Ba	In	Sw	LP
Walckenaeria arctica	0.213	43.200	0.538	8.115	Ba	In	Sw	LP
Walckenaeria atrotibialis	0.400	35.800	0.000	8.800	No	In	Sw	LP
Walckenaeria auranticeps	0.400	38.700	0.200	12.635	No	In	Sw	LP
Walckenaeria castanea	0.670	43.200	0.500	8.430	No	In	Sw	LP
Walckenaeria clavicornis	0.316	44.000	0.333	9.970	Ba	In	Sw	LP
Walckenaeria clavipalpis	0.551	36.700	0.286	8.415	No	In	Sw	LP
Walckenaeria communis	0.497	43.200	0.667	7.944	No	In	Sw	LP
Walckenaeria cuspidatabrevicula	0.336	43.200	0.250	8.105	No	In	Sw	LP
Walckenaeria directa	0.356	41.800	0.833	9.792	No	In	Sw	LP
Walckenaeria exigua	0.105	43.200	0.104	7.400	Ba	In	Sw	LP
Walckenaeria fallax	0.400	35.800	1.000	8.606	No	In	Sw	LP
Walckenaeria fraudatrix	0.302	41.700	0.000	11.199	Ba	In	Sw	LP
Walckenaeria karpinskii	0.279	49.600	0.083	8.442	Ba	In	Sw	LP
Walckenaeria kochii	0.579	43.200	1.000	7.897	No	In	Sw	LP
Walckenaeria minuta	0.087	36.700	0.200	8.456	Ba	In	Sw	LP
Walckenaeria pallida	0.378	40.000	0.250	7.692	No	In	Sw	LP
Walckenaeria palustris	0.114	36.700	1.000	8.391	Ba	In	Sw	LP
Walckenaeria redneri	0.229	36.700	1.000	8.396	Ba	In	Sw	LP
Walckenaeria sp.iralis	0.336	43.200	0.900	8.585	No	In	Sw	LP
Walckenaeria tibialis	0.135	36.700	1.000	8.434	Ba	In	Sw	LP
Walckenaeria tricornis	0.114	43.200	0.571	7.793	Ba	In	Sw	LP
Walckenaeria tumida	0.087	40.000	1.000	7.982	Ba	In	Sw	LP
Walckenaeria vigilax	0.316	43.200	0.000	9.350	Ba	In	Sw	LP
Walckenaerianus aimakensis	0.336	42.600	0.625	8.065	No	In	Sw	LP

Xysticus banksi	3.566	43.200	1.000	7.897	No	In	Am	LR
Xysticus britcheri	2.578	44.800	0.513	10.376	No	In	Am	LR
Xysticus deichmanni	3.045	44.100	0.202	10.113	No	In	Am	LR
Xysticus durus	5.207	43.200	0.000	8.507	No	In	Am	LR
Xysticus ellipticus	1.477	43.200	0.800	7.805	No	In	Am	LR
Xysticus emertoni	9.490	43.200	0.557	8.439	No	In	Am	LR
Xysticus ferox	4.790	43.200	0.621	7.705	No	In	Am	LR
Xysticus luctuosus	1.730	43.200	0.870	8.403	No	In	Am	LR
Xysticus montanensis	1.418	43.200	0.000	7.321	No	In	Am	LR
Xysticus obscurus	4.525	39.700	0.571	8.802	No	In	Am	LR
Zelotes fratris	7.307	43.200	0.447	7.868	No	In	Ac	DwLR
Zelotes puritanus	3.908	43.200	0.133	7.449	No	In	Ac	DwLR
Zelotes sula	2.243	41.500	0.333	11.704	No	In	Ac	DwLR

Appendix A3-3 List of all taxa and abundances from each site

Taxon	HAZ	BAN	CAM	IQA	KUG	TOM	CHU	SCH	NOR	YEL	GOB	MOO	Total
Acidota sp.			12										12
Aculepeira packardi											1		1
Aegialia lacustris							1					1	2
Agathidium sp. 1H							2						2
Agathidium sp. 1N									1				1
Agathidium sp. 1T						6							6
Agathidium sp. 2T						2							2
Agathidium sp. 3									6				6
Agonum affine							9		11			7	27
Agonum consimile									1				1
Agonum exaratum			2										2
Agonum gratiosum							3		29	100	1	23	156
Agonum metallescens												8	8
Agonum mutatum											2		2
Agonum quinquepunctatum							6		6				12
Agonum superioris												2	2
Agonum thoreyi												1	1
Agriotes limosus									2		5		7
Agyneta allosubtilis						6			3	3			12
Agyneta olivacea			2			1		43	22	74	1	2	145
Agyneta sp.1					58	33	23			1			115
Aleochara assiniboin										1			1
Aleocharine sp. 10M												8	8
Aleocharine sp. 10N									3				3
Aleocharine sp. 10Y										3			3
Aleocharine sp. 11N									1				1
Aleocharine sp. 1B		2											2
Aleocharine sp. 1G											16		16
Aleocharine sp. 1H							2						2
Aleocharine sp. 1K					1								1
Aleocharine sp. 1M												4	4
Aleocharine sp. 1N									29				29
Aleocharine sp. 1S								4					4
Aleocharine sp. 1T						1							1
Aleocharine sp. 1Y										34			34
Aleocharine sp. 2H							1						1
Aleocharine sp. 2I				1									1
Aleocharine sp. 2K					1								1
Aleocharine sp. 2M												20	20

