Determinants of trophic structure in ecological communities

Bу

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Dedication

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Abstract

Ecological communities are complex, and this complexity can obscure their underlying patterns and natural laws. One way to understand communities is to summarize their most important characteristics using consistent measures. Community structure is a set of measures of composition, abundance, distribution, and interaction that describe an ecological community over space and time. Trophic structure is an important aspect of community structure, and relates to energy and nutrient flow, especially the distribution of organisms across trophic levels. Trophic level is the energetic distance of an organism from the base of production – its average position in the food chains to which it belongs. Due to energetic inefficiencies, we generally predict that organisms decrease in number and biomass with trophic level, forming trophic pyramids (known as "pyramids of numbers" and "pyramids of biomass", respectively). Other, non-pyramidal trophic structures are also common, and trophic structure is affected by variables at multiple ecological scales. The objective of this thesis is to investigate determinants of trophic and community structure, including latitude, ecosystem type, biome transition, community composition, and body size.

While pyramids of numbers and pyramids of biomass are well-studied, few have investigated the trophic distribution of diversity. Using a meta-analysis approach, I found that, on average, large published food webs form pyramids of species richness, with a decrease in number of species with trophic level. The published food webs were more predator-poor, prey-rich, and hierarchical than three null models: random, niche, and cascade food web models. There was variation in trophic diversity structure amongst the food webs, and some food webs had uniform or inverse-pyramidal structure. Trophic diversity structure was correlated to centrality, latitude, ecosystem type, and study identity.

Community structure varies spatially, as can be seen even by a casual observer at interfaces between biomes. One such biome shift is between boreal forest and tundra, also known as the tree line. I studied how macroinvertebrate and soil prokaryote communities changed latitudinally along the forest-tundra ecotone in the Yukon, and how the communities responded to other environmental variables. I tested several hypotheses regarding changes in

community structure over the biome transition. I found that the communities differed between sites, changed along the latitudinal transect, and responded to environmental variables at multiple scales, including active layer depth, lichen cover, and road proximity.

Change in one aspect of community structure can affect other aspects of community structure. Loss of predators can have profound effects on the rest of the community. I used an experimental approach to investigate the effect of spider assemblage composition and diversity on prey consumption. I hypothesized that diverse assemblages would consume more prey due to niche complementarity and sampling effects. I found, however, that the spiders were generalist and intraguild predators, and that the one-species assemblage consumed the most prey. Spider body size affects its trophic niche, energy requirements, and interspecific interactions, and as a result, body size mediates the relationship between spider assemblage composition and prey consumption.

The body size of an organism affects how it interacts with other organisms and its biological rates. As a result, body size is central to many historical and modern ecological theories, involving implicit and explicit assumptions about the relationship between a predator body size and other variables. I used a meta-analytic approach to test several hypotheses regarding the relationship between body mass and trophic properties of terrestrial vertebrate predators: Accipitridae (hawks, eagles, and their relatives), Felidae (cats), and Serpentes (snakes). I found that the predators chose prey smaller than themselves, within a predictable mass range. Prey taxonomic diversity increased with Serpentes mass. Counter to theory, Felidae trophic level decreased with body mass, and Felidae and Accipitridae predator-prey body mass ratio increased with trophic level.

We currently live in the Anthropocene, an epoch characterized by anthropogenic geological, atmospheric, and biological change. These changes are affecting community structure, which in turn is affecting human access to the benefits provided by nature. Therefore, it is important that we continue to study community structure and the variables that affect it, so that we can predict and respond to ecological change in the Anthropocene.

Résumé

Les communautés écologiques sont complexes, et cette complexité peut masquer leurs modèles et leurs lois naturelles. Il possible de tenter de comprendre les communautés en résumant leurs caractéristiques les plus importantes avec des mesures reproductibles. La structure communautaire consiste en l'ensemble des mesures de la composition, de l'abondance, de la distribution et des interactions qui décrivent une communauté écologique dans l'espace et dans le temps. La structure trophique est un aspect important de la structure communautaire et concerne la circulation de l'énergie et des nutriments, en particulier la distribution des organismes entre les niveaux trophiques. Le niveau trophique est la distance énergétique entre un organisme et la base de la production - sa position moyenne dans les chaînes alimentaires auxquelles il appartient. En raison des inefficiences énergétiques, nous prédisons généralement que le nombre et la biomasse des organismes diminuent avec le niveau trophique, formant des pyramides trophiques (appelées respectivement « pyramides des nombres » et « pyramides des biomasses »). D'autres structures trophiques nonpyramidales sont également fréquentes, et la structure trophique est affectée par de multiples variables à différentes échelles écologiques. L'objectif de cette thèse est d'étudier les déterminants de la structure trophique et communautaire, incluant la latitude, le type d'écosystème, la transition du biome, la composition de la communauté et la taille du corps.

Bien que les pyramides des nombres et les pyramides des biomasses soient bien étudiées, peu ont étudié la distribution trophique de la diversité. En utilisant une méta-analyse, j'ai constaté qu'en moyenne, les grands réseaux trophiques publiés forment des pyramides de la richesse spécifique; le nombre d'espèces diminue avec le niveau trophique. Les réseaux trophiques publiés étaient plus pauvres en prédateurs, plus riches en proies et plus hiérarchiques comparé à trois modèles nuls : le modèle aléatoire, le modèle de niche et le modèle de cascade. La structure de la diversité trophique variait d'un réseau trophique à l'autre, et certains réseaux alimentaires avaient une structure uniforme ou en pyramide inversée. La structure de diversité trophique corrélait à la centralité, la latitude, le type d'écosystème et l'identité de l'étude.

La structure de la communauté varie dans l'espace, et ceci est particulièrement évident à l'interface entre les biomes. Le gradient entre forêt boréale et la toundra, également connue sous le nom de limite des arbres, est l'une de ses interfaces. J'ai étudié comment les communautés de macroinvertébrés et de procaryotes du sol changeaient le long de l'écotone entre la toundra et la forêt au Yukon, et comment les communautés réagissaient à d'autres variables environnementales. J'ai testé plusieurs hypothèses concernant les changements dans la structure de la communauté au cours de la transition du biome. J'ai constaté que les communautés étaient différentes entre les sites, qu'elles changeaient le long du transect latitudinal et réagissaient aux variables environnementales à de multiples échelles, y compris à la profondeur de la couche active, à la couverture de lichens et à la proximité de la route.

Le changement d'un aspect de la structure communautaire peut avoir une influence sur d'autres aspects de la structure communautaire. La perte de prédateurs peut avoir des effets profonds sur le reste de la communauté. J'ai utilisé une approche expérimentale pour étudier l'effet de la diversité et de la composition d'assemblages d'araignées sur la consommation de proies. J'ai posé l'hypothèse que les assemblages les plus divers consommeraient plus de proies en raison de la complémentarité des niches et des effets d'échantillonnage. Cependant, j'ai constaté que les araignées étaient des prédateurs généralistes et intraguildes, et que c'est l'assemblage d'une seule espèce qui consommait le plus de proies. La taille du corps de l'araignée affecte sa niche trophique, ses besoins en énergie et ses interactions interspécifiques et, par conséquent, la taille du corps sert de médiateur entre la composition de l'assemblage d'araignées et la consommation de proies.

La taille d'un organisme influe sur la façon dont il interagit avec d'autres organismes ainsi que sur ses taux biologiques. Par conséquent, la taille corporelle est au cœur de nombreuses théories écologiques historiques et modernes impliquant des hypothèses implicites et explicites sur la relation entre la taille corporelle d'un prédateur et d'autres variables. J'ai utilisé une approche méta-analytique pour tester plusieurs hypothèses concernant la relation entre la masse corporelle et les propriétés trophiques des prédateurs vertébrés terrestres : Accipitridae (faucons, aigles et leurs parents), Felidae (chats) et Serpentes (serpents). J'ai découvert que les

prédateurs choisissaient des proies plus petites qu'eux, dans une fourchette de masse prévisible. La diversité taxonomique des proies augmentait avec la masse des Serpentes. Contrairement à la théorie, le niveau trophique de Felidae diminuait avec la masse corporelle, et le ratio des masses prédateurs-proies de Felidae et Accipitridae augmentait avec le niveau trophique.

Nous vivons actuellement dans l'Anthropocène, une époque caractérisée par des changements géologiques, atmosphériques et biologiques anthropiques. Ces changements affectent la structure de la communauté, qui à son tour affecte l'accès humain aux richesses fournies par la nature. Il est donc important que nous continuions à étudier la structure des communautés et les variables qui l'affectent, afin de pouvoir prédire et répondre aux changements écologiques de l'Anthropocène.

Contributions to knowledge

1. I tested and found support for my original hypothesis that species richness typically decreases with trophic level (i.e., forming pyramids of species richness). A similar analysis has not been performed for several decades despite advancements in food web science. For the first time, I showed that trophic diversity structure is typically pyramidal and is correlated to centrality, latitude, ecosystem-type, and study identity.

2. I tested how macroinvertebrate and soil prokaryote communities respond to environmental variation together and independently. Never has this question been addressed in the forest-tundra interface. I demonstrated that the communities changed along this ecotone and responded to other environmental variables at multiple scales.

3. I found experimental evidence that body mass mediates the relationship between predator assemblage composition and prey consumption for spiders on the Yukon tundra. Body size is known to play a central role in predator-prey and food web dynamics, but few previous studies have addressed the role of predator body size in the relationship between predator diversity and prey consumption.

4. Using a meta-analytic approach, I tested hypotheses relating to the relationship between body size and trophic properties of terrestrial vertebrate predators (Accipitridae, Felidae, and Serpentes). Never have these hypotheses been tested for these taxa. I found that these predators were size-structured in their prey choice, but relationships related to trophic level were not as predicted by theory.

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Chapter 1: Introduction and Literature Review

It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us.

Charles Darwin, 1859, Origin of the Species (p. 490)

1.1 The shape of nature: Trophic structure and its determinants

1.1.1. Introduction

In the opening quote, above, Charles Darwin comments on the diverse and interdependent species of a river bank community, all produced by natural laws. The degree of complexity can be overwhelming to anyone who seeks to understand those underlying laws or generalities. Trophic structure is one approach to organize this complexity by summarizing essential characteristics of a community. Trophic structure is a body of measures that describe energy and nutrient flow in ecological communities, especially the distribution of organisms across trophic levels. This trophic distribution can be measured in terms including biomass, abundance, productivity, or diversity. The trophic level of an organism indicates its energetic distance from the base of production. Primary producers (usually plants and phytoplankton) have a trophic level of 1; primary consumers (consumers of primary producers) have a trophic level of 3; etc. Trophic structure therefore organizes organisms by their hierarchical relationship to energy flow through the community. It is a way of summarizing food webs, which are network maps of the consumer-resource relationships in an ecological community.

Charles Elton, the first to describe communities by their trophic structure, noted that the total number of individuals often decreases with trophic level. He referred to this pattern as a

"pyramid of numbers" (Elton 1927). It was later observed that there is frequently a parallel decrease in total biomass with trophic level, called a "pyramid of biomass" (Lindeman 1942). These two pyramids are driven by interspecific interactions (Hairston & Hairston 1993) and by the pyramid of energy: only a fraction of the energy at one trophic level is consumed and assimilated into the next (Lindeman 1942). Unlike the pyramids of numbers and biomass, which only sometimes occur, the 2nd law of thermodynamics requires that all closed communities at steady state conform to pyramids of energy. Energy is lost within trophic levels due to metabolic inefficiencies and it is lost between trophic levels due to inefficient energy transfer (Brown et al. 2004). Another trophic pyramid, the pyramid of species richness, is a decrease in the relative species richness (i.e., the proportion of species) at each trophic level. More generally, trophic diversity structure is the distribution of diversity across trophic levels, whether measured as species richness or any other diversity measure. If species richness generally increases with energy availability (Wright 1983; Gaston 2000; Allen et al. 2007), we can expect the pyramid of energy to generate a pyramid of species richness as it does for other trophic pyramids. This pyramid of species richness concept is tested in Chapter 2. While communities often conform to trophic pyramids, non-pyramidal trophic structures are also common, depending on organismal and ecosystem characteristics (Chapter 2; Shurin et al. 2006; Garvey & Whiles 2016).

The trophic structure of communities is strongly related to ecosystem functioning (Duffy et al. 2007). A classic example is trophic cascades (Hairston et al. 1960), which occur in three-level food chains when changes in the top predator's abundance causes reciprocal changes in the basal population's abundance. A reduction in carnivore biomass, for instance, could result in an increase in herbivore biomass, and thus a decrease in plant biomass. Trophic interactions are related to many ecosystem functions, including population regulation, nutrient cycling, stability, and decomposition. Ecosystem functions affect human well-being because they moderate the benefits which humanity receives from nature (i.e., ecosystem services; De Groot et al. 2002). The ability to predict and manage ecosystems for human well-being therefore motivates the study of trophic structure.

The study of trophic structure is one aspect of trophic ecology, which is the study of energy and nutrient transfer at all ecological scales (Table 1). Because trophic ecology spans ecological scales, it synthesizes often disparate disciplines, from organismal biology to ecosystem ecology. A notable trophic ecological approach is the Metabolic Theory of Ecology (Brown et al. 2004), a unifying framework which posits that the metabolic rate of organisms is a fundamental biological rate that governs many patterns observed in populations, communities, and ecosystems. All scales of trophic ecology are united by the principles of energy constraints and evolution, and all scales are hierarchically dependent on one another (Garvey & Whiles, 2016).

In this brief literature review, I begin by describing challenges to the concept of trophic structure. I then describe the relationship between trophic structure and several ecologically important variables: latitude, body size, aquatic versus terrestrial ecosystems, and phylogeny. For each variable, I discuss its effects on trophic structure at multiple ecological scales. I conclude by briefly discussing interactions between variables and the effects of global change on trophic structure.

1.1.2. Challenges to the trophic structure concept

Omnivory and detritivory are two types of consumption that challenge the concept of distinct and definable trophic levels. Trophic omnivores are organisms that consume resources from multiple trophic levels (Pimm & Lawton 1978), and typically have fractional (non-whole number) trophic levels. True omnivores are a subset of trophic omnivores that consume both plants and animals (Coll & Guershon 2002). Omnivory occurs when an organism shifts its diet depending on resource availability, internal state, or ontogenetic development. Omnivory has important effects on trophic structure and dynamics by influencing food web stability (McCann & Hastings 1997; Kratina et al. 2012). While omnivory might render the concept of distinct trophic levels somewhat simplistic, trophic levels are a useful approximation in many cases (Garvey and Whiles 2016). Although omnivory is common (Polis 1991), especially at high trophic levels (Lindeman 1942; Thompson et al. 2007), omnivorous links are often weak (e.g., accidental ingestion; Thompson et al. 2009). Many omnivores are only mildly omnivorous, with low variation in the trophic level of their food items (Williams & Martinez 2004). Trophic

cascades are consistent with linear food chains and are common in nature, perhaps because omnivores often strongly favour a single trophic level (Thompson et al. 2009). Because specialists should be better competitors for prey shared with generalist omnivores (Loxdale et al. 2011), natural selection generates distinct trophic roles which can be categorized approximately by trophic levels (Garvey & Whiles 2016). One way of conceptualizing trophic levels is that they are properties of the ecosystem rather than populations, and a population can perform functions at multiple trophic levels (Levine 1980). In this framing, there is no conflict between omnivory and discrete trophic levels.

Detritivory is another common consumption strategy that challenges a traditional understanding of trophic levels. Detritivores consume non-living organic matter (dead organisms and organic waste) and include many bacteria, fungi, invertebrates, and scavenger vertebrates. Most of the energy and organic matter in living organisms is not captured by consumers, but instead becomes detritus (Garvey & Whiles 2016). Detrital nutrients and energy re-enter the living food web when detritivores are consumed and when nutrients are absorbed by plants (Wolkovich et al. 2014; Zou et al. 2016). Detritivory generates loops in food webs, which renders the trophic level of organisms in these loops formally undefinable. Other consumption modes that generate loops, including cannibalism and intraguild predation (consumption of a resource competitor; Polis 1991), cause the same problem. In practice, detritivores are usually treated as having a trophic level of 2, with detritus considered to be the base of the detrital food web (e.g., Williams & Martinez 2004). While the loops created by detritivores make interpretation of trophic structure more complex, ultimately the energy in detritus comes from the classic trophic pyramid base, primary producers.

A final challenge to the trophic structure concept is that it implies food webs that are discrete and closed entities. In reality, the boundaries between ecological communities are fluid, with biomass, energy, and nutrients flowing between communities (Polis et al. 1997). Regardless, bounded communities are often a helpful approximation for ecological theorists and field workers.

1.1.3. Latitude

Solar energy and temperature decrease from the equator to the poles. At high, habitable temperatures, increased metabolic rates (Boltzmann 1872 as cited by Brown et al. 2004) lead to higher energy flux (Brown et al. 2004). Increased temperature is predicted to increase productivity and decrease biomass (i.e., standing stock biomass) at all trophic levels (Brown et al. 2004). In conjunction with a latitudinal gradient in solar energy availability for photosynthesis, the effect on primary producers is a global latitudinal gradient in terrestrial net primary productivity (NPP; Gillman et al. 2015). The global distribution of marine NPP, on the other hand, is driven more by nutrient availability than by latitude (Huston & Wolverston 2009). The effect of latitude on primary producers in turn affects higher trophic levels. More NPP at the trophic base may support a larger food web, consistent with the latitudinal diversity gradient (Hildebrand 2004). Although we might expect that more NPP will support more trophic levels, there is no evidence that food chain length decreases with latitude (Zanden & Fetzer 2007). With more NPP available to consume, and elevated metabolic rates, herbivory rates may also be more intense towards the equator (Hargreaves et al. 2018), although the evidence for such a gradient is mixed (Moles et al. 2011; Zhang et al. 2016). The intensity of biotic interactions at higher trophic levels (predation, parasitism, etc.) also tends to increase towards the equator (Schemske et al. 2009; Roslin et al. 2017). The increased consumer-resource interaction rate towards the equator may result in a greater proportion of energy transferred from one trophic level to the next (discussed further in Chapter 2).