Aleocharine sp. 2N								4					4
Aleocharine sp. 2T					1								1
Aleocharine sp. 2Y									4				4
Aleocharine sp. 3H						2							2
Aleocharine sp. 3K				1									1
Aleocharine sp. 3M												1	1
Aleocharine sp. 3N								5					5
Aleocharine sp. 3S							5						5
Aleocharine sp. 3T					1								1
Aleocharine sp. 3Y									6				6
Aleocharine sp. 4G										2			2
Aleocharine sp. 4K				1									1
Aleocharine sp. 4M												1	1
Aleocharine sp. 4N								12					12
Aleocharine sp. 4S							1						1
Aleocharine sp. 4T					4								4
Aleocharine sp. 4Y									1				1
Aleocharine sp. 5K				1									1
Aleocharine sp. 5M												5	5
Aleocharine sp. 5N								4					4
Aleocharine sp. 5S							3						3
Aleocharine sp. 5Y									9				9
Aleocharine sp. 6K				1									1
Aleocharine sp. 6M												3	3
Aleocharine sp. 6N								1					1
Aleocharine sp. 6S							29						29
Aleocharine sp. 6Y									2				2
Aleocharine sp. 7M												4	4
Aleocharine sp. 7S							1						1
Aleocharine sp. 8M												7	7
Aleocharine sp. 8N								19					19
Aleocharine sp. 8Y									7				7
Aleocharine sp. 9M												1	1
Aleocharine sp. 9N								4					4
Aleocharine sp. 9Y									7				7
Alopecosa aculeata					20	6	25	447	154	404	1		1057
Alopecosa exasp.erans	304	99											403
Alopecosa hirtipes		431				1	1						433
Alopecosa pictilis			13	168			24						205
Altica sp. 1								1					1
Altica sp. 2												13	13
Altica sp. 3									1				1

Altica sp. 4							1					1
Altica sp. 5										2		2
Alticine sp. 1H						1						1
Alticine sp. 1M											1	1
Alticine sp. 2M											1	1
Alticine sp. S							20					20
Amara alpina	303	804	111	213		28	3					1462
Amara erratica								1				1
Amara hyperborea							83	4	6			93
Amara laevipennis						1			4	21		26
Amara littoralis											1	1
Amara pseudobrunnea					1		10	1	2	1		15
Amara torrida								1			1	2
Amaurobiidae IM							2			6	1	9
Ampedus nigrinus								5				5
Ampedus pullus								9				9
Anisosticta bitriangularis								1			8	9
Anisotoma sp. 2								2				2
Anthaxia inornata								90	16		7	113
Anthicus sp. 1								16				16
Anthonomus nigrinus								1				1
Antistea brunnea											12	12
Aphid		5					2		5		1	13
Aphileta misera										1	21	22
Araneidae Immature					1			3				4
Araneus groenlandicola						1						1
Arctachaea sp.1								1				1
Arctella lapponica				5	2							7
Arcterigone pilifrons	17		7									24
Arctosa alpigena				1	2		27	15	10	1		56
Arctosa emertoni											2	2
Arctosa insignita				46	25	6	2	1	2			82
Arctosa raptor						66	90	33	11		60	260
Arctosa rubicunda								4		8	9	21
Argenna obesa								85	14		5	104
Ascoliocerus sanborni					16							16
Atomaria sp. 1M											3	3
Atomaria sp. 2M									1		18	19
Atomaria sp. M											75	75
Atomaria sp. T					1							1
Atomaria sp. Y									1			1
Auchenorrhyncha Nymph				12	380	18	78	51	109	26	1098	1772

Badister obtusus							1	2		1	4
Baeocera sp.									6		6
Baryphyma groenlandicum	28	62	141								231
Baryphyma kulczynskii	1	12			1		5	13		11	43
Baryphyma trifonsaffine						2					2
Bathyphantes brevipes										1	1
Bathyphantes brevis										3	3
Bathyphantes canadensis										3	3
Bathyphantes gracilis								1			1
Bathyphantes pallidus					2		15			3	20
Bathyphantes simillimus		1		4		19					24
Beckerus appressus						3					3
Bembidion bimaculatum										2	2
Bembidion dilaticolle										1	1
Bembidion diligens							2				2
Bembidion forestriatum								1		8	9
Bembidion grapei						1					1
Bembidion morulum					1		38	17			56
Bembidion quadratulum									1		1
Bembidion transparens							1			21	22
Bembidion versicolor										15	15
Blethisa catenaria			9								9
Blethisa quadricollis										2	2
Brachycepsis sp.					2						2
Bradycellus neglectus								2			2
Bradycellus nigrinus										4	4
Bryophacis arcticus			7		11						18
Bryophacis smetanai								1			1
Byrrhus sp. 1								1			1
Byrrhus sp. 1S						3					3
Byrrhus sp. 2								1			1
Byrrhus sp. 2H					1						1
Byrrhus sp. 2K			3								3
Byrrhus sp. 2N							1				1
Byrrhus sp. 2T				19							19
Byrrhus sp. 3								1			1
Byrrhus sp. 3M										37	37
Byrrhus sp. 3T				2							2
Caelifera sp.			9	2	2		133	15		68	229
Caelifera IM					22	5	86	7	20	78	218
Caenocara sp. 1H					5						5
Caenocara sp. 1T				1							1

Caenocara sp. 1Y							3			3
Calathus ingratus					2	9	10	9	3	33
Callilepis pluto							25			25
Carabus chamissonis		1		48		42				91
Carabus granulatus									174	174
Carabus maeander						30			6	36
Carabus serratus								27		27
Carabus taedatus				24						24
Carabus truncaticollis			100							100
Carabus vietinghoffii		6				8				14
Carorita limnaea						4	1	8	3	16
Catops sp.					1					1
Centromerus longibulbus					23			19	1	43
Ceraticelus bulbosus				2	36	6	6		5	55
Ceraticelus crassiceps				3	8		2			13
Ceraticelus emertoni									1	1
Ceraticelus laetabilis									1	1
Ceraticelus laetus									1	1
Ceraticelus rowensis							1			1
Ceraticelus silus					3					3
Ceraticelus similis									24	24
Ceraticelus sp.1							2			2
Ceratinella brunnea			1	1	9	12	1		3	27
Ceratinella buna					3					3
Ceratinella ornatula					5				2	7
Ceratinella parvula					3	1			3	7
Ceratinops latus						1		1		2
Ceratinopsis labradorensis					39	6		2		47
Ceratomegilla ulkei			5	2						7
Cercopidae		38	6			2			2	48
Cercyon sp. 1N						1				1
Cercyon sp. G								73		73
Cercyon sp. M									1	1
Chaetocnema sp. 1						2				2
Chaetocnema sp. 2									1	1
Chalcoscirtus alpicola							1			1
Cheniseo hagnicultor								1		1
Chlaenius alternatus						38	2			40
Chlaenius lithophilus									1	1
Chlaenius niger									1	1
Cicadellidae	2	33	185	13	39	147	66	7	750	1242
Cicindela limbalis						2				2

Cicindela longilabris longilabris								2				2
Cicurina brevis											1	1
Clivina fossor											5	5
Clubiona bryantae						1	4	1	26	1	11	44
Clubiona furcata							1				1	2
Clubiona kulczynskii											2	2
Clubiona norvegica								1			1	2
Clubiona opeongo										1		1
Clubiona praematura						2						2
Clubiona riparia											1	1
Clubiona trivialis							1					1
Clubionidae Immature						24	1	1	4	1	10	41
Cnephalocotes obscurus						1		9	7	5		22
Coccinella hieroglyphica								1				1
Coccinellid sp. 1								1	2			3
Coccinellid sp. 10										4		4
Coccinellid sp. 11				5								5
Coccinellid sp. 2								2				2
Coccinellid sp. 3								1				1
Coccinellid sp. 4								4				4
Coccinellid sp. 5								1				1
Coccinellid sp. 6									18			18
Coccinellid sp. 7									2			2
Coccinellid sp. 8					1							1
Coccinellid sp. 9						6						6
Coccoidea					1		1		2	2		6
Coleoptera Larva	17	9	8	6	28	24	35	20	8	3	65	223
Collinsia plumosa											21	21
Colon asperatum											26	26
Colon bidentatum											1	1
Colon dentatum											4	4
Colon oblongum								7	27		27	61
Colon politum											7	7
Coreidae					1							1
Corticaria sp.								18				18
Corticaria sp. 1G										4		4
Corticaria sp. 1K				1								1
Corticaria sp. 1T					20							20
Corticaria sp. 2T					2							2
Corticaria sp. 3T					2							2
Corticarina sp. 1								8				8
Corylophid sp. 1									19		6	25