Because of the tilt in the Earth's axis, environmental conditions undergo seasonal change, accompanied by seasonal changes in trophic structure. Evolution has generated numerous strategies to address the physiological challenges of cold winters, many of which involve reduced activity (Marchand 2014). Primary production, especially, is reduced during the winter at middle and high latitudes (Lisovski et al. 2017). Endotherms, in contrast, can maintain activity in the winter by metabolically generating heat. Productivity at the base of the food web is therefore reduced each winter, and organisms at higher trophic levels consume biomass generated during the summer pulse. Tropical regions have a different type of seasonality,

driven by water availability and hydroclimate (Guan et al. 2015), though seasonal NPP variation in tropical regions is less than in temperate and polar regions (Lisovski et al. 2017).

1.1.4. Organism size

Body size affects the interspecific interactions and biological rates of organisms, and so is central to many food web models (e.g., Brown et al. 2004; Loeuille & Loreau 2005; Petchy et al. 2008). Elton observed that many food chains are organized by body size differences (Elton 1927): prey are consumed by predators larger than themselves, which are in turn consumed by even larger predators. He argued that this size hierarchy drives the pyramid of numbers. Small organisms at the base of trophic pyramids can reproduce faster and reach greater densities than large organisms at higher trophic levels. Large organisms have a lower mass-specific metabolic rate than small organisms (Kleiber 1932), so populations of large organisms flux biomass more slowly. Therefore, size-structured food webs will have inverted pyramids of biomass if predators are sufficiently larger than their prey. The distribution of productivity across trophic levels is not affected by the distribution of body size across trophic levels because small organisms compensate for their lower per capita productivity with greater population density (Brown et al. 2004).

Empirical work confirms that predators are almost universally larger than their prey (Cohen et al. 1993; Brose et al. 2006; Chapter 5), with some exceptions such as cooperative hunters. On the other hand, trophic level increases with body mass in only some types of ecosystems (Shurin et al. 2006; Riede et al. 2011). The apparent discrepancy between these two facts arises because predator-prey relationships are not the only type of consumer-resource relationship. Parasites and many terrestrial herbivores, for example, are much smaller than their resource. When consumers are not larger than their resource, we predict a (non-inverted) pyramid of biomass. If body size decreases with trophic level (Burness et al. 2001), we predict an inverted pyramid of numbers.

1.1.5. Aquatic versus terrestrial ecosystems

Aquatic and terrestrial environments differ in their physical characteristics, and these differences have consequences for the trophic structure of communities (Portalier et al. 2018). Aquatic food webs are more size-structured than terrestrial food webs, meaning that body size increases with trophic level (Shurin et al. 2006). This begins with the primary producers, which in aquatic ecosystems (especially pelagic ecosystems) are usually small and unicellular phytoplankton, and which in terrestrial ecosystems are typically multicellular plants that can be very large. Terrestrial plants contain more cellulose and lignin and less nitrogen and phosphorus than phytoplankton, due to their structural and transport tissues, and so have lower nutritional quality (Elser et al. 2000). While NPP does not differ between aquatic and terrestrial ecosystems (Cebrian & Lartigue 2004), the standing stock of biomass for primary production is lower for aquatic ecosystems than terrestrial ecosystems. This difference is because of the small size of phytoplankton and because aquatic primary consumers remove the easilydigestible primary producer biomass at a faster rate than terrestrial primary consumers (Lindeman 1942; Brown et al. 2004). Consequently, aquatic ecosystems frequently have an inverted pyramid of biomass, while terrestrial ecosystem pyramids are usually not inverted (Del Giorgio et al. 1999; Shurin et al. 2006; Bar-On et al. 2018).

Detrital food webs also differ consistently between terrestrial and aquatic food webs. Detritus consumption rate is similar between terrestrial and aquatic ecosystems, but detritivores have greater biomass in terrestrial ecosystems (Cebrian 1999). This difference suggests aquatic detritivores accumulate less biomass due to a higher metabolic rate or that they are removed at a faster rate by predators (Cebrian 1999; Shurin et al. 2006). Greater consumption of detritivores by predators in aquatic ecosystems than terrestrial ecosystems may mean that more biomass re-enters the living food web in aquatic ecosystems (Shurin et al. 2006). In terrestrial ecosystems, decomposition rate depends largely on water availability, while in aquatic ecosystems decomposition rate depends on factors including water salinity, oxygen concentration, and pH (Garvey & Whiles 2016).

1.1.6. Phylogeny

The process of evolution by natural selection has resulted in organisms which can differ profoundly in their metabolic systems and response to their environment, with consequences for trophic structure. Body size and other traits that govern metabolism and interactions between organisms are determined in part by evolutionary history, and therefore trophic traits will vary with phylogeny (Naisbit et al. 2012). For instance, invertebrates consume prey smaller than themselves, on average, but closer to their own body size than vertebrate predators and their prey (Cohen et al. 1993). Across Animalia there is a strong phylogenetic signal in the prey body mass range of predators (Naisbit et al. 2011). This phylogenetic variation in predator-prey body size ratios may be due to the evolution of different feeding modes, such as whether the predator consumes prey whole (Nakazawa et al. 2013). Resource preference, beyond just prey body size, is strongly correlated to phylogeny in many groups (e.g., Vitt & Pianka, 2005). Resource preference can affect trophic structure; For instance, due to the similar size of invertebrate predators and prey, the biomass and abundance of invertebrate predators and prey should be more similar than for vertebrate predators and their prey. Endothermy and ectothermy are two metabolic strategies that have evolved in Animalia and affect trophic structure. Endotherms allocate a portion of their energy to maintaining their internal temperature. A trophic level made up largely of endotherms, therefore, will lose more energy to heat production than a trophic level with more ectotherms. Because of the correlation between phylogeny and trophic characteristics, inclusion of phylogeny in food web models can allow better prediction of trophic structure (Cattin et al. 2004; Loeuille & Loreau 2005; Naisbit et al. 2012)

1.1.7. Conclusion

Latitude, body size, ecosystem type, and phylogeny all affect trophic structure independently. Additionally, the effects of these variables on trophic structure interact with one another. For example, within some phylogenetic groups, animal body size increases with latitude because of temperature (Bergmann 1847 as cited by Meiri & Dayan 2003; Meiri & Dayan 2003) or productivity gradients (Geist 1987). Equatorial animals, therefore, may be both warmer and

smaller than polar animals. The effects of latitude and body size on trophic structure may be even more pronounced than latitude acting alone, since both small body size and increased temperature are associated with high mass-specific metabolic rate (Brown et al. 2004). Terrestrial and aquatic ecosystems change differently with latitude; and the implications of body size for foraging behaviour differs between phylogenetic groups. Because of the effects of these interacting ecological variables, trophic structure varies over space and time in complex ways.

We are currently living in the Anthropocene (Crutzen & Steffen 2003), a proposed epoch characterized by anthropogenic changes in global climate, nutrient dynamics, and diversity. We are only beginning to discover how the interacting effects of these variables are affecting trophic structure. As humans alter the planet, the plants, birds, insects, and worms of Darwin's tangled bank are under increasing risk of extinction. Their loss is ethically troubling, but also threatens our access to the natural goods and services humans require to survive. As the structure of ecological communities change due to anthropogenic activity, ecosystem functions and services will also be altered. It an urgent task to understand the laws and patterns underlying ecological complexity so that we may predict and respond to change.

1.2 Objectives of this thesis

The goal of my research is to investigate the determinants of community structure, especially trophic structure. I hypothesize that variation in community and trophic structure is predictable and correlated to variables that are internal (e.g., community composition, body size distribution) and external (e.g., latitude, ecosystem type, biome transition) to the community.

My main research questions are:

What is the typical distribution of species amongst trophic levels within large published food webs and what variables are correlated to this "trophic diversity structure"?

How do macroinvertebrate and soil prokaryote communities change along a forest-tundra ecotone and with environmental variables in the Yukon?

What is the relationship between tundra spider assemblage composition and prey consumption in the Taiga Cordillera Ecozone of the Yukon?

How does body size of terrestrial vertebrate predators correlate to their trophic properties, including trophic level and dietary niche?

The specific objectives of this thesis were:

Chapter 2: Describe the trophic diversity structure of large published food webs and identify correlations between trophic diversity structure and endogenous, exogenous, and methodological variables.

Chapter 3: Test hypotheses regarding changes in macroinvertebrate and soil prokaryote community structure across a forest-tundra ecotone of the Yukon. Describe correlations between environmental variables and macroinvertebrate and soil prokaryote community composition and structure.

Chapter 4: Use an experimental approach in the Yukon to investigate the relationship between spider community composition and prey consumption, with a focus on the wolf spider *Pardosa lapponica*.

Chapter 5: Test hypotheses regarding correlations between body mass and trophic properties of terrestrial vertebrate predators (Accipitridae, Felidae, and Serpentes) using published dietary inventories and trait databases.

Table 1.1. Examples of trophic ecology research domains at organismal to global ecological scales.

Ecological scale	Research domains
Organism	Metabolism; diet; evolutionary adaptations for predation; anti- predator adaptations; foraging behaviour
Population	Intraspecific competition; trophic niches
Community	Consumer-resource interactions (including predator-prey, herbivore-plant, parasite-host, pollinator-plant, etc.); food webs
Ecosystem	Trophic structure; energy flow; nutrient cycles
Global	Latitudinal interaction gradients; trophic effects of global change

Connecting Text:

I begin my investigation of trophic structure by describing the trophic diversity structure of published food webs across several ecosystem types and a global geographic extent. The motivation for this work is that important ecosystem functions are embedded within food webs, and the distribution of biodiversity across food web trophic levels will affect those ecosystem functions. It has been several decades since the distribution of species richness across trophic levels has been evaluated (Cohen et al. 1990; Martinez 1994). Over these decades, food web science has continued to advance as issues, especially lack of resolution (aggregation of species and missing species and consumed-resource links), are investigated and confronted (Hodkinson & Coulson 2004). Empirical food webs form the basis of food web theory, and so it may yield valuable insight to re-evaluate classic theory against currently-available published food webs. This chapter addresses the questions: *What is the typical trophic diversity structure of large published food webs and what variables are correlated to trophic diversity structure*?

Contributions of authors: The authors that contributed to this work are Shaun Turney¹ and Christopher M. Buddle¹. ST and CMB conceived the ideas and designed the methodology. ST collected and analysed the data and led the writing of the manuscript. Both authors contributed critically to the drafts.

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Chapter 2: Pyramids of species richness: the determinants and distribution of species diversity across trophic levels

2.1 Abstract

How species richness is distributed across trophic levels determines several dimensions of ecosystem functioning, including herbivory, predation, and decomposition rates. We perform a meta-analysis of 72 large food published food webs to investigate their trophic diversity structure and possible endogenous, exogenous, and methodological causal variables. Consistent with classic theory, we found that published food webs can generally be described as "pyramids of species richness". The food webs were more predator-poor, prey-rich, and hierarchical than is expected by chance or by the niche or cascade models. The trophic species richness distribution also depended on centrality, latitude, ecosystem-type, and methodological bias. Although trophic diversity structure is generally pyramidal, under many conditions the structure is consistently uniform or inverse-pyramidal. Our meta-analysis adds nuance to classic assumptions about food web structure: diversity decreases with trophic level, but not under all conditions, and the decrease may be scale-dependent.

2.2 Introduction

2.2.1 Biodiversity and food webs: Pyramids of species richness

Food webs are networks of species in a community, connected uni-directionally by their consumer-resource relationships. These relationships include predator-prey, plant-herbivore, plant-pollinator, host-parasite, or any other relationship involving biomass consumption. These ecological "road maps" (Pimm et al. 1991) are central to ecological theory and embedded within food webs are a number of important ecosystem functions: herbivory, predation, nutrient cycling, and decomposition, among other functions. A large body of evidence is building that biodiversity is intimately tied to ecosystem functioning (reviewed in Hooper et al. 2005) and ecosystem services (reviewed in Mace et al. 2012). The biodiversity of consumer and resource species affects ecosystem functioning directly and via trophic cascades (lves et al.

2005). Biodiversity loss from human activity, which may disproportionally affect predators (Estes et al. 2011), has a profound impact on ecosystem functioning and subsequently on human well-being (Cardinale et al. 2012). How biodiversity is structured and maintained across trophic levels is fundamental to conservation science and to the study of biodiversity and ecosystem functioning.

Elton's (1927) pyramid of numbers and pyramid of biomass hypothesize that there will be a large number of organisms and high biomass, respectively, at low trophic levels and progressively fewer/less at each increasing trophic level. Elton's work later found a theoretical basis in Lindeman's ecological efficiency theory (1942), which states that a large proportion of the energy at each trophic level is not transferred to the trophic level above. Typical speciesenergy curves suggest that, like numbers and biomass, species richness may also increase with energy availability (Evans et al. 2005). Thus, we could expect that biodiversity will be distributed such that it is greatest at basal levels and decreases with trophic level, forming a pyramid of species richness.

Since the early days of food web biology, researchers have noted consistent patterns in food web structure (Pimm et al. 1991; Cohen et al. 1990). These food web "laws" include scaleinvariant ratios of top predator: intermediate: basal species, and consumer: resource species richness. Although there is some variation in the ratios, some meta-analyses have found that species richness consistently decreases with trophic level (Pimm et al. 1991; Cohen et al. 1990). Recent evidence (Hatton et al. 2015) suggests that the proportions of pyramids of biomass may not be scale-invariant. Predator biomass increases following a ¾-power law relationship with prey biomass, suggestive of a connection to the ¾-power law relationship between metabolism and biomass described by Kleiber's law (van der Meer 2006). It has not yet been investigated whether the proportions of the pyramid of numbers or the pyramid of species richness are scale-variant.

2.2.2 Drivers of food web diversity structure: Endogenous, exogenous, and bias

The pyramid shape of food webs and other observed patterns in food web structure arises from three sources: endogenously, exogenously, and from methodological bias. Endogenously, a pyramid shape in food web trophic structure could arise from hierarchical predator-prey networks. This hierarchical hypothesis is inherent in two widely-used food web models: the cascade (Cohen & Newman 1985) and the niche models (Williams & Martinez 2000). A hierarchical structure such as is described mathematically by the cascade and niche models, could emerge from body size constraints in predator-prey relationships (Woodward & Hildren 2002). Food webs may also be structured endogenously by evolutionary processes, although these processes will not be discussed in detail here (for example, Eklöf et al. 2012).

There is evidence that climatic or environmental variables may also affect food web structure (Petchey et al. 1999; Barton et al. 2009; Ferreira et al. 2014). Community structure, including food web structure, is known to differ between terrestrial and aquatic communities (Shurin et al. 2006). Predator-prey relationships are influenced by temperature (Petchey et al. 2010) and competition between consumers is influenced by nutrient availability (Tilman et al. 1982). Changes to consumer-resource relationships between species due to abiotic variables will in turn have an effect on food web structure.

Observed patterns in food web structure may be methodological artifacts and some or all of the patterns may not exist in actual ecological communities. Published food webs may be overly simplistic, lacking the species richness, omnivory and looping present in the real food webs they describe and they may also over-represent top predators (Polis 1991). Furthermore, described food webs are only subsets of real food webs; study systems are almost always artificially delineated by the scope of the sampling.

2.2.3 Meta-analysis

Over time, as food web biology has developed as a science, food webs have become more species-rich and have less grouping of diverse taxa into tropho-species, among other changes (Layman et al. 2015). Much of the science surrounding scale-invariant trophic ratios was

developed based on food webs that, in view of research over the past decades, are now considered flawed. Shurin and colleagues pointed out in 2006 that remarkably little information is available concerning diversity within trophic levels in terrestrial and aquatic webs. The study that comes closest to analyzing trophic diversity distribution in recent decades is Fath and Killian's 2007 study of 17 commonly studied ecosystems, both terrestrial and aquatic. They found that the majority of the trophic pyramids were inverted in regards to species richness. An updated look at the distribution of diversity across food webs is needed to re-evaluate our classic understanding of food web diversity structure.

In this study we performed a meta-analysis of 72 large (>50 species), recent (mean year = 2001) food webs from GlobalWeb (University of Canberra 2015). First, we determined the average species richness at several trophic levels, as well as the prey: predator ratio. Next, to investigate endogenous structuring mechanisms, we quantified food web structure, including hierarchy and centralization, using several measures from network theory. We determined whether prey: predator ratio is scale-variant. We then tested the degree to which random, cascade, and niche models produced agreeing values. We investigated the effect of exogenous variables on the trophic structure, including both geographic and climatic variables. We considered the problem of bias presented by the authors' methodological choices. Finally, we determined the proportion of variance explained by endogenous, exogenous, and author bias.

2.3 Methods

Published food webs

The food webs were downloaded from the online database, University of Canberra's GlobalWeb (University of Canberra 2015). We downloaded all the food webs in the database but used only the food webs with 50 or greater species, a total of 72 food webs (Table S2.1).

Endogenous variables

We made use of the *analyse.list* function of the *foodweb* package (Perdomo et al.) in R Statistical Software Version 3.1.1 (R Development Core Team 2008) to calculate a number of variables for each GlobalWeb food web: species richness, total number of links, fraction omnivory, fraction cannibalism, total trophic positions, fraction basal, fraction intermediate, fraction top, fraction herbivore, and the prey: predator ratio. The "fractions" are the number of species belonging to the given class (omnivore, cannibal, basal, etc.) divided by the total species richness. Predator: prey ratio is the number of consumer and intermediate species divided by the number of basal and intermediate species.

Additionally, we calculated five more variables for each food web. We calculated nestedness using the function *NODF* of the package *RInSp* (Zaccarelli et al. 2015). NODF (Almeida-Neto et al., 2008) is a Nestedness metric based on Overlap and Decreasing Fill. We calculated in-reach centralization and out-reach centralization using the function *centr_clo* from the package *igraph* (Csardi and Nepusz 2006), with "mode" set to "in" and "out", respectively. In-reach and out-reach centralization are the degree of similarity of the food web to an in- or out-, respectively, star network of equal size. A star network, in the context of food webs, is a single consumer for which all other species are resources (in-star) or a single resource for which all other species are consumers (out-star).

GRC is a measure of the variation in node centrality, with the idea that variation in centrality is a measure of hierarchy in a network (Mones et al. 2012). Centrality can be "in" or "out", and so a measure of GRC was calculated for each: GRCo for out-reach centrality and GRCi for in-reach centrality. GRCi and GRCo can be understood as measures of top-down and bottom-up, respectively, hierarchy in the food web.

Food web models

We used a classic null model approach (Harvey et al. 1983) to compare the structure of published food webs to the structure predicted by null models. The three null models used were the random, niche, and cascade models. In the random model, for a food web of given species richness, *S*, and a given connectance, *C*, links are assigned between any two species with equal probability (Williams and Martinez, 2000). In the cascade model (Cohen and Newman, 1985) given *S* and *C*, each species is randomly assigned a value drawn uniformly from the interval [0,1]. Each species consumes a given species with a value less than its own with a

probability P= 2CS/(S-1), creating a nested hierarchy structure of predators and prey. The niche model (Williams and Martinez, 2000) builds on the cascade model with the concept of the "niche value" – a range of values within which all of prey of a given species fall. Instead of preying upon any species with a value less than its own, a species preys upon species which fall within a certain interval of values less than its own value.

Given the number of species and the number of links in a food web, we generated simulated food webs according to the random model (Hart. 2014). For each published food web, we generated 25 simulated food webs. We calculated the same food web variables for the simulated food webs as we did for the published food webs. We repeated the same process of model simulation for the cascade (Hart 2014) and niche (Petchey 2014) models.

Exogenous variables and bias

For each food web, we determined the approximate latitude, maximum annual temperature, average monthly precipitation, whether it was are terrestrial or aquatic, and the ecosystem type. We calculated the approximate longitude and latitude of the food webs based on locations as described in the source paper for each food web. We determined the maximum annual temperature and average monthly precipitation for the approximate location of the food webs. Climate variables were obtained from WorldClim (Hijmans et al. 2005), high resolution data which was accessed via the *getData* function of the *raster* package in R (Hijmans 2014). We assigned a value of 1 to aquatic food webs and 0 to terrestrial food webs because a number of authors have noted systematic differences between aquatic and terrestrial food webs (Shurin et al. 2006). Ecosystem type of each food web was supplied by GlobalWeb.

Many of the food webs in the GlobalWeb database were published together within the same research paper. Food webs which were described as part of the same study were subject to most of the same potential biasing factors. These sets of concurrently-produced food webs shared the same authors, the same sampling methods, and the same descriptive methods. Therefore, as a proxy for the biases introduced by the particular methodologies used in each study, we used study identity.

Ordination

In order to collapse the variation in the proportions of species at multiple trophic levels into fewer dimensions, we used ordination analysis. We used the function *metaMDS* from the package *vegan* (Oksanen et al. 2015) to perform NMDS on the fraction of basal, herbivore, omnivore, intermediate, cannibal, and top predator species. We then used the function *envfit*, also from the *vegan* package, to fit variables to the ordination.

For the first ordination analysis, we performed NMDS on all the food webs, published and simulated. We then fit the food web type (published, random, cascade, and niche) to the ordination to determine the goodness of fit (R²) and the empirical p-value of food web type. Next, we performed NMDS ordination on only the published food webs. We fit the endogenous, exogenous, and study identity variables to the published food web ordination.

Linear models

We used linear models of various types in order to quantify patterns in prey: predator ratio and nestedness (NODF). First we used a linear mixed effects model (function *lmer* from package *lme4*; Bates et al. 2014) to detect differences between food web types (published, random, niche, and cascade) in regards to prey: predator ratio. Web type and study identity were fixed effects and food web identity (remember that equivalent simulated webs were generated for each food web) was a random effect. We used a Tukey post-hoc test with the function *glht* from the function *multcomp* (Torsten et al. 2008) to detect the location of significant differences between food web types. We performed an equivalent analysis to detect differences between food web types in regards to nestedness.

Using a one-sample t-test (*t.test* function from the R *stats* package), we tested the difference of prey: predator ratio of each food web type from 1. In order to determine whether prey: predator ratio is scale variant, we tested a linear regression model of predator species richness with prey species richness as the sole explanatory variable. We also tested the same model but with the log of the two variables in order to evaluate a power-law relationship, and compared the R² of the two models.
In order to determine the endogenous and exogenous variables that determine prey: predator ratio and nestedness (NODF), we used the function *Im* from the R *stats* package. We then subjected the models to step-wise selection using the function *stepAIC* from the R *stats* package, which uses AIC to determine the model with the most parsimonious fit. In the first model, we included all endogenous variables as predictors of prey: predator ratio. In the second model, we included all exogenous variables as predictors of prey: predator ratio. In the third model we included all exogenous variables as predictors of nestedness. In the final set of models, we tested study identity as a predictor of prey: predator ratio, and then of nestedness.

Variance partitioning

To determine the relative contributions of each set of variables (endogenous, exogenous, and bias) to trophic biodiversity structure, we used variance partitioning (function *varpart* from the package *vegan*). Our response variable matrix was the proportions of basal, herbivore, omnivore, intermediate, cannibal, and top predator species. Our set of exogenous variables did not included the terrestrial versus aquatic variable because this variable was collinear with the ecosystem type variable. In the first variance partitioning analysis we included the exogenous and endogenous variable sets. In the second variance partitioning analysis we included all three variable sets (endogenous, exogenous, bias).

2.4 Results

Published food webs

Our meta-analysis included 72 published food webs from 24 different studies. The selected food webs were large, included recent studies, and covered a wide range of ecosystems. The webs had a mean species richness of 90.03 (SD=31.34) with a range from 50 to 209 species. The mean year in which the food webs were published was 2001.1 (SD=16.214), with a range from 1929 to 2013. Food webs were from both aquatic (n=56) and terrestrial (n=16), from 12 different ecosystem types (terrestrial, parasitoid community, tree log, carrion, stream, marine, pond, lake, shrubland, forest, wetland, pitcher plant), and distributed broadly around the world.

Comparison of published and model food webs

Ordination analysis of the proportions of species richness at each trophic level of published, random, cascade, and niche food webs revealed a significant effect of food web type (R²=0.494, p<0.0001). The differences in species richness distribution across trophic levels are visible in Fig. 2.1: published food webs had a bottom-rich top-poor structure which is not found in the model food webs. The LME model of prey: predator ratio with all food web types found that the ratio was higher for published food webs than for any of the food web models (F=79.893; p<0.0001; Fig 2.2A). T-tests, which tested the difference of each food web type prey: predator ratio from 1, found that published food webs had a ratio significantly greater than one (mean=1.835; t=5.86; p<0.0001). The LME model of nestedness (NODF) found that, like for the prey: predator ratio, published food web nestedness was strongly and significantly greater than for any of the model food webs (F=32.844; p<0.0001; Fig 2.2B). The predator species richness increased with prey species richness (β =0.29; p=0.006; R²=0.103). The log-log model resulted in a slightly worse fit (β =0.346; p=0.0431; R²=0.057). If the food webs are restricted to belong to the stream ecosystem type, the only ecosystem type for which there were >10 food webs, the model fit improved dramatically for both the linear (β =0.405; p<0.0001; R²=0.392) and the log-log model (Fig 2.3; β=0.748; p<0.0001; R²=0.345).

Endogenous variables

Ordination analysis of the proportions of species richness at each trophic level of published food webs found significant effects of several endogenous variables: GRCo (R^2 =0.709; p<0.0001), GRCi (R^2 =0.317; p<0.0001), in-reach centralization (R^2 =0.192; p=0.001), out-reach centralization (R^2 =0.3879; p<0.0001), number of trophic levels (R^2 =0.683; p<0.0001), and link density (R^2 =0.489; p<0.0001). Out-reach centralization, in-reach centralization, trophic position, and GRCo formed one directionally-similar group in the ordination space. After stepwise selection, the linear model of prey: predator ratio of published food webs with endogenous variables found that GRCo (β =-1.428; p<0.0001), GRCi (β =1.186; p<0.0001), and link density (β =-0.1; p<0.0001) all had a significant effect on prey: predator ratio.

Exogenous variables

Ordination analysis of the proportions of species richness at each trophic level of published food webs alone found significant effects of absolute latitude ($R^2=0.271$; p<0.0001) and ecosystem type ($R^2=0.649$; p<0.0001). Temperature and latitude were strongly negatively correlated ($R^2=0.54$). Aquatic (n=56) and high absolute latitude (>41°; n=41) food webs were bottom-rich top-poor in topology, while in contrast terrestrial (n=16) and low absolute latitude (<41°; n=31) food webs were uniform. The proportion of species in the top trophic level was less in the aquatic (mean = 0.16; SD = 0.19; SE = 0.03) than the terrestrial food webs (mean = 0.35; SD = 0.25; SE = 0.06). The proportion of species in the basal trophic level was greater in the aquatic (mean = 0.47; SD = 0.24; SE = 0.03) than the terrestrial food webs (mean = 0.32; SD = 0.25; SE = 0.06).

After stepwise selection, the linear model of prey: predator ratio of published food webs with exogenous variables found that ecosystem type (F=30.31; p<0.0001), latitude (β =0.029; p<0.0001), and precipitation (β =-0.0253; p=0.047) all had a significant effect. Wetland ecosystems had a significantly higher prey: predator ratio than any other ecosystem type (mean = 5.81), followed by the stream ecosystem, which was significantly higher than most other biomes (mean = 2.13). Together, all other ecosystems had a mean ratio of about 1 (mean = 1.06, SD=0.587). Findings were similar, after stepwise selection, for the linear model of nestedness (NODF) for published food webs with exogenous variables. Ecosystem type again had a significant effect (F=11.8; p<0.0001), while temperature and latitude were retained in the model but had no significant effect. Marine ecosystem food webs had the greatest nestedness, with a mean significantly greater than most other ecosystem types (mean = 46.71), while forest food webs had the lowest nestedness, significantly lower than most other ecosystems (mean = 6.75).

Study identity

The ordination analysis of the proportions of species richness at each trophic level of published food webs alone found that study identity was highly significant and explained more variation than any other single variable (R²=0.896; p<0.0001). The linear model of prey: predator ratio for

published food webs with study identity as the sole explanatory factor was also highly significant with a high explanatory power (R^2 =0.952; p<0.0001). Likewise, the linear model of nestedness for published food webs with study identity was highly significant with a high explanatory power (R^2 =0.781; p<0.0001).

Variance partitioning

Variance partitioning of all three variable classes (endogenous, exogenous, and bias) found that together the variables explained 95% of the variation in trophic diversity structure (proportions of basal, herbivore, omnivore, intermediate, cannibal, and carnivore species). Endogenous variables, exogenous variables, and study identity accounted respectively for 9%, 0%, and 2% of the variation independently. 53% of the variation was shared by all three sets of variables, 18% was shared between study identity and endogenous variables, and 12% was shared between study identity and endogenous variables, and 12% was shared between study identity and endogenous variables, and 12% was shared between study identity and endogenous variables, and 12% was shared between study identity and endogenous variables, and 12% was shared between study identity and endogenous variables, and 12% was shared between study identity and endogenous variables, and 12% was shared between study identity and endogenous variables, and 12% was shared between study identity and endogenous variables, and 12% was shared between study identity and endogenous variables, and 12% was shared between study identity and endogenous variables, and 12% was shared between study identity and the two other variable classes, however, the values produced by variance partitioning are not reliable. Variance partitioning of only endogenous and exogenous variables together explained 93% of the variation in the data. 53% of the variation was shared between the two variable sets, while endogenous variables explained 28% independently, and exogenous variables explained 12% independently.

2.5 Discussion

2.5.1 How is diversity distributed across trophic levels?

Published food webs form "pyramids of species richness" (Fig 2.1A). That is to say, their diversity structure is bottom-heavy-top-poor. Published food webs have multiple prey for every predator and they have a strong nested hierarchy structure. These patterns are not generated by chance (random model), nor can they be fully explained by simple hierarchical models (cascade and niche models). This decrease in species richness with trophic level parallels the well-known pyramids of biomass and numbers, first recognized by Elton (1927). In the case of all these pyramids, the source of the pyramid structure is the energy loss at each trophic level

(Lindeman 1942). If energy availability drives species richness, either at an evolutionary- or community-level, we can expect fewer species at higher trophic levels (Evans et al. 2005).

Ordination found that neither the random, cascade, nor niche models generated similar trophic diversity structure to the published food web (Fig 2.1), therefore pyramids of species richness are not generated by chance, nor are they generated by simple hierarchical food web models. The cascade model food webs most closely resembled the published food webs, except with many more species belonging to intermediate trophic levels. The average prey: predator ratio of the published food webs was significantly greater than 1, with nearly two prey for every predator (Fig 2.2A). Only the cascade model, among the food web models, produced a mean prey: predator ratio significantly above 1. Even still, the published food web prey: predator ratio was significantly greater than all food web models, including the cascade model. The degree of nestedness, a measure of hierarchy, found in the published food webs was also significantly greater than the nestedness of any of the food web models (Fig 2.2B). That is, in the published food webs, consumers at given trophic levels tended to consume a nested subset of the resources consumed by the trophic level above them.

The partial success of the cascade model may indicate that the hierarchical structuring mechanisms implicit in the cascade model are also found in published food webs. The published food webs, however, were even more nested, prey-heavy, and pyramid shaped than the cascade model food webs. Taken together, these results suggest that food webs have strong structuring mechanisms that produce a stronger hierarchical pattern than that produced by the cascade model.

If prey: predator ratio is constant, we would expect a linear relationship between predator and prey species richness and a slope of 1 in a log-log regression. The proportion of variation explained by the linear model was only slightly greater than the log-log model, for both the full model and the stream-only model. The slopes of the log-log regression models were <1, although the 95% CI of the stream model overlapped with 1 (β =0.748 ± 0.324). The log-log stream model suggest a possible ¾-power law relationship of prey: predator species richness, as was found by Hatton and colleagues (2015) for prey: predator biomass (Fig 2.3). The results,

however, are most consistent with a scale-invariant predator-prey ratio, though further analysis with greater statistical power may be warranted.

2.5.2 What determines trophic diversity distribution?

The distribution of species richness across trophic levels in food webs is determined by variables that are either endogenous or exogenous to the food webs. The role of these structuring variables is obscured to an unknown extent by biases introduced by methodology.

Food webs with a strong pyramid structure and a high prey: predator ratio tended to have high GRCi and in-reach centralization. Food webs with weak or absent pyramid structure and a low prey: predator ratio tended to have high GRCo and out-reach centralization. These correlations provide clues to species-level consumer-resource relationships that lead to a food web-level pyramid structure. In particular, our data suggests that the centrality of species in the food web plays a role in determining the food web's trophic diversity structure. In terms commonly used in ecology, a species with high in-reach centrality is a generalist and a species with low in-reach centrality is a specialist; we are unaware of a corresponding ecological term for describing outreach centrality. If a food web contains one or more species that are strong generalists, the modules contributed by those species will tend to make the food web more prey-rich. Similarly, if a food web tends to be made up of consumers which have multiple resources, each of which have several resources, and so on, this hierarchical structure will likewise generate a pyramid of species richness. The inverse is also true: if a food web contains one or more species that have many predators or if a food web tends to be made up of resources that have several consumers, each of which have several consumers, and so on, the food web will tend towards an inverted pyramid of species richness with a low prey: predator ratio. One common example in natural ecosystems is a plant with multiple arthropod herbivores, each of which is parasitized by multiple parasitoids, each of which is hyper-parasitized (for example, Poelman et al. 2013). The out-reach centrality of a species clearly has a relationship to the structure of its community, yet this trait is so little considered in ecology that, unlike in-reach centrality, no common term exists to describe the degree of out-centrality. It is unclear if consumer-resource relationships at the species-level determine trophic biodiversity structure, if the causal relationship is in the

other direction, or if the relationship is reciprocal. Further investigation is required to determine the causal relationship.

Food webs in aquatic and high latitude ecosystems tended to have a top-poor bottom-rich pyramid of species richness structure and a high prey: predator ratio. The trophic biodiversity structure also differed between ecosystem types, with some of the aquatic ecosystem types having a high prey: predator ratio (stream and wetland) and high nestedness (marine). It seems likely that there are two variables at play: (1) latitude and the variables which co-vary with latitude, and (2) aquatic versus terrestrial ecosystems, within which there are some differences between the types of terrestrial and aquatic habitat. Published food webs of communities which are far from the equator and/or aquatic tend to have a pyramid of species richness structure, while communities which are close-to the equator and/or terrestrial tend to have a uniform trophic diversity distribution (Fig 2.4).

Latitude can act as a proxy for a large number of inter-related variables, including temperature, primary productivity, sunlight intensity, and human population density; we do not know which of these latitudinal covariates is driving food web trophic structure. Overall, species richness was greater in the low-latitude than the high-latitude food webs (means = 96.2 and 85.4, respectively). It has long been noted that diversity decreases with latitude (Pianka 1966; Hillebrand 2004), but in the communities represented by the food webs in our meta-analysis, the diversity-latitude effect seems to be stronger for producers than for consumers. High diversity at low latitudes is not surprising; the puzzling thing is that diversity trickles up the trophic levels in low-latitude but not nearly to the same extent in high-latitude food webs. Solar energy is at a maximum near the earth's equator, which could drive diversification of plants (Partel et al. 2007). High plant diversity could also be driven by accelerated evolution rates at high temperatures (Brown 2014).

Although terrestrial and aquatic ecosystem are not fundamentally different, they differ in some consistent ways (Webb 2012). Their distribution of diversity across trophic levels appears to be one of those differences: aquatic food webs form pyramids of species richness while terrestrial food webs have a uniform distribution (Fig 2.4). One consistent difference between terrestrial

and aquatic ecosystems is the distribution of body size across trophic levels (Shurin et al. 2006). In pelagic food webs, there is a positive correlation between trophic level and body size, whereas there is no such relationship in terrestrial food webs. The strong pyramid of species richness structure seen in aquatic food webs may therefore be a result of scale. Within a community that researchers have sampled to create a food web, a large diversity of small phytoplankton species is easily found, while large predators will tend to have low density and thus low diversity in a given area. Still, as with high-latitude food webs, the question remains of why diversity is not lost with the loss of energy at each trophic level in terrestrial food webs.