Corylophid sp. 2										1		1	2
Corylophid sp. 3										1		1	2
Corylophid sp. 4										1		1	2
Crepidodera sp.												8	8
Cryptophagus sp. 1H							4						4
Cryptophagus sp. 1N									55				55
Cryptophagus sp. 1T						2							2
Cryptophagus sp. 1Y										31			31
Cryptophagus sp. 2N									1				1
Cryptophagus sp. G											45		45
Cryptophagus sp. S								9					9
Curimopsis setulosa										1			1
Curimopsis sp. S								1					1
Curimopsis sp. T						3							3
Cybaeopsis euopla								8	1		9	12	30
Cymindis unicolor					2	1	1						4
Cyphon sp. 1G											1		1
Cyphon sp. 1M												3	3
Cyphon sp. 1N									7				7
Cytilus alternatus									4	3		13	20
Dalopius pallidus												21	21
Delphacidae					3	23	11	4	72	33	15	121	282
Diacheila arctica									1				1
Diacheila polita						16							16
Dicheirotrichus cognatus												5	5
Dichelotarsus laevicollis								1					1
Dichelotarsus puberulus								6				1	7
Dichelotarsus sp. 1							29						29
Dictyna arundinacea											3		3
Dictyna brevitarsus									1		1		2
Dictyna major												1	1
Dictynidae Immature	1		6		7	6			4				24
Dicymbium elongatum									1				1
Diplocentria bidentata				3		1	8	75	30	31	15		163
Diplocentria perplexa								1					1
Diplocentria rectangulata								31			1		32
Diplocephalus barbiger	2	7	1		5								15
Diplocephalus cristatus												1	1
Diplopoda			2									2	4
Dipoena nigra											1		1
Dismodicus decemoculatus												1	1
Dolomedes striatus											9	2	11

Dolomedes triton												1	1
Drassodes mirus							1			2			3
Drassodes neglectus									6	6			12
Dyschirius frigidus						1							1
Dyschirius globulosus										1			1
Dyschirius hiemalis							13	1	3	15			32
Dyschirius integer												18	18
Dyschirius melanocholicus					2	16							18
Dyschirius nigricornis							6						6
Dyschirius subarcticus						1							1
Eanus decoratus						2	5	1			1		9
Eanus maculipennis								1			3		4
Elaphrus clairvillei							6		4			4	14
Elaphrus fuliginosus										1			1
Elaphrus lapponicus						27	16		9	4			56
Elaphrus lecontei												1	1
Ellescus ephippiatus							1						1
Emblyna annulipes				1					8			3	12
Emblyna borealis	3		29		2								34
Emblyna phylax											1		1
Enicmus sp. 1B		21											21
Enicmus sp. 1G											7		7
Enoplognatha caricis										3		1	4
Entelecara sombra									1				1
Epuraea sp. 1G											1		1
Epuraea sp. 1H							10						10
Epuraea sp. 1M												1	1
Epuraea sp. 1N									35				35
Epuraea sp. 1S								2					2
Epuraea sp. 1T						2							2
Epuraea sp. 1Y										83			83
Erigone arctica		40	43										83
Erigone arctophylacis												13	13
Erigone atra									1			77	78
Erigone dentigera							1		2			44	47
Erigone psychrophila	149	128	20	3	1								301
Erigone sp.1				4									4
Erigone tirolensis				5									5
Estrandia grandaeva							1	1					2
Euaesthetus sp. 1												13	13
Eucinetus haemorrhoidalis									6				6

Euryopis argentea									42	20			62
Eusphalerum sp. 1										1			1
Eusphalerum sp. T						34							34
Evarcha proszynskii									6	8			14
Flatidae									1				1
Floricomus rostratus							6	48					54
Formicidae						17	1		273	912	4		1207
Glischrochilus siepmanni										2			2
Glyphesis idahoanus												1	1
Glyphesis scopulifer									3			2	5
Glyptina sp.									1				1
Gnaphosa borea					80	32	15		26	17	5		175
Gnaphosa brumalis					5			26	4	1	2		38
Gnaphosa microps						39	6	4	10	5	1		65
Gnaphosa muscorum							2	7	13	12			34
Gnaphosa orites					5	1	38						44
Gnaphosa parvula							1	1	6		2	11	21
Gnaphosidae Immature					52	9	31	17	45	57	22	3	236
Gnypeta ashei	14												14
Gonatium crassipalpum						11	1		4		1		17
Grammonota angusta									1		1		2
Grammonota gigas								186			1	52	239
Grammonota maritima							7			2			9
Grammonota sp.1										2			2
Grypus equiseti												32	32
Habronattus borealis									1				1
Hahnia cinerea										1	1		2
Hahnia glacialis								20	6				26
Hahnia ononidum									8	1			9
Hahniidae Immature								5	3	8		34	50
Haplodrassus eunis									8	3	13		24
Haplodrassus hiemalis					9	57	6		14	23	3		112
Haplodrassus signifer						1		22	6		9		38
Harpalus nigritarsis						6			9	3			18
Harpalus pleuritieus									1				1
Harpalus solitaris									1	1			2
Heteroptera Nymph			68	5	32	1	7		6	7	28	6	160
Hilaira canaliculata							1		2				3
Hilaira herniosa						3		4	1				8
Hilaira proletaria		1	9										10
Hilaira vexatrix	301	117	1	19									438
Hippodamia sp. 1								2					2