Although, on average, food webs form pyramids of species richness, large and important subsets of described communities form uniform distributions or inverse pyramids; these include terrestrial and low-latitude food webs. Considering that the vast majority of humans live in terrestrial and low-latitude ecosystems, these are very important exceptions indeed.

Food webs are caricatures of complex systems (Hallam 2009). The caricature cartoonist and the scientist both hope to capture the essential characters of their subject despite the unavoidability of approximation and simplification. In our research, the effect of endogenous and exogenous variables on food web structure is obscured by methodological bias to an unknown degree. The study identity was strongly correlated with the trophic diversity distribution, the prey: predator ratio, and the nestedness of published food webs, and in all cases explained a majority of the variation. The high explanatory power of study identity suggests that food web diversity structure was determined more by who made the food web than by properties of the community being described. An equally plausible explanation, however, is that authors tended to choose study systems which were ecologically similar. Indeed, there was a high degree of collinearity between study identity and several endogenous and exogenous variables.

When endogenous and exogenous variables were considered without study identity, they together explained the vast majority of variation in trophic diversity distribution (90%). Centrality, latitude, and ecosystem type (aquatic versus terrestrial) are the endogenous and exogenous variables that drive the high explanatory power. Because of collinearity between the

endogenous and exogenous variables with study identity, we cannot be sure of the role of methodological bias in determining food web trophic diversity distribution.

2.5.3 Conclusions and future directions

Directly analogous to Elton's pyramids of numbers and biomass, diversity is distributed across trophic levels in a pyramid of species richness. That is to say, food webs have the highest species richness at the basal trophic level and increasingly less species richness as trophic level increases. The proportions of the pyramid of species richness in some ecosystems may be scale-variant according to a ¾-power law. Food webs are more consumer-poor and resource-rich than is expected by chance or by simple hierarchical food web models. The distribution of species richness across trophic levels is driven by endogenous and exogenous variables, especially by centrality, latitude, and ecosystem type. Patterns in trophic diversity distribution are obscured to an unknown extent by methodological bias.

Our meta-analysis leads naturally to a number of questions: Does prey: predator species richness vary according to a ¾-power law? What is the role of out-centrality in determining ecosystem structure? How do sampling methods differ in their ability to capture biodiversity at each trophic level? Why is biodiversity not lost with trophic level in terrestrial and low-latitude ecosystems? Research about the distribution of biodiversity across trophic levels will lend new perspective to ongoing scientific dialogue about biodiversity and ecosystem functioning and services (Hooper et al. 2005; Mace et al. 2012).

2.6 Acknowledgements

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Figure 2.1. The average proportion of species present at basal, herbivore, intermediate trophic level for A) the published food webs (n = 72), and the corresponding B) random, C) cascade, and D) niche model food webs. The model food webs correspond to the published food webs in their number of species and links. The length of each line flanking the bars is the SE/2.



Figure 2.2. A) The prey: predator ratio and B) the nestedness (NODF) of published food webs (n = 72), and the corresponding random, cascade, and niche model food webs. The model food webs correspond to the published food webs in their number of species and links. Note the log scale of the y-axes for both plots. Bars represent the median, first and third quartiles, and 95% confidence intervals. A) All food web types were significantly different from 1 (*** indicates p < 0.001) and significantly different from one another in regards to prey: predator ratio with published food webs having the highest predator-prey ratio. B) All food web types were significantly different from each other in nestedness, with published food webs having the highest nestedness.



Figure 2.3. Simple linear regression model of log(predator species richness) and log(prey species richness) of stream habitats is given as a black line (n=41; β =0.748; p<0.0001; R2=0.345). Slope of 1 is given as a dotted line.



Figure 2.4. The average proportion of species present at basal, herbivore, intermediate trophic level for A) aquatic (n=56), B) terrestrial (n=16), C) high absolute latitude (>41°; n=41) D) a low absolute latitude (<41°; n=31) published food webs. The length of each line flanking the bars is the SE/2. Note the strong pyramid structure of A) and C) and the uniform structure of B) and D).

Connecting Text:

The following two chapters, Chapters 3 and 4, concern the community structure of tundra organisms and are based on my field work in the Yukon, Canada. In Chapter 3, I describe correlations between environmental variables and macroinvertebrate and soil prokaryote communities in the Yukon. I collected samples along a forest-tundra ecotone, which allowed me to test several hypotheses regarding the effect of the latitudinal biome transition on community structure. Few previous studies have described and contrasted co-occurrent invertebrate and microbial community responses to environmental variables. I found that the trophic structure of communities became more bottom-heavy, top-poor as latitude increased. I tested whether the same pattern was found for the sampled macroinvertebrate communities. This chapter addresses the question: *How do macroinvertebrate and soil prokaryotes communities change along a forest-tundra ecotone and with environmental variables in the Yukon?*

Contributions of authors: The authors that contributed to this work are Shaun Turney¹, Ianina Altshuler¹, Lyle G. Whyte¹, and Christopher M. Buddle¹. ST, IA, and CMB conceived the ideas and designed the methodology. ST collectsed and analysed the data and led the writing of the manuscript. IA led the soil microbial analysis. All authors contributed critically to the drafts.

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Chapter 3: Macroinvertebrate and soil prokaryote communities in the forest-tundra ecotone of the Subarctic Yukon.

3.1 Abstract

The forest-tundra interface is the world's largest ecotone, and is globally important due to its biodiversity, climatic sensitivity, and natural resources. The ecological communities which characterize this ecotone, and which provide local and global ecosystem services, are affected by environmental variation at multiple scales. We explored correlations between environmental variables and macroinvertebrate and soil prokaryote communities in the foresttundra ecotone of the Yukon, Canada. We found that each tussock tundra site possessed a distinct community of macroinvertebrates and prokaryotes, and therefore represented a unique contribution to regional biodiversity. Prokaryote diversity increased with active layer depth, which could be an effect of temperature, or could be evidence of a species-area effect. Prokaryote diversity decreased with lichen cover, which could be due to antimicrobial properties of lichen. The macroinvertebrate community composition was affected by proximity to a human disturbance, the Dempster Highway. Both macroinvertebrate and prokaryote community composition changed along the latitudinal transect, as the biome transitioned from taiga to tundra. We also found that the abundance of carnivores relative to herbivores decreased with latitude, which adds to recent evidence that predation decreases with latitude. Our survey yielded new insights about how macro- and microorganisms vary together and independently in relation to environmental variables at multiple scales in a forest-tundra ecotone.

3.2 Introduction

Macroorganisms and microorganisms respond to environmental variation in different ways, and often at different scales (Fierer & Jackson 2006). Global biodiversity of plants and animals forms a latitudinal gradient, peaking at the equatorial band formed by the tropics (Gaston 2000).

Many other spatially and temporally large-scale variables, including elevation, glacial history, and geographic barriers affect macroorganism communities (Polis 1999; Badgley & Fox 2000; Martiny et al. 2006). Recent studies have suggested a decrease in predation with latitude (Chapter 2; Roslin et al. 2017), indicating that interactions among macroorganisms are also affected by latitude (Schemske et al. 2009). While large-scale environmental variables are often invoked to explain abundance and distribution of macroorganisms, theory holds that local contemporary variables are more important for microorganisms (Fierer & Jackson 2006). A foundational theory of microbial ecology is that "Everything is everywhere, but, the environment selects" (Beijerinck 1913; Baas Becking 1934). In other words, all microbes are cosmopolitan, but contemporary local conditions will determine which microbes dominate at a given location (De Wit & Bouvier 2006). Microorganisms have high dispersal rates and large population sizes, and so geography has historically been thought to play a minor role (O'Malley 2007).

Due to the many interactions between micro- and macroorganisms, however, we can expect that microorganisms will respond indirectly to variables that affect macroorganisms. Micro- and macroorganisms are connected through networks of consumption, mutualism, competition, and parasitism. Soil microbes play important roles in nutrient and decomposition processes (Rodriguez & Fraga 1999; Lavelle et al. 2006; van der Hijden et al. 2008). Soil microbes increase plant productivity by solubilizing phosphate (Rodriguez and Fraga 1999) and fixing nitrogen (van der Hijden et al. 2008). Prokaryotes and macroinvertebrates compete for nutrients in soil and detritus (Berg et al. 2001). Macroinvertebrates, such as bacteriophagous nematodes, affect soil bacterial structure through consumption, resulting in energy and nutrient flow from bacteria to macroinvertebrates (Blanc et al. 2006).

It is increasingly recognized that micro- and macroorganisms both respond to environmental variation at multiple spatial scales (Martiny et al. 2006; Hanson et al. 2012). Studies in a variety of ecosystems have demonstrated that both macroinvertebrates and bacteria respond to environmental variation from the scale of centimeters, such as soil quality (Nielsen et al. 2010) and trophic interactions (Wardle et al. 2004; Wardle 2006), to the landscape or regional scale, such as vegetation (Bokhorst et al. 2014; Bokhorst et al. 2016) and latitude (Yergeau et al. 2007;

Yergeau et al. 2009). A better understanding of the shared and contrasting drivers of micro- and macroorganism biogeography will provide vital insight into the processes controlling Earth's biodiversity and biogeochemistry (Fierer & Jackson 2006).

The forest-tundra ecotone is a polar region that is undergoing rapid social and environmental change (Callaghan et al. 2002). It is the world's largest ecotone (Ranson et al. 2004) and is ecologically important at a global level due to its resources, its contribution to land-atmosphere interactions, and its biodiversity (Callaghan et al. 2002). Research on the relationships between environmental variation and ecological communities is especially important in polar regions, where rapid climate change is impacting environmental variation. Polar regions are more sensitive to the effects of global change than temperate and equatorial regions (Ford et al. 2006; McGuire et al. 2009). Subarctic and Arctic tundra communities are undergoing rapid changes, such as changes in shrub encroachment and density (Myers-Smith et al. 2015; Rich et al. 2013). Warming experiments indicate that as climatic warming continues, tundra emissions of greenhouse gasses will increase (Voigt et al. 2016), primary productivity and nutrient cycling rates will increase (Xue et al. 2016), and interspecific interactions will be altered (Barrio et al. 2016). In the Yukon, melting permafrost due to climate change has led to severe erosion of the Dempster Highway (CBC News 2015). These developing challenges highlight the urgency of gaining a fundamental understanding of Northern tundra ecology and its relationship to environmental variables.

The microbial ecology of Yukon tundra soil has so far received little attention, although there have been studies in neighbouring regions, including Alaska (Wallenstein et al. 2007; Kim et al. 2014) and the Northwest Territories (Chu et al. 2011). Previous research has described components of Yukon tundra macroinvertebrate community ecology, especially spider (Bowden & Buddle 2010; Bowden & Buddle 2012a; Bowden & Buddle 2012b) and beetle communities (Ernst and Buddle 2015). Very few studies have investigated correlations between macroinvertebrate and soil microbial communities in the tundra context (but see Sørensen et al. 2006).

In this study, we describe the macroinvertebrate and soil prokaryote communities at five tussock tundra sites in the Yukon, Canada. These sites were located along a latitudinal transect covering 280 km and the transition from taiga to tundra (CCEA 2016). This provided significant environmental variation that allowed us to examine relationships between environmental factors and the structure and composition of biological communities. We investigated correlations between the macroinvertebrate and soil prokaryote communities, and correlations with environmental variables, including latitude, road proximity, vegetation, soil type, and active layer depth. We predicted that community composition of both macroinvertebrate and soil prokaryotes would correlate to environmental variation at multiple scales: local (e.g., soil type, active layer depth, vegetation cover), landscape (e.g., road proximity), and regional (e.g., latitude). The taiga-tundra biome transition allowed us to test hypotheses about how the communities changed across this ecotone. First, we predicted that macroinvertebrate abundance and diversity would decrease with latitude, from the taiga ecozone in the south to the tundra ecozone in the north, following classic latitudinal gradients in diversity and productivity (Gaston 2000). Second, in accordance with the classic view that "everything is everywhere", we predicted that prokaryote diversity would be constant over our study region. Third, we predicted that the relative abundance and diversity of carnivores would decrease with latitude.

3.3 Methods

3.3.1 Site Description and Study Design

In July 2015, we assessed the soil prokaryote and terrestrial macroinvertebrate communities at five sites located along the Dempster highway in the Yukon Territory (Fig 3.1). Our 280-km sampling transect captured a transition from a taiga biome in the south (Site 5, 64.60°N; Fig 3.1) to a tundra biome in the north (Site 1, 66.97°N). The Dempster Highway, officially opened in 1979, is a 746-km, two-lane, all-season gravel road which extends from 40 km north of Dawson City, Yukon, to Inuvik, Northwest Territories. The climate of the region is typical of northwestern North America, with a short growing season (June-August) and harsh winters. The

average temperature in July 2015 at Rock River (66.98°N, 136.22°W) was 10.8°C with a total of 69.2 mm of precipitation (Environmental Canada 2017).

In the region surrounding Sites 1 and 2, there were spruce-tamarack shrub stands and riverine poplar-spruce shrub stands. In the region surrounding Site 3, there were spruce stands and riverine poplar-spruce stands. In the regions surrounding Sites 4 and 5, there were closed conifer forests and riverine willow stands (Stanek et al., 1981). Overall, the size and density of these trees and shrubs decreased steeply with latitude over the studied region. The altitude of the sites decreased with latitude, with the two north-most sites being between 665-690 AMSL, and the most southern site being 1187-1202 AMSL (Table 3.1). Sites 4 and 5 were within the Ogilvie Mountain range.

At each of the five sites, we sampled five 1 m² quadrats that were placed 50 m apart and were 50-450 m from the Dempster Highway. We haphazardly chose tundra sites and quadrats that were dry (no open water), on level ground, dominated by cotton grass tussocks, and contained no trees or shrubs taller than 0.4 m. The sites had no signs of previous human disturbance besides the nearby highway. Samples were collected in 2015 on July 5th (Site 1), 8th (Site 2), 14th (Site 3), 18th (Site 4), and 22nd (Site 5).

We delineated the 1 m² perimeter of each quadrat with a ~20 cm deep narrow trench in which we inserted and secured the base of a 1.35 m tall mesh tent (Style of Mine Fashion and Outdoor Products Co. Ltd., Anti-Mosquito Meditation Tent, light grey; Fig 3.2). The tent created a closed environment which effectively prevented macroinvertebrates, except for soil invertebrates deeper than ~20 cm under the soil surface, from entering or leaving the ~1.35 m³ space.

3.3.2 Macroinvertebrate and soil collection

Immediately after securing each tent, we hung a glue trap (Catchmaster[®] Spider and Insect Glue Trap) from the top of the tent on the inside. We set a yellow pan trap (filled with 50% propylene glycol, 50% water, with a small amount of dishwashing detergent) nestled in the ground within the tent. All manipulations within the tent were performed by opening the tent door zipper only to the extent required for the manipulation, to avoid dispersal of

macroinvertebrates into and out of the tent. We allowed the traps to collect surface-dwelling and flying macroinvertebrates for a period of 40-48 hours.

Upon returning to the tents, we removed the glue and pan traps. We wrapped the glue traps in plastic wrap and stored the drained contents of the pan traps in 90% ethanol for later identification in the lab. We collected invertebrates and debris within the tent using a D-vac which was applied thoroughly within the tent, including the soil surface, for two minutes. The vacuum was designed after Stewart and Wright's (1995) sampling apparatus, and was made by modifying the commercial leaf vacuum, Weed Eater[®] 25cc Leaf Blower/Vacuum. We stored the material collected by the D-vac in 90% ethanol for later identification in the lab.

For each quadrat, after applying the vacuum, we took three 10 cm diameter soil cores from the surface vegetation to the permafrost, from three arbitrary locations in each of the quadrats. We placed the first soil core in a Winkler funnel (Besuchet et al. 1987), which was remixed daily and allowed to collect soil macroinvertebrates for three nights. Winkler funnels can be equally as effective at extracting macroinvertebrates from substrate as Berlese funnels (Smith et al. 2008; Sabu et al. 2011) but have the added advantage of not requiring electricity (which was not available to us). In the field, we picked apart the second core meticulously within three days of collection, removing any macroinvertebrates visible without a microscope. We stored these soil macroinvertebrates and the output of the Berlese funnels in 90% ethanol for later identification in the lab. In total, we therefore sampled macroinvertebrates from 1.57% of the total soil volume underlying the quadrat ([2*(3.1415*(5cm)²)]/(100cm)²). We oven-dried the final soil core to remove moisture for quantification of soil and vegetation biomass.

By using common sampling methods (pan trap, D-vac, glue trap) within a tent, the size of the area sampled was known because the tent prevented dispersal into and out of the sampled area. In contrast, when a tent or other barrier is not used, the area sampled is undefined, so very little can be inferred about density or relative abundance. This tent method therefore allowed us to answer questions about relative macroinvertebrate abundance among sampling locations and within sites for surface-dwelling macroinvertebrates. However, for invertebrates <~1 mm, our density estimates will be substantially less than true density. This was because our

methods (pan traps, D-vac, sticky trap) were designed for trapping macroinvertebrates > 1 mm and because we did not have access to a microscope in the field. For soil invertebrates >20 cm below the surface, dispersal into and out of the tent was possible. For fast-moving macroinvertebrates, individuals may have fled as we set down the tent. Because the sampling effort and method was consistent, we assumed that the degree of underestimation was constant across samples, and therefore the relative abundance of macroinvertebrates could be compared across samples.

For 16S prokaryote community analysis we collected one smaller (~5 g) soil sample from the top 15cm of the soil of each quadrat and preserved samples in absolute ethanol as described by Harry et al. (2000). Due to the cost of DNA sequencing, we selected soil samples from four out of the five randomly selected quadrats at each site, for a total of 20 samples for soil 16S community sequencing.

3.3.3 Abiotic variables

At each quadrat, we measured several abiotic variables. We paced the distance from the Dempster highway to the quadrats to estimate the distance. We measured the active layer depth as the depth of the hole left by the soil core to determine the distance between the soil surface and the permafrost. We used a GPS to record the latitude, longitude, and altitude of each quadrat. After removing the tent, we photographed the quadrat at chest height (~1.2 m) from directly above. We analyzed each quadrat photo using the software ImageJ (Schneider et al. 2012) on the platform Fiji (Schindelin et al. 2012). We first measured the surface areas of the different vegetation types in each photo (grass, forb, shrub, moss, and lichen), which we then converted to a proportion cover for each vegetation type at each quadrat. We separately weighed the vegetation biomass that was removed from the third soil core in each quadrat. We assessed the soil type visually and categorized it as sandy, silty, clay, peaty, chalky, or loamy.

3.3.4 Identification of invertebrates

In the lab, using a microscope, we identified all samples from the soil cores, Winkler funnels, glue traps, pan traps, and D-vac which had previously been preserved in the field. We identified

insects and spiders to the family level, except for damaged or juvenile individuals and Thysanoptera, which were identified only to order. We did not identify the specimens to species or morphospecies. Non-insect groups (Acari, Collembola, Annelida, Gastropoda, Nematoda, and Myriapoda) were identified to varying levels, typically to order. We also classified taxa, when possible, by trophic group. We excluded microinvertebrates from our analysis (Enchytraeidae and Rotifera) because they were not the focus of our study and because our methods strongly under-sampled microinvertebrates.

3.3.5 16S rRNA microbial community profiling – prokaryote DNA extraction, sequencing, and analysis

For 16S microbial analysis, we extracted DNA from soil samples using 2 g of soil and the DNeasy PowerSoil Kit from MoBio Laboratories, following the manufacturer's guidelines. The extracted DNA was concentrated using a centrifugal evaporator. The 2 g soil samples were weighed out from the ~ 5 g of soil per quadrat that was collected and preserved in the field. Molecular Research DNA Lab (MR DNA; www.mrdnalab.com; Shallowater, TX, USA) sequenced the DNA. The 16S rRNA gene V4 variable region was amplified using 515F/806R primers that target both bacteria and archaea (Caporaso et al., 2012). The DNA was amplified using 28-cycle PCR with HotStarTaq Plus Master Mix Kit (Qiagen, USA) using the program: 94°C initial denaturation for 3 minutes, followed by 28 cycles at 94°C for 30 seconds, 53°C for 40 seconds and 72°C for 1 minute, with a final elongation step at 72°C for 5 minutes. PCR products were checked on a 2% agarose gel.

The separately indexed samples were pooled in equal proportion for sequencing and purified using Ampure XP beads (Beckman Coulter). The indexing of individual samples allows them to be sequenced simultaneously, while retaining the ability to distinguish the samples. The samples were then used to make an Illumina DNA library and sequenced at MR DNA on a MiSeq 2x300bp following the manufacturer's guidelines. Sequencing data were processed using MR DNA analysis pipeline (MR DNA, Shallowater, TX, USA). Briefly, the forward and reverse read sequences were joined, depleted of indexes, the sequences were then denoised, operational taxonomic units (OTUs) were generated and chimeras were removed. OTUs were defined by

clustering at 97% similarity and were taxonomically classified using BLASTn against a curated database derived from RDPII and NCBI (<u>www.ncbi.nlm.nih.gov</u>, <u>http://rdp.cme.msu.edu</u>). Sequence data has been deposited on GenBank (BioProject accession number = PRJNA385195).

3.3.6 Statistical analyses

Ordination: To check for variance inflation among continuous environmental variables (Table 3.1), we used the *HH* function, *vif* (Heiberger & Robbins 2014). In subsequent analyses involving environmental variables as explanatory variables, we excluded variables strongly correlated with latitude to resolve elevated variance inflation. We used the *R* Statistical Package (R Core Team, 2016) for all analyses.

We carried out two NMDS ordinations: one for the macroinvertebrate community and one for the soil prokaryote community. NMDS ordination is a process that places communities within the ordination space in such a way that reproduces the actual pairwise rank-order distances between communities. We set the ordination space to have two dimensions to optimize visualization. We removed some taxa from the community matrices to reduce bias from lowabundance groups. For the macroinvertebrates, we excluded singleton, doubleton, and "unknown" taxa from the community matrix. For the soil microbial community, we excluded any phyla with fewer than 1000 total (across all samples) sequence reads. All analyses of the bacteria and archaea community were at the phylum or OTU level. We performed the ordination using the function *metaMDS* in the package, *vegan* (Oksanen et al. 2016), using a Bray-Curtis dissimilarity matrix with 20 runs. We judged the goodness-of-fit of the ordinations from the stress and the linear R^2 (the correlation between the original rank-order distance matrix and the ordination distances). We then fitted the environmental variables to the ordination using the *vegan* function, *envfit*. Site centroids in the ordination space represent the average community composition of quadrats at that site. Sites with centroids close to each other within the ordination space indicate that the community composition of quadrats at these sites are similar. The location of a taxon within the ordination space indicates its correlation with the ordination axes, and therefore also its rank abundance at the sites.

Similarly, the length and direction of an environmental variable vector indicates its correlation with the ordination axes, and therefore its correlation to community composition.

To confirm the results of the NMDS data fitting, we also carried out a PERMANOVA using the *vegan* function, *adonis*, with option = "margin" to measure the marginal effects of each term. We used a Bray-Curtis dissimilarity matrix and 999 permutations. We only included site and the explanatory variables found to be significant by the NMDS.

Mantel tests: Next, we tested for correlations among the vegetation, macroinvertebrates, and soil prokaryote communities. The vegetation community matrix was simply the proportion ground cover of the five vegetation types. To test for correlations among the three communities' distance matrices, we carried out three Mantel tests and one partial Mantel test using *vegan* functions, *mantel* and *mantel.partial*.

Hypothesis testing: We tested our three hypotheses using mixed effects models with site as a random effect and latitude as a fixed effect. Site was treated as a random effect to account for the non-independence of samples from the same site, and latitude was treated as a fixed effect because we wished to test the effect of latitude on other variables. For all mixed effects model analyses, we scaled latitude to a mean of 0 and standard deviation of 1. We used the *nlme* function, *lme*, for response variables with normal distributions (diversity and total macroinvertebrate abundance). For response variables with Poisson distributions (herbivore and carnivore abundance), we used the *lme4* function, *glmer* (Pinheiro et al. 2016).

To calculate macroinvertebrate and soil prokaryote diversity we used two measures: rarefied richness and Shannon diversity. We rarefied taxonomic richness for macroinvertebrate taxa and prokaryote phyla, using the *vegan* function, *rarefy*, with the sub-sample size set to 19 individuals for macroinvertebrates, and 37108 reads for prokaryotes (the number of individuals or reads in the quadrat with the smallest sample size). We also used prokaryote OTU richness as a measure of prokaryote diversity. OTUs were well-sampled so rarefaction was unnecessary (raw and rarefied richness were essentially equal). We calculated the Shannon diversity index for macroinvertebrate taxa and prokaryote phyla, using the *vegan* function, *diversity*, followed by a Box-Cox transformation to normalize the distribution, using the *car* function,

powerTransform (Fox & Weisberg, 2011). We therefore had two measures of macroinvertebrate diversity (taxon richness and Shannon diversity), and three measures of prokaryote diversity (phylum richness, Shannon diversity, and OTU richness).

We calculated the relative herbivore abundance as herbivore abundance/[herbivore abundance + carnivore abundance], and relative carnivore abundance as carnivore abundance/[herbivore abundance + carnivore abundance]. We did not include parasitoids as carnivores, nor did we include detritivores as herbivores.

Exploratory modeling: Finally, we performed exploratory analyses to determine which environmental variables best accounted for variation in six response variables: three macroinvertebrate response variables (abundance, taxon richness, and Shannon diversity) and three prokaryote response variables (OTU richness, phylum richness, and Shannon diversity). For each of the six response variables, we calculated model parameters and AICc model weights for the set of models that contained all possible combinations of the environmental variables, including the empty model and excluding interactions (a total of 2¹¹ = 2048 models for each response variable). The models were mixed-effects models (*lme*), with site as a random effect and the environmental variables as fixed effects, and with all continuous variables scaled (mean = 0; SD = 1). For each combination of response and explanatory variable, we calculated the sum of the AICc model weights for all models containing the explanatory variable (cumulative weight; Arnold 2010). We also calculated the average coefficient value (β) and standard error (SE) for all models containing the explanatory variable. We used the *MuMIn* function, *dredge* (Barton 2017), to generate the models and model averages. We interpreted the cumulative weight as a measure of the relative importance of the explanatory variable, and the modelaveraged coefficient and standard error as measures of the effect size and confidence, respectively (Burnham & Anderson 2004). We calculated the 95% confidence interval of each coefficient as $\beta \pm 1.96 * SE$.

3.4 Results

Description of the environmental variables

Overall, grass covered the largest proportion of ground in the quadrats (Table 3.1; mean \pm SD = 0.41 \pm 0.15; throughout, values are given as the mean \pm SD of the quadrats), followed by shrubs (0.19 \pm 0.13), lichen (0.10 \pm 0.10), forbs (0.07 \pm 0.11), and then moss (0.06 \pm 0.09). Site 3 differed the most in vegetation from the other sites, with a higher proportion of forbs and shrubs. All quadrats had peaty soil, except for one quadrat at Site 2 and two quadrats at Site 3, which had clay soil. The mean vegetation dry mass was 24.5 \pm 9.2 g, the mean active layer depth was 34 \pm 9 cm, and the mean distance from the Dempster Highway was 159.6 \pm 127.5 m.

Several of the environmental variables were correlated (VIF >> 10 for most of the variables; Table 3.1; Fig 3.3A). When longitude and altitude were excluded, correlation amongst the variables was much lower (VIF <10 for all remaining variables). Therefore, these two variables were excluded as explanatory variables from subsequent analyses.

Description of the macroinvertebrate communities

In total, we collected 1760 macroinvertebrates, or 70.4 m⁻² (Table 3.2). These belonged to 38 taxa. By class, Collembola accounted for the largest number of the sampled macroinvertebrates ($25.9 \pm 15 \text{ m}^{-2}$), followed by Arachnida ($21.7 \pm 11.5 \text{ m}^{-2}$), and Insecta ($19.9 \pm 13.5 \text{ m}^{-2}$). Within Arachnida, Acari (mites) accounted for the most individuals ($13.9 \pm 8.3 \text{ m}^{-2}$). Within Insecta, Hemiptera were the most abundant order ($6.8 \pm 4.5 \text{ m}^{-2}$), followed by Hymenoptera ($6.6 \pm 9. \text{ m}^{-2}$), and Diptera ($4.5 \pm 4.5 \text{ m}^{-2}$). The most numerically dominant insect families were, in descending order, Formicidae, Cicadellidae, and Cecidomyiidae.

At Site 1 and Site 4, one tent was blown over by the wind. We were therefore unable to collect the pan trap, D-vac, or glue trap samples for these two quadrats. The total abundance of macroinvertebrate collected at these two sites, however, was not lower than the total abundance at other sites (Table 3.2), and we therefore did not modify the data analysis to account for these events. The macroinvertebrate communities differed significantly among sites (*NMDS*: $R^2 = 0.45$; *PERMANOVA*: $F_{4,24} = 2.87$; $R^2 = 0.33$; p = 0.001; Fig 3.3B). Macroinvertebrate communities also differed with latitude (*NMDS*: $R^2 = 0.33$; *PERMANOVA*: $F_{1,24} = 2.49$; $R^2 = 0.08$; p = 0.01), such that some groups, including Culicidae, increased with latitude, and other groups, including Tingidae and Thomisidae, decreased (Table 3.2; Fig 3.3B). Macroinvertebrate communities also differed with highway proximity (*NMDS*: $R^2 = 0.43$; *PERMANOVA*: $F_{1,24} = 2.29$; $R^2 = 0.07$; p = 0.03), such that some groups, including Pteromalidae, were more abundant close to the Highway, and other groups, including Culicidae and Formicidae, were less abundant (Fig 3.3A). The NMDS had moderate goodness-of-fit (*stress* = 0.2) and most of the variation in the rank-order distance matrix was accounted for by the ordination ($R^2 = 0.82$).

Description of the soil prokaryotic communities

The 16S rRNA analysis yielded an average of 47,941.5 ± 8453.2 reads/sample, belonging to a total of 7203 OTUs. Based on 16S rRNA community profiling, the dominant bacterial phyla across all sites were Proteobacteria (28%), Acidobacteria (23%), Verrumicrobia (11%), Bacterioidetes (8%), Firmicutes (7%), to a lesser extent Chloroflexi (5%), Planctomycetes (3%), and Gemmatimonadetes (1%; Fig 3.4 shows phyla by site). Archaea were much less abundant (0 - 0.2% of reads, Sites 1-4) and sequences were predominately comprised of Euryarchaeota and Thaumarchaeota. However, Site 5 had a higher relative abundance of archaeal sequences (0.1 - 5.1%) compared to the other sites. Most of these sequences belonged to Euryarchaeota and Crenarchaeota, with the most abundant OTUs classifying as Methanosarcinales and Methanobacteriales. Site 5 also had a higher relative abundance of fermentative anaerobic Firmictures (Class Clostridia), averaging 15.1% of bacterial reads across the biological replicates.

The soil prokaryote communities differed significantly among sites (*NMDS*: $R^2 = 0.63$; *PERMANOVA*: $F_{4,18} = 2.37$; $R^2 = 0.3$; p = 0.01). Soil prokaryotic communities also differed with latitude (*NMDS*: $R^2 = 0.34$; *PERMANOVA*: $F_{1,18} = 6.8$; $R^2 = 0.23$; p = 0.001), such that some phyla, including Armatimonadetes, increased with latitude, and other phyla, including Firmicutes and Euryarchaeota, decreased with latitude (Fig 3.3B). Soil prokaryotic communities also differed with active layer depth (*NMDS*: $R^2 = 0.45$; *PERMANOVA*: $F_{1,18} = 2.98$; $R^2 = 0.1$; p = 0.03), such that some phyla, including Chloroflexi, increased with active layer depth, and other phyla, including Fusobacteria, decreased with active layer depth. The NMDS had high goodness-of-fit (*stress* = 0.08), and most of the variation in the rank-order distance matrix was accounted for by the ordination (R^2 = 0.98).

Correlations among vegetation, macroinvertebrate, and prokaryote communities

There were no correlations among the vegetation, macroinvertebrate, and prokaryote communities (r = 0.06; p = 0.33). There were also no correlations between vegetation and macroinvertebrate communities (r = 0.09; p = 0.24), vegetation and prokaryote communities (r = 0.07; p = 0.32), or macroinvertebrate and prokaryote communities (r = 0.02; p = 0.3).

Changes in diversity and abundance with latitude

Our data did not support our first hypothesis. For macroinvertebrates, abundance (β = 4.49; t_{19} = 0.93; p = 0.37), taxon richness (β = -0.14; t_{19} = -0.52; p = 0.61), and Shannon diversity (β = -0.39; t_{19} = -0.88; p = 0.391) were not related to latitude.

Our data supported our second hypothesis. For prokaryotes, phylum richness (β = -1.08; t_{14} = -1.57; p = 0.14), Shannon diversity (β = -2.25; t14 = -2.05; p = 0.06), and OTU richness (β = 60.49; t_{14} = 0.62; p = 0.55) did not change significantly with latitude.

Our data supported our third hypothesis. Herbivore abundance increased with latitude (β = 0.23; z = 3.32; p = 0.001). The trend for carnivore abundance was negative with latitude but the relationship was not significant (β = -0.28; z = -1.84; p = 0.07). Thus, the abundance of herbivores relative to carnivores increased with latitude, while the abundance of carnivores relative to herbivores decreased (Fig 3.5).

Correlations between diversity and environmental factors

No explanatory variables in any of the macroinvertebrate exploratory models had high relative importance or confidence intervals that excluded 0.

Prokaryote diversity decreased with lichen cover and increased with active layer depth. OTU richness decreased with lichen cover, and the relative importance of this explanatory variable

was moderate (β = -0.53, SE = 0.24; $\sum w_i$ = 0.66; Fig 3.6). Phylum richness increased with active layer depth, and the relative importance of this explanatory variable was moderate (β = 0.4, SE = 0.2; $\sum w_i$ = 0.54; Fig 3.7). All other explanatory variables for the three Prokaryote exploratory models had low relative importance and confidence intervals that overlapped with 0.

3.5 Discussion

Macroinvertebrate and prokaryote communities responded to environmental variation within and across the forest-tundra ecotone of the subarctic Yukon. These environmental correlations were at multiple scales, from local (lichen cover, active layer depth), to landscape (road proximity), to regional (biome transition).

3.5.1 Macroinvertebrates and Prokaryotes of the Yukon tussock tundra

We found that Collembola and Acari were numerically dominant. Together, these two groups numbered more than half of the total invertebrates identified (Table 3.2). This is despite that our methods underestimated small soil invertebrate abundance because the hand-sorted soil cores were sorted without the aid of a microscope. The density of soil invertebrates is often greater in Arctic soils than in temperate soils (Peterson & Luxton 1982), with Collembola and Acari numbering upwards of 10 000 individuals m⁻² (Maclean et al. 1977; Sørensen et al. 2006). Average Collembola densities in our study were 798 m⁻², which is substantially lower, likely because small Collembola and Acari were poorly detected by our methods. The dominance of Collembola and Acari, despite their underestimation, reinforces the notion that much of the ecological activity of the tundra takes place below-ground. It also suggests a strong link between tundra macroinvertebrates and soil prokaryotes, given that Collembola, Acari, and soil microbes are known to directly interact, especially through their roles in decomposition (Sørensen et al., 2006).

Spiders are abundant across the Arctic, and the Yukon is no exception (Bowden & Buddle 2010; Bowden & Buddle 2012b). Our finding that Lycosidae (wolf spiders) had an average density of 2.0 individual/m² highlights the predominance of these animals in the tundra ecosystem. This density estimate is greater than a previous estimate by Bowden and Buddle (2012b) in the

same region, who found that the average density of the three most abundant wolf spider species was 0.52 individuals/m². The difference may have been due to inter-annual variation or differences in sampling methods. We found that the D-vac, which Bowden and Buddle did not use, was an effective method for sampling wolf spiders. Spiders are generalist consumers and are themselves consumed by a wide variety of predators, thereby linking above- and belowground systems, as well as vertebrate and invertebrate systems. The high density of spiders may contribute to ecosystem stability on the tundra, through their role in linking these food web compartments (Rooney et al. 2006).