Hippodamia sp. 2									1			1
Histeridae sp. 1										1		1
Hogna frondicola							1			8		9
Horcotes quadricristatus				41	5	4	76					126
Hybauchenidium aquilonare	38	14		1								53
Hybauchenidium gibbosum							57					57
Hydnobius sp.											12	12
Hydraena sp. 1						1						1
Hylesinine sp.									1			1
Hylobius congener										63		63
Hypera diversipunctata				1	1							2
Hypera sp. C		1										1
Hypera sp. T					1							1
Hypnoidus abbreviatus											5	5
Hypnoidus bicolor					4		28	1	5	1	1	40
Hypnoidus rivularius					1			1				2
Hypomma subarcticum									1			1
Hypselistes florens								1				1
Hypselistes semiflavus								1				1
Hypsosinga groenlandica					17	1		2				20
Hypsosinga pygmaea							7	1	1	1		10
Hypsosinga rubens								9	4	1		14
Improphantes complicatus					8	2	16		1			27
Incestophantes washingtoni					1		4		1			6
Ischnosoma pictum						1				10		11
Ischnosoma splendidum									3			3
Ischnosoma timbriatum									3			3
Islandiana falsifica						2		1	2			5
Islandiana longisetosa											17	17
Islandiana princeps						1						1
Isochnus arcticus	24	1										25
Ivielum sibiricum					8							8
Kaestneria pullata								1			8	9
Kaestneria rufula							2	1			1	4
Lampyrid sp. 1M											1	1
Lampyrid sp. 1S							1					1
Lampyrid sp. 2											3	3
Larinioides cornutus										1	1	2
Lathys pallida									1			1
Latridius sp. 1C		3										3
Latridius sp. 1N								1				1

Leiodes assimilis												7	7
Leiodes neglecta												23	23
Leiodes punctostriata									2	24		2	28
Leiodes sp. 1M												2	2
Leiodes sp. 1M F												32	32
Leiodes sp. 1N									1				1
Lepidophorus lineatocollis						1			27				28
Lepidoptera Larva	16	21	16	3	14	18	88	8	16	21	38	35	294
Lepthyphantes alpinus							2	2	3				7
Lepthyphantes zebra							1						1
Lepyrus gemellus					1								1
Lepyrus nordenskioeldi			2		8								10
Lepyrus sp. C			10										10
Lepyrus sp. H							21						21
Lepyrus sp. N									4				4
Lepyrus sp. T						1							1
Limonius aeger											3		3
Linyphiidae Immature	554	296	69	100	48	22	70	177	37	35	99	86	1593
Liogluta nigropolita				1									1
Listronotus humilis							1				1		2
Lithobiidae Immature						42							42
Lordithon fungicola										3			3
Loricera pilicornis							1						1
Lycosidae Immature	414	194	308	659	237	280	333	93	253	179	131	173	3254
Lygaeidae Immature									6	3	2		11
Mantura sp.									1				1
Masikia indistincta		39	6	2									47
Mecynargus borealis					7		5						12
Mecynargus monticola					5								5
Mecynargus paetulus		3				1		3	5				12
Mecynargus sphagnicola				4	3	2							9
Mecynargus tungusicus						1							1
Megasternum sp.												1	1
Meioneta amersaxatilis			2		1		2	8	2			1	16
Meioneta fabra							21						21
Meioneta jacksoni						17	11	79		8	1	3	119
Meioneta maritima		10	5		3	1							19
Meioneta nigripes		1		1									2
Meioneta simplex					1	1	1	96	40	25	89		253
Melanophthalma sp. 1N									9				9
Melanophthalma sp. 1Y										26			26
Melanophthalma sp. G											1		1

Melanophthalma sp. M									7	7
Melanthaxia inornata						3				3
Mermessus entomologicus					2			15		17
Mermessus tridentata					3			1		4
Mermessus undulatus				6	2	2	1		39	50
Metopobactrus prominulus		23	1	12		3				39
Micaria aenea						15	6	11		32
Micaria alpina			15	17		1				33
Micaria constricta				5						5
Micaria pulicaria			1	6		5	19	2		33
Micaria rossica						20	10			30
Microlinyphia dana							6			6
Microlinyphia mandibulata									1	1
Microlinyphia pusilla									1	1
Microneta viaria						1		1		2
Miridae	6				1	1				8
Misumena vatia						1		1		2
Mordellochroa scapularis						1				1
Muscidae Larva	2							2	2	6
Mycetoporus nigrans		3		5			1			9
Mycetoporus smetanai							1			1
Nabidae									2	2
Nebria gyllenhali					3					3
Negastrius arnetti									1	1
Neoantistea agilis								13		13
Neoantistea magna									17	17
Neogalerucella pusilla				1					4	5
Neohypdonus gentilis									4	4
Neriene clathrata							1			1
Nicrophorus defodiens						2	1			3
Notaris aethiops			1	2		3	6			12
Notiophilus aquaticus					1					1
Notiophilus borealis		22	5	9	3					39
Notiophilus intermedius						1	1			2
Notiophilus semistriatus							2	1		3
Oedothorax trilobatus					2	19	1		7	29
Olophrum latum	7									7
Omaliine sp. 1G								1		1
Omaliine sp. 1H				5						5
Omaliine sp. 1K		3								3
Omaliine sp. 1M									3	3

Omaliine sp. 1N								1				1
Omaliine sp. 1S							10					10
Omaliine sp. 1T					1							1
Omaliine sp. 1Y									5			5
Omaliine sp. 2H						1						1
Omaliine sp. 2M											2	2
Omaliine sp. 2N								1				1
Omaliine sp. 2S							3					3
Omaliine sp. 2T					1							1
Omaliine sp. 2Y									1			1
Omaliine sp. 3H						3						3
Omaliine sp. 3N								3				3
Omaliine sp. 3S							1					1
Omaliine sp. 3T					1							1
Omaliine sp. 4S							2					2
Omaliine sp. 4T					3							3
Omaliine sp. 5T					4							4
Omaliine sp. 6T					1							1
Omalline sp. 3Y									1			1
Opiliones											7	7
Oreoneta beringiana			5									5
OReoneta brunnea				5		1	1					7
Oreoneta sp.1			1									1
Oreonetides flavescens										3		3
Oreonetides rectangulatus								1			4	5
Oreonetides vaginatus							4	3	3			10
Oreophantes recurvatus											1	1
Otiorhynchus ovatus										2		2
Oxyporus occipitalis									1			1
Oxyporus sp. 1M											8	8
Ozyptila arctica				18	12	5						35
Ozyptila curvata											1	1
Ozyptila gertschi								2	4		15	21
Ozyptila praticola						2						2
Ozyptila sinceracanadensis						1		50	38	20	1	110
Pachygnatha clerckii		8						2	3			13
Paederine sp. 1N								34				34
Paederine sp. 1Y									42			42
Pardosa albomaculata							1					1
Pardosa algens	413	2773	95	14			1		2			3298
Pardosa concinna				290	757	1564	2	18	24	1	1	2657
Pardosa furcifera					73	322	215		10			620

Pardosa fuscula				1	70	90	154	74	8	357	754
Pardosa glacialis	410	110	985		7						1512
Pardosa groenlandica								1			1
Pardosa hyperborea				3	60	156	256	18	425	12	930
Pardosa labradorensis				1		8					9
Pardosa mackenziana						2	59	23			84
Pardosa modica							4				4
Pardosa moesta				59			199	1282	1	775	2316
Pardosa podhorskii			95	2							97
Pardosa rubicunda										1	1
Pardosa sodalis			273	5							278
Pardosa uintana					1	20	17	3	3		44
Pardosa xerampelina				1			117	7	3	71	199
Patrobus foveocollis						3		1			4
Patrobus longicornis										5	5
Patrobus septentrionis						3	10				13
Patrobus stygicus							3				3
Pelecopsis mengei							2	3			5
Pelegrina montana										3	3
Pellenes montanus							11				11
Pentatomidae						1	3	13			17
Perregrinus deformis						1		7			8
Phaenonotum sp. 1N							1				1
Phaenonotum sp. 1S						1					1
Phidippus whitmani							1	2			3
Philodromidae Immature			7	10	78		4	5			104
Philodromus alascensis						1					1
Philodromus cesp.itum								1			1
Phlattothrata parva							1				1
Pidonia scripta								1			1
Pirata bryantae						4	5			2	11
Pirata canadensis										14	14
Pirata cantralli						81	6		7	59	153
Pirata piraticus					12	22	15	2		194	245
Pissodes nemorensis									5		5
Pityohyphantes subarcticus										2	2
Pityokteines sp. 1								1			1
Platycerus sp. 1								1			1
Platynus decentis										1	1
Platynus mannerheimii						1				2	3
Pocadicnemis americana						22	22	8	27	1	80
Poeciloneta vakkhanka				1							1