Hemiptera, Hymenoptera, and Diptera were also abundant macroinvertebrates in our samples. Very few ant species are known to live on the tundra (Shellford 1963), and so we were surprised to find a higher abundance of Formicidae than any other hymenopteran (*Leptothorax muscorum, Leptothorax acervorum,* and *Formica neorufibarbis*; identified using Francoeur 1997). Perhaps disturbance from the nearby Dempster Highway generates tundra conditions favourable to these ants. Lepidoptera had low relative abundance in our samples, likely because we selected sites with low densities of shrubs and forbs, which are common lepidopteran food items (Barrio et al. 2016).

The dominant soil prokaryote phyla at our sites (Proteobactera, Acidobacteria, Actinobacteria, Verrucomicrobia, and Bacteroidetes) are typical of soil bacteria across the Arctic (Yergeau et al. 2010; Chu et al. 2010; Hultman et al. 2015). The largest discrepancy with other Arctic studies was the much greater relative abundance of Verrucomicrobia at our sites. This may be due to methodological differences, as many PCR primers strongly underestimate Verrucomicrobia abundance (Bergmann et al. 2011), leading to an underestimation of Verrucomicrobia by other authors. Most of the Verrucomicrobia we detected belonged to the orders Verrucomicrobiales and Opitutales.

Overall, bacteria and archaea present in the soils included members capable of a variety of functional processes including, heterotrophy, fermentation, methanogenesis, nitrogen fixation, methylotrophy, ammonia oxidation, and cellulose degradation. This suggests that if the active layer deepens due to climate change and permafrost thaw, the bacteria and archaea in the soils

are capable of degrading newly available organic carbon stores (Graham et al. 2012; Voigt et al. 2016; Xue et al. 2016).

3.5.2 Active layer depth

The soil prokaryote community increased in diversity and changed in composition with active layer depth (Fig 3.3B; Fig 3.7), suggesting a mechanism through which climate change may affect soil communities. The active layer depth, which is the depth at which the permafrost begins, is an indicator of average annual temperature. We observed an increase in the bacteria Chloroflexi and a decrease in the bacteria Fusobacteria with depth (Fig 3.3B). The coldest soils, therefore, may not be optimal for the growth of the Chloroflexi taxa present, while the Fusobacteria taxa may be better cold-adapted. Prokaryotic diversity increased with active layer depth (Fig 3.7), which may be because a warmer environment is hospitable to a wider range of taxa. Alternatively, the positive relationship between active layer depth and prokaryotic diversity may be the result of a taxa-area relationship (Horner-Devine et al. 2004), because greater active layer depth means a larger soil volume. As the tundra warms due to climate change, the active layer will deepen, and our results suggest that this will change the soil prokaryote communities of the tundra. These changes may include increased soil prokaryote diversity or the loss of cold-adapted taxa.

3.5.3 Vegetation

Prokaryote diversity increased with lichen cover (Fig 3.6), an association which may be driven by soil chemistry or the inhibitory activity of lichen. Tundra lichen can grow in soil conditions that are unfavourable to other vegetation types (Johnson 1981), such as low moisture (Kranner et al. 2008) or nutrient availability. These conditions may also be poor for many soil prokaryotes, leading to a negative correlation between prokaryote diversity and lichen cover. Additionally, lichen may create inhospitable conditions for prokaryotes by producing antimicrobial compounds (Shukla et al. 2010). As shrub density expands due to climate change, lichen density and diversity is decreasing (Cornelisson et al. 2001; Lang et al. 2012), which may cause changes in prokaryotic soil communities. We were surprised to find no other correlations between vegetation and macroinvertebrate or prokaryote communities, given that previous Arctic studies have consistently found that vegetation drives prokaryote (E.g., Wallenstein et al. 2007; Chu et al. 2011) and macroinvertebrate community composition (E.g., Rich et al. 2013; Sweet et al. 2015). Possibly the vegetation taxonomic resolution was too coarse to detect correlations. Alternatively, the degree of variation in vegetation among sites may have been too low to affect the macroinvertebrate community, considering that the sites were all selected to be within tussock tundra habitats.

3.5.4 Road proximity

Proximity to the Dempster Highway affected the macroinvertebrate community composition (Fig 3.3), an observation that merits further study given the forecasted development of the Canadian North (Lamy 2016). Several taxonomic groups had higher abundance close to the road, including Tingidae, while Formicidae and Culicidae were more abundant far from the road. The change in macroinvertebrate community with road proximity suggests that groups differ in their sensitivity to the road disturbance. Roads affect adjacent communities by generating edge habitats, which can differ strongly from the conditions in the surrounding region (Coffin 2007; Muñoz et al. 2015). In the case of the Dempster Highway and other Northern gravel roads, this edge habitat has altered soil properties (Gill et al. 2014), increased moisture due to permafrost thaw (Gill et al. 2014; O'Neill & Burn 2015), and causes changes in vegetation (Kershaw & Kershaw, 1987; Myers-Smith et al., 2006; Cameron & Lantz, 2016). The changes in macroinvertebrate community composition could be driven by the altered soil and hydrological properties or by associated changes in the plant composition.

The effect of road proximity was not explicitly part of our sampling design, because we did not expect that it would have an effect. These findings in this study inspired us to carry out a more systematic study of the Dempster Highway's impact on macroinvertebrate communities (Ste-Marie et al., 2018).

3.5.5 Biome transition

As the biome transitioned from taiga to tundra along our latitudinal transect, we found that macroinvertebrate and prokaryote community composition changed as well. Consistent with other studies (Oswood 1989), we did find that Diptera (Culicidae, and to a lesser extent, Cecidomyiidae and Empididae) were associated with our higher latitude sites. Diptera predominate in the North because many species are well-adapted to cold environments (Downes 1965). At the higher latitude sites, the decrease in Tingidae, an herbivorous true bug (Hemiptera), could be due to decreased vegetation density. The decrease in Thomisidae at the tundra sites was unexpected, given that a previous study of spiders in the same region found constant densities of thomisid spiders across the same 280-km latitudinal transect (Bowden and Buddle 2010). The differences in the relative abundances of prokaryote taxa among our sites were notable, although these results are more difficult to interpret because their functional ecology is not fully described. One interesting pattern however, was a relatively higher abundance of methanogenic archaea and anaerobic Firimicutes at the southmost site (Site 5). This could suggest a more anaerobic environment and possible increased methane flux from these soils (Hultman et al. 2015; Mackelprang et al. 2016).

While the macroinvertebrate and prokaryote communities changed along with the biome transition, their diversity and macroinvertebrate abundance remained constant. We had predicted (Hypothesis 1) that macroinvertebrate abundance and diversity would decrease with latitude, with greater diversity and abundance in the southern (taiga) sites than the northern (tundra) sites, reflecting observations at a global scale for many taxa (Gaston 2000). The absence of these negative correlations in our study may be because the pattern observed globally is due to direct latitudinal effects, rather than latitude on diversity and abundance (Bowden and Buddle 2010). Another possibility is that there is no general relationship for all macroinvertebrate taxa and the shift from taiga to tundra: some taxa increase, some decrease, while others have a hump-shaped relationship (Gaston 2000). We did not observe any correlation between latitude and diversity in the soil bacteria and archaea. This lack of

correlation was as we had predicted (Hypothesis 2) and as has been observed by other authors (Fierer & Jackson 2006; Chu et al. 2010).

The abundance of carnivores relative to herbivores decreased with latitude (Hypotheses 3; Fig 3.5), suggesting a decrease in predation intensity along the forest-tundra biome transition. Several recent studies have observed a decrease in predation with latitude, including a decrease in predation risk (Roslin et al. 2017) and a decrease in the ratio of herbivorous to carnivorous animal species (Turney & Buddle 2016). The decrease in predation with latitude may relate to a more general decrease in intensity of biotic interactions with latitude (Schemske et al. 2009). Or, the decrease might be due to increased ecological isolation or decreased resource availability in northern biomes compared to southern biomes, factors which have both been linked to decreased food chain length (Post 2002).

With climate change and permafrost thaw, the Arctic is predicted to become warmer and wetter (Graham et al. 2012), and so it is possible that, in the future, the more northern sites will more closely resemble the present-day conditions of the more southern sites. We might expect changes such as fewer Diptera or more carnivorous taxa in macroinvertebrate communities. Prokaryotic communities may become more anaerobic and methanogenic as they become wetter due to permafrost melt, resembling more closely the communities observed at Site 5.

3.6 Conclusion

Although the tussock tundra in the forest-tundra ecotone of the Northern Yukon appears superficially homogenous in terms of plants and vertebrates, we found diverse and distinct macroinvertebrate and prokaryote communities among our five study sites. We found that macroinvertebrate and soil prokaryote community composition and trophic structure changed along a forest-tundra ecotone. We also found that local- and regional-scale abiotic variables, including human disturbance (Dempster Highway) and variables affected by climate change (active layer depth), explained variation among samples. As the Canadian north continues to be developed by industry, these findings have important implications: environmental mitigation and conservation efforts should not treat tussock tundra habitat as a homogenous or interchangeable. Loss of any single region of tundra entails the loss of a distinct community and a decrease in regional diversity. This hidden biodiversity could be obscured if only plants and vertebrates are considered, rather than the macroinvertebrate and soil prokaryote communities on which these larger organisms depend.

3.7 Permits and ethical approval:

This research was permitted under the Yukon Scientists and Explorer's Act, License Number: 15-10SandE. Research activity within Tombstone Territorial Park (Sites 4 and 5) was permitted by a Research and Education Park Permit, Permit Number 15-RE-TP-01. Additionally, permission was sought and granted from all relevant First Nations (Tr'ondek Hwech'in, Tetlit Gwich'in, and Vuntut Gwitchin). All applicable international, national, and institutional guidelines for the care and use of animals were followed.

3.8 Acknowledgements:

Thank you to Anne-Sophie Caron for her dedicated field work assistance. Thanks to Scot E. Dowd for his excellent DNA sequencing services. Thank you to the anonymous reviewers and to guest editor Lauren Culler who provided helpful feedback. This project was possible due to funding from the National Science and Engineering Research Council of Canada: A Discovery Grant and Northern Research Supplement to CMB and a Postgraduate Scholarship-Doctoral to ST. This study was further supported by a W. Garfield Weston Award for Northern Research (Doctoral) from the Canadian Northern Studies Trust to ST. **Table 3.1.** Environmental variables measured in July 2015 at 25 quadrats on the Yukon tundra, Canada. The mean (and standard deviation) of each environmental variable is given for each site. Further description of how the variables were measured is given in Methods.

Environmental variable	Site 1	Site 2	Site 3	Site 4	Site 5
Latitude	66.97	66.59	65.81	64.84	64.6
Longitude	-136.22	-136.29	-137.76	-138.32	-138.32
Altitude	687 (3)	670 (4.4)	806.6 (8.9)	1003.4 (0.5)	1189.2 (9.9)
Soil type	Peat	Peat, clay	Peat, clay	Peat	Peat
Grass cover	0.58 (0.11)	0.3 (0.13)	0.35 (0.11)	0.34 (0.08)	0.49 (0.16)
Moss cover	0.06 (0.06)	0.13 (0.16)	0.01 (0.01)	0.02 (0.02)	0.09 (0.04)
Lichen cover	0.08 (0.05)	0.09 (0.08)	0.07 (0.15)	0.17 (0.09)	0.07 (0.08)
Shrub cover	0.14 (0.07)	0.19 (0.08)	0.33 (0.21)	0.22 (0.04)	0.07 (0.03)
Forb cover	0.07 (0.04)	0.05 (0.03)	0.19 (0.2)	0.02 (0.04)	0 (0.01)
Vegetation dry mass (g)	20.5 (6.9)	18.6 (8.2)	24.6 (6.3)	34.7 (8.3)	24.2 (9.3)
Active layer depth (cm)	26.3 (3.6)	33.6 (4.9)	42.6 (15.9)	31.8 (1.1)	34.2 (4.1)
Highway proximity (m)	101 (40.4)	400 (39.5)	80 (27.4)	117 (29.7)	100 (39.5)
Table 3.2. The density of individuals collected at each of the five sites for each macroinvertebrate taxon. Macroinvertebrates were sampled using pan traps, glue traps, D-vac, hand-sorting of soil, and Winkler funnels. Each value is the mean number of individuals from all quadrats and trapping methods for the given site and taxon, with the standard deviation given in brackets. The "multiple" trophic group indicates that there is variation in trophic strategy within the taxon. Samples were collected in July of 2015 from the Yukon, Canada.

			Density (individuals/m ²) at each site (SD)						
			(North)				(South)		
Order or class	Family	Trophic	1	2	3	4	5	Average	
		group							
Araneae	Linyphiidae	Carnivore	4.4 (4)	1.6 (2)	5.6 (5.4)	2.6 (2.9)	11.0 (4.9)	5 (8.3)	
	Lycosidae	Carnivore	0.7 (1.1)	0.6 (0.9)	3.4 (1.1)	3.2 (3.9)	2.0 (2)	2.0 (2.3)	
	Thomisidae	Carnivore	0	0.2 (0.5)	1.0 (1.4)	0.4 (0.6)	2.2 (1.9)	0.8 (1.3)	
	Dictynidae	Carnivore	0	0.2 (0.5)	0	0	0	0 (0.2)	
Hymenoptera	Formicidae	Multiple	0.2 (0.5)	17.0 (16.8)	1.0 (1.2)	3.0 (2.7)	0	4.2 (9.6)	
	Braconidae	Parasitoid	0.2 (0.5)	1.6 (1.7)	1.6 (0.6)	0.6 (0.9)	0.2 (0.5)	0.8 (1.1)	
	Chalcidoidea	Parasitoid	1.0 (1)	1.0 (1)	0.2 (0.5)	0.4 (0.9)	1.0 (1.4)	0.7 (1)	
	Ichneumonidae	Parasitoid	0	0.6 (0.9)	0.4 (0.6)	0	0.4 (0.6)	0.3 (0.5)	
	Pteromalidae	Parasitoid	0.2 (0.5)	0	0.2 (0.5)	0	0.4 (0.6)	0.2 (0.4)	
	Dryinidae	Parasitoid	0	0	0.2 (0.5)	0.2 (0.5)	0	0.1 (0.4)	
	Eulophidae	Parasitoid	0.2 (0.5)	0	0	0	0	0 (0.2)	
	Platygastridae	Parasitoid	0	0.2 (0.5)	0	0	0	0 (0.2)	
	Unknown	NA	0	0.4 (0.6)	0	0.4 (0.9)	0	0.2 (0.5)	
	Hymenoptera								
Hemiptera	Cicadellidae	Herbivore	4.8 (4)	3.4 (2.1)	4.8 (3.7)	2.0 (1.4)	4.2 (0.8)	3.8 (2.7)	
	Tingidae	Herbivore	0	0	0	0.4 (0.9)	0.4 (0.6)	0.2 (0.5)	
	Aphidoidea	Herbivore	0	0.2 (0.5)	0	0	0	0 (0.2)	
	Reduvidae	Carnivore	0	0	0	0.2 (0.5)	0	0 (0.2)	
	Psylloidae	Herbivore	0	0	0	0.2 (0.5)	0	0 (0.2)	

	lmmature Hemiptera	NA	0.4 (0.9)	1.4 (1.7)	5.6 (4.3)	3.0 (3)	3.0 (3.3)	2.7 (3.2)
Diptera	Cecidomyiidae	Herbivore	4.4 (7.1)	5.2 (4.2)	2.6 (2.2)	1.6 (1.1)	1.4 (1.1)	3 (3.9)
	Phoridae	Multiple	0	0	0.2 (0.5)	1.2 (1.1)	0.8 (0.8)	0.4 (0.8)
	Culicidae	Blood- feeding	0.6 (0.9)	1.0 (0.7)	0	0.2 (0.5)	0	0.4 (0.6)
	Mycetophilidae	Feed little as adults	0	0	0	0.4 (0.6)	0	0.1 (0.3)
	Empididae	Multiple	0.2 (0.5)	0.2 (0.5)	0	0	0	0.1 (0.3)
	Muscidae	Multiple	0	0.2 (0.5)	0.2 (0.5)	0	0	0.1 (0.3)
	Pipunculidae	Parasitoid	0.2 (0.5)	0	0	0	0	0 (0.2)
	Anthomyiidae	Herbivore	0.2 (0.5)	0	0	0	0	0 (0.2)
	Chironomidae	Feed little as adults	0	0	0.2 (0.5)	0	0	0 (0.2)
	Dolichopodidae	Carnivore	0	0.2 (0.5)	0	0	0	0 (0.2)
	Tipulidae	Feed little as adults	0	0.2 (0.5)	0	0	0	0 (0.2)
	Unknown Brachycera	NA	0	0	0	0	0.1 (0.9)	0.1 (0.4)
	Unknown Nematocera	NA	0.2 (0.5)	0.2 (0.5)	0	0.2 (0.5)	0	0.1 (0.3)
Coleoptera	Carabidae	Carnivore	0.6 (0.9)	1.2 (1.6)	0	0	0	0.4 (0.9)
	Staphylinidae	Carnivore	0.6 (0.9)	0.4 (0.9)	0.4 (0.6)	0	0.2 (0.5)	0.3 (0.6)
	Unknown Coleoptera	NA	0	0.2 (0.5)	0	0	0	0 (0.2)
Lepidoptera		Herbivore	0.2 (0.5)	0	0.4 (0.6)	0.2 (0.5)	0.2 (0.5)	0.2 (0.4)
Thysanoptera		Herbivore	0.6 (1.3)	2.8 (1.8)	1.0 (2.4)	0.4 (0.9)	0.6 (0.9)	1.0 (1.7)
Collembola		Omnivore	29.2 (18.8)	22.8 (9.4)	38.8 (17)	22.8 (11.1)	13.8 (7.9)	25.5 (15)
Acari		Multiple	19.6 (8.6)	5.0 (2)	13.8 (7.2)	19.4 (7.7)	11.6 (6.2)	13.9 (8.3)
Unknown larva	a	NA	0.8 (1.3)	0.2 (0.5)	0	0.8 (1.1)	0.4 (0.6)	0.4 (0.8)
Chilopoda		Carnivore	0.6 (0.9)	0.2 (0.5)	1.8 (2.5)	0.8 (0.8)	0	0.7 (1.3)

Oligochaeta		Detritivore	2.4 (1.8)	0.2 (0.5)	0.2 (0.5)	0.6 (0.9)	4 (2.6)	1.5 (2)
Gastropoda		Herbivore	0	0	1.6 (3.1)	0.6 (0.9)	0.2 (0.5)	0.5 (1.5)
Nematoda		Multiple	0.6 (1.3)	0	0.6 (0.9)	0	0	0.2 (0.7)
Total	Abundance		73.2 (37.7)	68.6 (23.9)	85.8 (17)	65.8 (22)	58.6 (9.7)	70.4 (23.7)
	Taxonomic		22	25	24	23	18	38
	richness							







Figure 3.2. Photograph of the tent used to enclose the quadrat, with one of the authors (ST) using the D-vac to sample within the quadrat. Five quadrats were placed at each of the five sites in the Yukon, Canada, in July 2015. The tent had a 1m² base and was 1.35m in height (Style of Mine Fashion and Outdoor Products Co. Ltd., Anti-Mosquito Meditation Tent, light grey). The D-vac was designed after Stewart and Wright (1995) and was made by modifying a Weed Eater[®] 25cc Leaf Blower/Vacuum.