Poeciloneta variegata						1						1
Poecilus lucublandis											6	6
Priognathus monilicornis										1		1
Procas lecontei									1			1
Proteinine sp. 1N								1				1
Proteinus sp. 1S							3					3
Pselaphine sp. 1G										1		1
Pselaphine sp. 1M											1	1
Pselaphine sp. 1N								2				2
Pseudanostirus ochreipennis									2			2
Pseudanostirus triundulatus									1	5	1	7
Pseudoscorpionida											1	1
Psyllidae		23		1	7			5	2		7	45
Pterostichus adstrictus								20	4		15	39
Pterostichus arcticola					18	1	2					21
Pterostichus barryorum				10								10
Pterostichus brevicornis		2		392	64	80	3					541
Pterostichus caribou	154	846		325		69						1394
Pterostichus haematopus			306	106	6	54	110	3	1			586
Pterostichus hudsonicus				4								4
Pterostichus melanarius											204	204
Pterostichus parasimilis					244							244
Pterostichus patruelis								6	2	1	9	18
Pterostichus pensylvanicus								19		6		25
Pterostichus pinguedineus							1					1
Pterostichus punctatissimus						71		18	22			111
Pterostichus tareumiut	197											197
Pterostichus tenuis											4	4
Pterostichus vermiculosus		1		42								43
Ptiliid sp. 1M											9	9
Ptiliid sp. 1Y									1			1
Quedius fellmanii				2								2
Reduviidae					1			10	2			13
Reichenbachia sp.											1	1
Rhagium inquisitor										6		6
Rhagonycha fraxini										28	1	29
Rhagonycha mandibularis						87						87
Rhagonycha sp. 1K				2								2
Rhyncolus brunneus									2			2
Robertus borealis										2	3	5

Robertus fuscus								1	12				13
Rugathodes aurantius												1	1
Saldidae		1806	216		1	2	1		11	16	1	187	2241
Saldidae Nymph		43	1				8					100	152
Salticidae Immature						2	10		7	12	3	1	35
Satilatlas carens					6								6
Satilatlas gertschi										1			1
Satilatlas marxii							2						2
Scaphinotus bilobus												1	1
Sciaphilus asperatus												1	1
Sciastes dubius								1					1
Sciastes mentasta									2				2
Sciastes truncatus								1	16	2			19
Scironis tarsalis									10				10
Scolytine sp. 1											1		1
Scotinotylus pallidus											2		2
Scotinotylus sacer								3	3	4			10
Scydmaenid sp.								6		1			7
Scyletria inflata												75	75
Selatosomus aeripennis										15			15
Semljicola beringianus		243	3	16		2							264
Semljicola obtusus							1	6					7
Sergiolus montanus												1	1
Sericus incongruus									2	5	4		11
Setasomus aratus										1			1
Siagonium punctatum											1		1
Silometopoides pampia	160		6	2		2				1			171
Simplocara sp. 1							1						1
Sisicottus montanus								15					15
Sisicottus quoylei								1					1
Sisicus penifusifer											1		1
Sisis rotundus								19	9				28
Sitona lineellus									1				1
Sitticus cutleri									1				1
Sitticus floricolapalustris								1					1
Sitticus ranieri						1	3	1	12	10	1		28
Sitticus striatus							2	1	1				4
Sphaeroderus stenostomus												5	5
Sphenophorus costipennis												1	1
Staphylinine sp. 1H							4						4
Staphylinine sp. 1M												1	1
Staphylinine sp. 1N									8				8

Staphylinine sp. 1T					1								1
Staphylinine sp. 1Y									5				5
Staphylinine sp. 2H						2							2
Staphylinine sp. 2N								4					4
Staphylinine sp. 2T					1								1
Staphylinine sp. 2Y									9				9
Staphylinine sp. 3M												2	2
Staphylinine sp. 3N								9					9
Staphylinine sp. 3T					4								4
Staphylinine sp. 3Y									1				1
Staphylinine sp. 4M												4	4
Staphylinine sp. 4N								4					4
Staphylinine sp. 4T					6								6
Staphylinine sp. 5M												2	2
Staphylinine sp. 5T					7								7
Staphylinine sp. 6M												7	7
Staphylinine sp. 7M												2	2
Staphylinine sp. 8M												5	5
Staphylinine sp. 9M												1	1
Stemonyphantes blauveltae									4				4
Stenus frigidus			2										2
Stenus sp. 1B		1											1
Stenus sp. 1C			3										3
Stenus sp. 1G										2			2
Stenus sp. 1H						2							2
Stenus sp. 1K				4									4
Stenus sp. 1M												16	16
Stenus sp. 1N								21					21
Stenus sp. 1S							2						2
Stenus sp. 1T					1								1
Stenus sp. 1Y									6				6
Steotoda albomaculata									2				2
Stilbus sp.												2	2
Stratiomyidae Larva					1				1	1		1	4
Styloctetor stativus								17	9	18			44
Sylvanelater mendax								1					1
Symphyta Larva	3	19		1	9		1	2	8			7	50
Syntomus americanus								3	2	1			6
Synuchus impunctatus												1	1
Tachinus basalis					1								1
Tachinus elongatus					3	3			6				12
Tachyporine sp. 1M												4	4

Tachyporine sp. 1N								3					3
Tachyporine sp. 1S							23						23
Tachyporine sp. 2M												6	6
Tachyporine sp. 2N								7					7
Tachyporine sp. 2S							1						1
Tachyporine sp. 2Y									1				1
Tachyporine sp. 3M												9	9
Tachyporine sp. 3N								8					8
Tachyporine sp. 3S							1						1
Tachyporine sp. 4H						1							1
Tachyporine sp. 4M												1	1
Tachyporine sp. 4N								3					3
Tachyporine sp. 4S							3						3
Tachyporine sp. 5M												3	3
Tachyporine sp. 5N								12					12
Tachyporine sp. 5S							10						10
Tachyporine sp. 5Y									1				1
Tachyporine sp. 6N								1					1
Tachyporine sp. 6Y									1				1
Tachyporine sp. 7S							1						1
Tachyporine sp. 7Y									10				10
Tachyporus borealis									7				7
Tachyporus nimbicola						1							1
Tachyporus nitidulus									3				3
Tachyporus rulomus									5				5
Talavera minuta							1	12	6	1			20
Tapinocyba bicarinata						1	24	3	19	7	1		55
Tapinocyba minuta							29	8	6	14	1		58
Tapinocyba simplex							2	1		3			6
Tapinocyba sp.1							1						1
Tarsiphantes latithorax	16	13	1		4								34
Tennesseellum formicum									3				3
Tetragnatha caudata												7	7
Tetragnatha extansa							1						1
Tetragnatha versicolor										1			1
Tetragnathidae Immature			5		2			1	5				13
Thanatophilus lapponicus						4							4
Thanatophilus sagax						19		65	2				86
Thanatus arcticus					12	26	57	1	4	7			107
Thanatus formicinus								1					1
Thanatus striatus								4	15				19
Theonoe stridula									2	1			3

Theridiidae Immature						1				1	3	1	6
Theridion differens									1				1
Thomisidae Immature	16			15	4	16	42	20	13	9	9	17	161
Thripidae									2	9	50		61
Thymoites minnesota												2	2
Tibellus maritimus									2	6	6	3	17
Tibellus oblongus									1				1
Tingidae					7	19	4					2	32
Tipulidae Larva			2	1	1	3	1			1		1	10
Tisactia sp.									1				1
Tiso aestivus									3				3
Tmeticus ornatus												1	1
Trebacosa marxi												1	1
Trechus crassiscapus								1					1
Trichodes ornatus									40				40
Tricholochmaea ribicola									3			6	9
Tricholochmaea vaccinii								2			3		5
trochosa terricola											13	9	22
tunagyna debilis								1			2	2	5
Tympanophorus puncticollis												1	1
Upis ceramboides										2			2
Vermontia thoracica						3			4	2	1	1	11
Wabasso cacuminatus								63		1	78		142
Wabasso quaestio							12	2	8	3			25
Walckenaeria arctica								4	2	1	2	4	13
Walckenaeria atrotibialis												1	1
Walckenaeria auranticeps							5						5
Walckenaeria castanea								2	1			1	4
Walckenaeria clavicornis		1				1	1						3
Walckenaeria clavipalpis								7					7
Walckenaeria communis								2	1	3			6
Walckenaeria cuspidatabrevicula								3	1				4
Walckenaeria directa							2	3				1	6
Walckenaeria exigua									39	4	178		221
Walckenaeria fallax												2	2
Walckenaeria fraudatrix						1							1
Walckenaeria karpinskii		8	1		8			54	1				72
Walckenaeria kochii									1				1
Walckenaeria minuta								5					5
Walckenaeria pallida								1			3		4
Walckenaeria palustris								12					12

Walckenaeria redneri								3					3
Walckenaeria sp.iralis							1	1	2	2		4	10
Walckenaeria tibialis								1					1
Walckenaeria tricornis								17	25	10	4		56
Walckenaeria tumida								1			1		2
Walckenaeria vigilax						1			1				2
Walckenaerianus aimakensis										25		15	40
Xysticus banksi									1				1
Xysticus britcheri					1	68	23	14	5	3		36	150
Xysticus deichmanni	47		26	17	4								94
Xysticus durus							4	3	6	7			20
Xysticus ellipticus							2		2	12	24		40
Xysticus emertoni						16			30	23	5	5	79
Xysticus ferox									28			1	29
Xysticus luctuosus							1	15	3	3		1	23
Xysticus montanensis									7				7
Xysticus obscurus				1				6					7
Zelotes fratris							2		13	12	11		38
Zelotes puritanus									8	7			15
Zelotes sula							5				1		6
Total abundance	**2106**	**4481**	**5937**	**1603**	**4020**	**3148**	**3941**	**3036**	**4494**	**4579**	**2410**	**6254**	**46009**
Observed species richness	**15**	**31**	**50**	**36**	**85**	**138**	**149**	**180**	**274**	**234**	**148**	**247**	**809**