Figure 3.3. NMDS ordinations of data sampled from the five sites. The red circles delineate the 95% confidence intervals of the centroids for each site. Only environmental variables with a significant fit are plotted (p < 0.05). Each green point corresponds to the closest green label and indicates the loading of the taxon. A) Ordination of macroinvertebrates. The taxa with scores >0.4 on one or both axes are plotted. B) Ordination of bacteria and archaea. The taxa with scores >0.2 on one or both axes are plotted. A species score is the rank-abundance weighted centroid of all the samples in which the taxon occurs, indicating the taxon's correlation to the ordination axes.



Figure 3.4. The relative abundance of bacteria and archaea phyla based on 16S rRNA gene sequencing from soil samples at five tundra sites in the Yukon, Canada in July 2015. The relative abundance of phyla at each site is based on an average of four biological replicates. The phyla are listed in the legend in the same order as they are stacked in the bar graph.





(herbivore/[herbivore+carnivore] at each quadrat) increased with latitude. Macroinvertebrates were sampled from the soil and surface in quadrats at five tundra sites in the Yukon, Canada in July 2015, and were categorized by trophic group (Table 3.2). The grey line at y=0.5 indicates an equal abundance of herbivores and carnivores.



Figure 3.6. Prokaryote diversity (OTU richness) decreased with the lichen cover in quadrats at five tundra sites in the Yukon, Canada in July 2015. OTU richness was calculated from 16S microbial sequencing. Lichen cover was measured as the proportion of the quadrat surface covered by lichen.



Figure 3.7. Prokaryote diversity (rarefied phylum richness) increased with active layer depth in quadrats at five tundra sites in the Yukon, Canada in July 2015. Rarefied phylum richness was calculated from 16S microbial sequencing. Active layer depth was measured as the distances from the surface vegetation to the permafrost.

Connecting Text:

In the meta-analysis described in Chapter 2, I demonstrated that trophic structure responds to variation both outside of and within communities. In the study described in Chapter 3, I found that tundra macroinvertebrate communities respond to environmental variation. In this chapter, I investigate how variation at one trophic level of tundra macroinvertebrate communities, assemblage composition of tundra spiders, affects variation at another trophic, prey abundance. In Chapter 3, I also found that wolf spiders (*Lycosidae*) are highly abundant on the Yukon tundra: on average there were two wolf spiders per square meter (Table 3.2). I therefore chose wolf spiders as my focal organisms, since their abundance made them easier to study and implies that they are ecologically important. Biodiversity loss, especially of predators, is changing ecological communities worldwide (Estes et al. 2011; Ripple et al. 2014). The motivation of this chapter is to better predict the effects of changing predator assemblages. This chapter addresses the question: *What is the relationship between spider assemblage composition on the tundra of the Yukon*?

Contributions of authors: The authors that contributed to this work are Shaun Turney¹ and Christopher M. Buddle¹. ST and CMB conceived the ideas and designed methodology; ST collected and analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts.

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Chapter 4: Body size mediates the relationship between spider (Arachnida: Araneae) assemblage composition and prey consumption rate: Results of a mesocosm experiment in the Yukon, Canada.

4.1 Abstract

Many ecological communities are undergoing rapid changes in composition and diversity, and changes at one trophic level can have direct and cascading effects on other trophic levels. Prey consumption typically increases with predator diversity due to niche complementarity and sampling effects. However, the effect of functional traits and interactions between predator species mean that the relationship is far from simple. In July 2016, we performed a series of experiments in the Yukon, Canada, to investigate the relationship between spider assemblage composition and prey consumption, with a focus on the wolf spider Pardosa lapponica (Thorell 1872). We carried out feeding trials, in which *P. lapponica* and other spider species were offered potential prey, as well as mesocosm experiments, in which we varied spider assemblage composition within small enclosures. We confirmed that *P. lapponica* is a generalist consumer, that individual consumption rate increased with spider body size, and that intraguild predation is present. We found that the total number of prey consumed was greatest in the least diverse assemblage but consumption did increase with predator functional trait variation and biomass. The best model (lowest AIC) of prey consumption included predator assemblage composition, variation in predator body mass, total predator biomass, and all interactions. The body size of a spider affects its trophic niche, energy requirements, and its interactions with other spiders. As a result, body size mediates the relationship between spider assemblage composition and prey consumption. A deeper understanding of the relationships between traits and functions will allow us to better predict the effect of species loss or gain on ecosystem functions.

4.2 Introduction

Many ecological communities are undergoing rapid change in the Anthropocene (Crutzen and Steffen 2003). Species are lost to extinction (Butchart et al. 2010; Hooper et al. 2012) or gained due to invasions (Pimentel et al. 2005), both often the result of human activity. Changes in community composition and diversity are worrisome given their relationships to ecosystem functions (Cardinale et al. 2005; Hooper et al. 2005; Naeem et al. 2012). Species diversity has been associated with productivity, stability, decomposition rate, and invasibility, amongst other ecosystem functions (Hooper et al. 2012; Tilman et al. 2014; Hautier et al. 2015). Biodiversity-ecosystem functioning literature is, however, somewhat biased towards studies of basal trophic levels, and of trophic levels treated in isolation (Loreau et al. 2001; Duffy et al. 2007; Griffin et al. 2013; Soliveres et al. 2016). In this study, we investigate the relationship between spider (Arachnida: Araneae) assemblage composition and prey consumption, by directly testing several unresolved hypotheses.

Simple Lotka-Volterra-like models (Ives et al. 2005) predict that, in general, prey density will decrease with predator species richness, due to interspecific niche complementarity and a sampling effect (Aarssen 1997; Ives et al. 2005; Griffin et al. 2013). These predictions, however, only hold true under certain conditions: when predators are extreme generalists or intraguild predation is strong, the models predict little to no relationship between predator diversity and prey density (Ives et al. 2005; Sitvarin & Rypstra 2014). If predators are generalists, then their niche complementarity will be low, and if predators consume each other (i.e., if intraguild predation occurs), then they will consume fewer of their shared prey.

Experimental results, while somewhat idiosyncratic, largely support these model predictions. Overall, species-rich predator assemblages are associated with greater prey suppression (Griffin et al. 2013). Furthermore, the strength of the effect increases with the taxonomic distinctness of the predators, presumably because taxonomically distinct predators have greater niche differentiation. In agricultural ecosystems, top-down control of arthropod herbivores increases with the species richness of natural enemies (Letourneau et al. 2009; However, the same metaanalysis found no such relationship for non-agricultural systems). Although the minority, some

experiments have demonstrated a negative relationship between predator diversity and prey suppression (Finke & Denno 2005; Griffin et al. 2013). Finally, the nature of the relationship between predator species diversity and prey suppression may also depend on variables such as habitat (Schmitz 2007) or prey identity (Wilby et al. 2005).

Given the central role of niche complementarity, predator functional diversity may more directly predict their consumption rate than taxonomic or phylogenetic diversity (Schmitz 2007; Gagic et al. 2015). Many have argued that functional diversity is a better predictor of ecosystem function than phylogenetic diversity, both generally (Petchey & Gaston 2006; Cadotte et al. 2011; Gagic et al. 2015), and specifically in the case of predator diversity and prey suppression (Chalcraft & Resetartis 2003; Schmitz 2007; Griffin et al. 2013). On the other hand, grassland experiments indicate that phylogenetic and functional diversity may both be independently valuable predictors of ecosystem functioning (Flynn et al. 2011).

Diversity does not act alone in determining ecosystem functioning: Several studies have demonstrated that functional identity is more important than diversity for some ecosystem functions (Mokany et al. 2008; Roscher et al. 2012; Gagic et al. 2015). In the case of predation, predator body size is perhaps the most important trait determining consumption rate, niche width, and intraguild predation (Woodward & Hildrew 2002). Metabolic rate increases with body mass (Kleiber 1932), so larger predators must consume a greater amount of prey biomass per capita (Brown et al. 2004). Population density being equal, the community with the greatest predation rate may simply be the community with the largest predator species.

In July 2016 in the Yukon, Canada, we carried out a set of experiments to investigate the predatory behaviour of the wolf spider, *Pardosa lapponica* (Thorell 1872). The density of wolf spiders in our study region is high (2 individuals/m²; Chapter 3), and they play important ecological roles, by linking invertebrate and vertebrate food webs, and above- and belowground food webs (Scheu 2001; Wirta et al. 2015). In general, predators, including spiders, often have strong top-down effects, shaping ecosystem structure at lower trophic levels (Schmitz 2003). Polar regions are disproportionately sensitive to the effects of climate change (Ford et al. 2006; McGuire et al. 2009), and the resulting range shifts will likely affect

Yukon predator assemblage composition (Pöyry et al. 2009; Fossheim et al. 2015), with unknown effects at lower trophic levels.. Furthermore, climate change may also cause changes in average body size (Sheridan and Bickford 2011), and wolf spider body mass has been observed to increase with warming in the Arctic (Høye et al. 2009; Koltz et al. 2018). Given these anticipated changes, it is important to understand the effects of predator assemblage composition and body size distribution on the top-down effects of an abundant tundra predator guild.

We conducted feeding trials on *P. lapponica*, and to a lesser extent, wolf spiders *Pardosa moesta* (Banks 1892) and *Pardosa sodalis* (Holm 1970), and crab spider *Xysticus obscurus* (Collett 1877). Neither wolf spiders nor crab spiders are web-builders: Wolf spiders sit and wait for prey or hunt them down, while crab spiders hunt down prey (Dondale et al. 1997). We investigated the degree of dietary specialization, niche differentiation, and the presence of intraguild predation amongst the spiders, as well as whether consumption rate would increase with spider body size. Next, we varied the spider assemblage composition in a mesocosm experiment (Table 4.1) and counted the unconsumed prey items remaining after the experimental period. We tested three contrasting hypotheses: (1) The number of unconsumed prey will decrease with the phylogenetic diversity of the predators. (2) The number of unconsumed prey will decrease with predator body size variation (SD). (3) The number of unconsumed prey will decrease with predator biomass.

4.3 Methods

4.3.1 Study sites

We collected arthropods at three tundra sites in July 2016 in the Yukon, Canada (Fig. 4.1). Site 1 (64.60°N, 138.32°W) was dominated by grass tussocks and small shrubs, with some moss and lichen. Site 2 (64.50°N, 138.22°W) was dominated by large bushes and moss, with some lichen. These two sites were within the Ogilvie Mountain range and within Tombstone Territorial Park. Site 3 (67.02°N, 136.20°W), about 280 km north of Sites 1 and 2, was dominated by moss and lichen, with some grass and small shrubs. All sites were adjacent to the Dempster Highway, an

all-season gravel road traversing the northern Yukon. The climate in the region is typical of northwestern North America, with a short growing season, permafrost, and cold winters.

4.3.2 Specimen collection

Spiders and prey were all live-caught in the Yukon, Canada in July 2016. We hand-caught adult *P. lapponica* at Site 1, and *P. sodalis* and *P. moesta* at Site 3. We collected *X. obscurus* at Site 1 using a specialized vacuum (D-vac), constructed by modifying a commercial leaf vacuum (Weed Eater[®] 25cc Leaf Blower/Vacuum; Stewart & Wright 1995). We also used the D-vac to collect potential prey items from Site 1 and Site 2. We collected a range of small, tundra-dwelling arthropods: springtails (Collembola), dwarf spiders (Linyphiidae), leafhoppers (Cicadellidae), mites (Acari), small caterpillars (Lepidoptera), small ground beetles (Carabidae), midges (Diptera, mostly Cecidomyiidae), and mosquitoes (Culicidae). We selected these arthropods because they are abundant in the study region and similar in size or smaller than *P. lapponica*.

We housed all arthropods in 100mL clear plastic containers, with moist paper towel and a small ventilation hole (blocked with gauze) in each container. We housed the wolf and crab spiders individually and housed the prey communally (by taxon).

4.3.3 Feeding trials

The feeding trials took place throughout July 2016. Spiders were starved for a minimum of 48 hours before the feeding trials. We conducted two types of feeding trials: prey identification trials and feeding rate trials.

In each prey identification trial, we added one potential prey individual to the container of a spider. In some cases, the potential prey was another crab or wolf spider, to test for cannibalism or intra-guild predation. For the first three hours, we checked every hour to see if the potential prey was still present. For the next week, we checked every 12 hours (9am and 9pm). If the potential prey was absent, we assumed that the spider had consumed it. If it was present but dead, we replaced it with a new live prey of the same type. The prey identification trials ended when either the spider consumed the prey, the spider died, or a week had passed.

For the feeding rate trials, we added five springtails (mostly 1-2 mm long *Entomobryomorpha*) to the container of a spider. Again, for the first three hours we checked every hour to see how many springtails had been consumed, and for the next week we checked every 12 hours (9am and 9pm). After each check, we replenished the springtails such that there were again five live springtails per container. The feeding rate trials ended when either the spider died or a week had passed. Because of logistics in the field, *X. obscurus* feeding rate trials were terminated early (before 12 hours had passed).

4.3.4 Mesocosm experiment

Each of the 40 mesocosms consisted of a 7.57 L, 23 cm diameter, heavy-duty white plastic bucket (Canadian Tire Bucket, 2-G). In the bottom of each bucket we drilled three small drainage holes, over which we glued mesh screen. Over the top of each bucket we attached a mesh lid (0.88 mm hole size). The mesocosms were laid out on the tundra (Site 1), arranged in a 5x8 grid with about 1m between mesocosms. We gathered moss and lichen substrate from the immediately surrounding area and collected it in a large container. We then gently broke the moss and lichen into smaller pieces and mixed it together, to reduce any spatial effects. We spread 250mL (unpacked) of the substrate on the floor of each mesocosm.

Each mesocosms received one of four randomly-assigned treatments, with ten replicates of each treatment (Table 4.1). The treatments manipulated the spider assemblage of the mesocosms. The treatments were as follows: Control (C): no spiders were added; One-species treatment (1S): two *P. lapponica*; Two-species treatment (2S): one *P. lapponica* and one conspecific *Pardosa*; Two-family treatment (F): one *P. lapponica* and *X. obscurus*.

The 2S and F treatments were divided into sub-treatments, each of which had five replicates. The subtreatments of 2S were as follows: one *P. lapponica* and one *P. sodalis* (2SS); one *P. lapponica* and one *P. moesta* (2SM). The subtreatments of F were as follows: one *P. lapponica* and one *X. obscurus* (F1); one *P. lapponica* and four *X. obscurus* (F4). For F1, the abundance of *X. obscurus* and *P. lapponica* were matched, while for F4, the mass of *X. obscurus* and *P. lapponica* were (roughly) matched. Only female *Pardosa* were selected for the mesocosm experiment, while for *X. obscurus*, both sexes were selected (due to their relative rarity). The mesocosms ran for two weeks, from the 15 - 29 of July 2016. If any spiders died during the two weeks, they were not replaced. At the end of the two weeks we removed the wolf spiders from the mesocosms, except when we were unable to find the wolf spider.

We determined the mass of each spider before and after the mesocosm experiment, using an electronic balance. Due to limited access to electricity in the field, we were unable to weigh the feeding trial spiders. Instead we relied on body length to indicate the body size of these spiders. All spiders, from both the feeding trial and the mesocosm experiments, were preserved in ethanol at the end of their respective experiments. We measured the body length of each spider, from the anterior-most end of its cephalothorax to the posterior-most end of its abdomen (not including its mouthparts or spinnerets). We carefully removed the substrate (moss and lichen) from each mesocosm and placed them in separate, sealed plastic bags. We transported the bags in a cooler back to our laboratory in Montreal, QC, Canada.

4.3.5 Prey extraction using Tullgren funnels

After about 70 hours in transportation, we used Tullgren-type funnels (Tullgren 1918 as cited by Macfadyen 1953) to extract invertebrates from the moss and lichen mesocosm substrate. We had access to 30 Tullgren funnels, and so the first 30 samples were immediately processed in the funnels. For the first hour, we kept the lightbulbs off. Then, for 24 hours we kept the lights at 50% brightness. Finally, we turned the light to full brightness and allowed the funnels to run for four full additional days.

After processing the first 30 samples, we processed the remaining 10 samples, which had meanwhile been refrigerated (4°C). We placed the samples in the funnels and kept the lightbulbs off for five hours, to allow the samples to reach room temperature. As before, for 24 hours we kept the light at 50% brightness. We then turned the light to full brightness and allowed the funnels to run for six more days. From previous experimentation, we had found that when samples had spent some time in refrigeration they required longer in the funnels to

extract all invertebrates. We then counted the extracted invertebrates, identified each specimen to order, and measured their body length.

4.3.6 Statistical analyses

To compare the body length of the *P. lapponica*, *P. sodalis*, *P. moesta*, and *X. obscurus*, we used an ANOVA (function *anova*, R base package; R Core Team, 2016; significant findings for all ANOVA were followed with a Tukey's HSD). We repeated the same analysis comparing log (body mass) rather than body length.

To compare the springtail consumption rate (from the feeding rate trials) of the four spider species we also used an ANOVA (function *anova*). We compared only the first three hours and averaged each individual's rate over these three hours. To test for a positive relationship between spider body length and springtail consumption rate we used a linear regression (function *Im*, R base package). We also tested a multiple regression model of consumption rate, which included both body length, species, and an interaction between the two (function *Anova* from the *car* package; Fox & Weisberg 2011).

To test for differences in prey consumption between the mesocosm treatments and subtreatments, we tested general linear models of "prey remaining" (function *glm*, Poisson-family; followed by function *Anova*, type-II; significant results were followed by a post-hoc test using the function *glht* in the package *multcomp*; Hothorn et al. 2008). These models tested whether spider assemblage composition affected prey consumption. "Prey remaining" was the total number of verified prey items extracted by the Tullgren funnels. That is, we only included the invertebrate types that were consumed during the feeding trial experiments (Table 4.2). We considered the number of prey remaining to (inversely) indicate the number of prey consumed. We tested two models which differed in their explanatory variables: one model contained the Tullgren funnel extraction date as an explanatory covariate in these mesocosm models, as well as all the following mesocosm models.

To test whether the number of prey remaining decreased with the total biomass or variation in body mass of the predator assemblage, we used general linear models (function *glm*, Poissonfamily). The first model contained the number of prey remaining as a response variable and predator biomass (mass sum) and extraction date as explanatory variables (Model 3 in Table 4.3). The second model contained the number of prey remaining as a response variable and standard deviation of predator mass (mass SD) and extraction date as explanatory variables (Model 4 in Table 4.3). Significantly negative values for the mass sum or mass SD coefficients were considered to support the hypothesis that prey consumption increases with predator biomass or predator body mass variation, respectively. The control treatments were not included in these two models because there were no predators in these treatments, so the sum and standard deviation of predator mass were not meaningful.

Finally, we compared general linear models that contained all 15 possible combinations of the three explanatory variables: subtreatment, total predator mass, and standard deviation of predator mass (function *glm*, Poisson-family; followed by function *Anova*, type-II; Table 4.3). The response variable was prey remaining and we did not include control treatments. We calculated AICc, Δ AICc, and Akaike weight for each model (*MuMIn* function *model.sel*; Barton 2017) and selected the model with the lowest AICc as the best model. AICc is the small-sample-size corrected version of the Akaike Information Criterion, a measure of the relative quality of models, for which a smaller value indicates a better model. We also calculated a pseudo-R² for each model (1 – [Residual deviance/Null deviance]; Faraway 2016). This approach allowed us to compare which combination of explanatory variables best explain variation in prey consumption.

4.4 Results

4.4.1 Spider specimens

We collected a total of 184 spiders for the feeding trials and mesocosm experiment: 144 *P. lapponica*, 27 *P. sodalis*, 9 *P. moesta*, and 44 *X. obscurus*. 134 of these spiders were used for the feeding trials: 64 *P. lapponica*, 22 *P. sodalis*, 4 *P. moesta*, and 19 *X. obscurus*.

Body length differed significantly between the species (F(3,150) = 11.47; p < 0.0001), as did body mass (Fig. 4.2; F(3,76) = 129.4; p < 0.0001). Body length of *P. sodalis* was significantly greater than the three other species, and body mass differed between all species except for *P. lapponica* and *P. moesta* (Fig. 4.2). *Pardosa sodalis* had the largest body length at 6.212 mm (Fig. 4.2; standard deviation = SD = 0.851 mm; n = 26) and the greatest body mass at 0.0431 g (SD = 0.0084 g; n = 5). *Pardosa lapponica* was the next largest species, with a body length of 5.144 mm (SD = 0.721 mm; n = 94) and a body mass of 0.0188 g (SD = 0.0045 g; n = 40). *Pardosa moesta* had a similar size, with a body length of 4.417 mm (SD = 0.376 mm; n = 6) and a body mass of 0.0147 g (SD = 0.0013 g; n = 5). *Xysticus obscurus* was the smallest, with a body length of 2.615 mm (SD = 0.300 mm; n = 13) and a body mass of 0.004 g (SD = 0.0024 g; n = 30).

4.4.2 Prey identification feeding trials

We carried out a total of 79 prey identification feeding trials (Table 4.2). The spiders consumed a wide range of prey, and we observed intraguild predation. *Pardosa lapponica* consumed caterpillars, centipedes, springtails, midges, dwarf spiders, leafhoppers, mites, mosquitoes, and crab spiders. However, they consumed caterpillars, centipedes, mites, and crab spiders in \leq 50% of the trials in which they were offered these items. They did not consume beetles or other *Pardosa*. *Pardosa sodalis* consumed midges, dwarf spiders, leafhoppers, mosquitoes, and *Pardosa spp*. They consumed all these items in every trial in which they had been offered them. *P. sodalis* did not consumed mosquitoes, mites, or *P. lapponica*. We only performed one prey identification feeding trial on *P. moesta*; this individual consumed a leafhopper. *X. obscurus* consumed springtails, a midge, and a leafhopper. They did not consume *P. lapponica* nor did they cannibalize *X. obscurus*.

4.4.3 Feeding rate trials

We carried out feeding rate trials on a total of 20 spiders. The mean consumption rate during the first three hours of the feeding rate trials for all spiders was 1.025 springtails/hour (SD = 0.658; n = 20). The feeding rate was not significantly different between spider species (F(3,16) = 2.667; p = 0.083). *Pardosa sodalis* had the highest mean consumption rate during the first three hours, at 1.50 springtails/hour (SD = 0.882; n = 4). *Pardosa lapponica* had the next

greatest rate, at 1.15 springtails/hour (SD = 0.558; n = 10), followed by *X. obscurus*, at 0.533 springtails/hour (SD = 0.298; n = 5), and *P. moesta*, at 0.33 springtails/hour (n = 1).

Consumption rate during the first three hours increased significantly with body length (Fig. 4.3; β =0.238; t=2.691; df=18; p=0.015; adj. R²=0.247). There was no significant interaction between body size and species (χ^2 (2,13) = 0.584; p = 0.476). Body length and log (body mass) were positively correlated (R² = 0.655). Six of the feeding rate trials were terminated early. This included one *P. lapponica* trial, in which the individual died after 60 hours, and all five *X. obscurus* trials, which were terminated before 12 hours due to logistics. The mean consumption rate was greatest during the first three hours of the feeding rate trials, then quickly dropped. The mean consumption rate over the full week (for all spiders that completed the full week) was 0.260 springtails/hour (SD = 0.126; n = 14). This is the equivalent of 43.75 springtails/week.

4.4.4 Mesocosm experiment: Extracted invertebrates

The mean number of invertebrates extracted by the Tullgren funnels was 303.80 (SD = 107.04; n = 40). On the first extraction date, a mean of 322.87 invertebrates were extracted (SD = 115.06; n = 30), while on the second extraction date a mean of 246.60 invertebrates were extracted (SD = 46.21; n = 10).

Most of the invertebrates extracted were mites and springtails. On average, mites made up 54.96% of invertebrates extracted (SD = 10.51 %; n = 40), and springtails made up 43.53% (SD = 10.87 %; n = 40). We also extracted (in descending order of abundance): insect larvae, small spiders (all < 5 mm in body length), true bugs (*Hemiptera*), centipedes, beetles, Hymenoptera, and flies.

Based on the results of the prey identity trials, the following invertebrate types were considered as prey items in the calculation of "prey remaining": springtails, all spiders, true bugs, and flies with body length < 5 mm. Almost all of these extracted prey were springtails (98.4%). The mean number of prey remaining (i.e., prey extracted by the Tullgren funnels) was 137.65 invertebrates (SD = 68.43; n = 40).

We retrieved the highest proportion of *P. lapponica* from the 2SM mesocosms (5/5 *P. lapponica* retrieved) and the F4 mesocosms (5/5), followed by the F1 mesocosms (4/5), the 1S mesocosms (13/20; note that there were 10 trials with two *P. lapponica* each = 20 *P. lapponica*), and finally the 2SS mesocosms (2/5). We retrieved 3/5 *P. moesta* from the 2SM mesocosms, and 4/5 *P. sodalis* from the 2SS mesocosms. We do not report the number of *X. obscurus* retrieved because there is a high probability that missing *X. obscurus* were due simply to the difficulty of spotting these small individuals amongst the like-coloured substrate.

4.4.5 Mesocosm experiment: Effects of predator diversity and biomass Our hypothesis that the number of prey remaining would decrease with phylogenetic diversity was not fully supported. There were significant differences between the four treatments in the number of prey remaining (Fig. 4.4; χ^2 (3, N=40) = 167.85; p<0.0001), but the number of prey remaining in 1S mesocosms (lowest diversity) was significantly less than all other treatments. There were no other significant differences between treatments. There were also significant differences between the six subtreatments in the number of prey remaining (Fig. 4.4; χ^2 (5, N=40) = 200.2; p<0.0001). As with the treatment model, the prey remaining in 1S was significantly less than all subtreatments. The number of prey remaining in the subtreatment F1 was significantly greater than for 1S, but significantly less than all other treatments except 2SM.

Our hypotheses that the number of prey remaining would decrease with predator biomass and variation in mass were supported. The number of prey remaining decreased with the total mass of the predator assemblage (β = -4.647; z = -3.496; p < 0.001; Fig 4.5). The prey remaining also decreased with the standard deviation of the predator mass (β = -5.051; z = -2.199; p = 0.028).

The model of prey remaining with the lowest AICc was the model that included all three explanatory variables and their interactions (Model 15 in Table 4.3). This model accounted for most of the variation in the data (pseudo- $R^2 = 0.88$), and all variables and their interactions were significant (p < 0.0001) except for extraction date. The Aikake weight of this model was 1, while all others had a weight of 0, meaning that we can essentially be certain that the full model (Model 15) was the best of all those compared.

4.5 Discussion

The objective of our experiments was to determine the effect of assemblage composition and body size on the prey consumption rate by tundra spider assemblages. We showed that assemblage composition, functional trait variation, and functional trait identity all act together in determining the prey consumption rate. These findings highlight that the relationship between predator species diversity and consumption rate is far from simple. The effect of the loss or gain of a species will depend on the traits of that species, as well as the traits of other species in the assemblage. As we discuss below, body size is an important functional trait that plays a central role in determining the trophic characteristic of spider communities, including niche complementarity, individual prey consumption rate, and intraguild predation.

4.5.1 The role of phylogenetic diversity

Our hypothesis that the prey consumption of the spider assemblage would increase with its phylogenetic diversity was not fully supported. While the F1 (two-family) subtreatment resulted in fewer prey remaining than the control treatment, the 1S (one-species) treatment resulted in substantially fewer prey remaining (Fig 4.4). Although a positive relationship between predation diversity and consumption rate is most commonly reported, our study and others demonstrate that other relationships are possible (Finke & Denno 2005; Griffin et al. 2013). Theory predicts that when predators are extreme generalists or strong intraguild predation is present, prey suppression will not increase with predator diversity (Ives et al. 2005; Sytvarin & Rypstra 2014). From our feeding trials, we demonstrated that *P. lapponica* is a highly generalist species, eating prey that ranged widely in size, phylogeny, and morphology (Table 4.2). Our prey identification feeding trials of the other spider species, while limited, did suggest that these species had similarly wide trophic niches. Generalist feeding behaviours by spiders is aligned with the common perception of what spiders eat (Foelix 1996). Other authors have also demonstrated that Pardosa and Xysticus are highly generalist (Nentwig 1986; Nyffeler & Benz 1988; Nyffeler 1999), and gut content DNA sequencing has revealed that coexisting Pardosa and *Xysticus* in Greenland have extensive niche overlap (Wirta et al. 2015). Because niche

breadth of all spider species was wide, the addition of a second predator taxon may not have represented an increase in the types of prey the assemblage could together consume.

The presence of intraguild predation also explains the lack of positive relationship between phylogenetic diversity and prey consumption in our mesocosm experiment. We observed three instances of intraguild predation in our feeding trials (Table 4.2; *P. sodalis* consumed *Pardosa spp.*, and *P. lapponica* consumed *X. obscurus*). Other authors have also noted that intraguild predation is common amongst spiders (Hodge 1999; Sitvarin & Rypstra 2014). We did not observe any cannibalism in our feeding trials, perhaps because spiders of the same species were of a similar size (Fig 4.2; Woodward & Hildrew 2002). Predation between spiders of similar size, however, can occur (Petersen et al. 2010). The low proportion of *P. lapponica* due to predation by the larger *P. sodalis*. A larger proportion of *P. lapponica* were retrieved from the 1S mesocosms (13/20), suggesting that seven *P. lapponica* may have been cannibalized. Because intraguild predation was present, the addition of a second predator taxon may have resulted in increased mortality (and other predator effects) for the smaller or similar-sized predator taxon.

The absence of a significant difference between subtreatments 2S and F4 and the control treatment (Fig 4.4) suggests that spiders in these mesocosms were consuming little to no prey. On a small time-scale, intraguild predation effectively eliminates both predators: one predator because it has been eaten, the other because it is satiated. However, we can be certain that most *Pardosa* were not consumed by intraguild predation, since the majority of *Pardosa* were retrieved alive at the end of the treatment period. The low consumption rates of 2S and F4 may therefore be due to non-consumptive predator effects (Schmitz et al. 1997; Preisser et al. 2005). The spiders may have reduced their foraging behaviour (Verdolin 2006) when sharing a mesocosm with a spider of a different species to avoid intraguild predation.

There were significantly fewer prey remaining in F1 and F4, and while it might be too small to be biologically important, could be because of an increase in intraguild predation with *X*.

obscurus density. Intraguild predation would therefore be greater in the F4 mesocosms, and thus prey consumption rate would be reduced.

4.5.2 The role of body mass variation

As we had hypothesized, the number of prey remaining in the mesocosms decreased with variation in predator body mass(Fig. 4.5). The increase in prey consumption with body mass variation, but not phylogenetic diversity, could be because body mass is more important than species identity in determining the diet of these spiders. Other authors have observed that spider trophic position and niche size is influenced by body size (Sanders et al. 2015), and ontogenetic dietary shifts can be substantial as a spider grows (Pekár & Toft 2015). If the niche of a spider is determined largely by its body mass, then the niche complementarity of a spider assemblage will by driven by variation in body mass.

Authors of a previous meta-analysis argued that prey suppression increases with phylogenetic distance due to a correlation between phylogenetic and functional diversity (Griffin et al. 2013). Functional and phylogenetic diversity are indeed often linked (Devictor et al. 2010; Flynn et al. 2011), but this was not the case for our experimental spider assemblages (Table 4.1); The spider species in our study had substantial within-species and within-family body size variation. Spider species of similar size often coexist in nature, so phylogenetic diversity and body size variation may also be unlinked in many natural communities.

The relationship between body size variation and prey consumption could be also driven by an interaction between intraguild predator effects and body size variation. Intraguild predation in spiders usually consists of a larger individual consuming a smaller or similar-sized individual (Balfour et al. 2003; Rypstra & Samu 2005). Therefore, it may be that when a pair of spiders are of similar size, they will both experience predator effects; while when spiders are of different sizes, only the smaller of the pair will experience predator effects. If this is the case, we would expect intraguild predatory effects to decrease with body size variation, which is consistent with our results.

Although overall there was a negative relationship between the number of prey remaining and body size variation, the relationship differed between subtreatments (Fig. 4.5). The relationship was not negative for the 1S treatment, which may be because within-species size variation was low compared to between-species diversity. Another possibility is that intraguild predator effects were less pronounced in the 1S mesocosms because *P. lapponica* were inhibited in cannibalism relative to intraguild predation. Further study is required to better understand the interacting effects of predator body size and intraguild predation on prey consumption.

4.5.3 The role of biomass

As we had hypothesized, the number of prey remaining decreased with the total spider biomass (Fig. 4.5). The increase in prey consumption rate with predator biomass was almost certainly driven by an increase in prey consumption with predator mass at the level of the individual spider (Fig. 4.3). The springtail consumption rate of a spider was determined by its size, and not by the species to which it belonged. This finding of increased prey consumption with predator biomass is predicted by basic tenets of biology, including Kleiber's law (Kleiber 1932) and Lotka-Volterra models. Biomass is determined jointly by body size and population density. In our mesocosms, we controlled predator density experimentally and so differences in biomass were largely due to differences in body size (except for differences between F1 and F4). In natural communities, population density is correlated to body size, such large organisms are more sparsely distributed than small organisms (Damuth 1981). Furthermore, mass-specific metabolic rate decreases with body mass, which may further decrease the top-down effects of large predators (Brown et al. 2004). The studied tundra spider assemblages, however, did not seem to conform to this general rule: for instance, the small X. obscurus spiders were rare compared to the extremely abundant *P. lapponica* spiders. The relationship between predator body size and biomass in natural tundra assemblages may differ from our artificial assemblages, though it is difficult to predict exactly how without a clear relationship between spider body size and population density.

The relationship between predator body size and prey consumption may be affected by its feeding mode (Nakazawa et al. 2013). If this experiment were repeated using web-building

spiders, we might expect a weaker effect of spider body size on prey body size or prey consumption rate. Instead, spider prey consumption may be controlled more by web size and design (Murakami 1983). *Pardosa*, which often use a sit-and-wait strategy, may be able to consume prey of a greater relative size than *Xysticus*, which forage (Griffiths 1980). If *Xysticus* consume smaller prey relative to their body size, they may consume numerically more prey than an equal sized *Pardosa*. This may partly explain the greater prey consumption in F1 mesocosms (Fig 4.4). The relationship between predator biomass and prey remaining was negative for all treatments, but the slope of the relationship was less steep for treatment 1S and subtreatment F1 than for the other treatments (Fig 4.5). These two (sub)treatments were also the two for which the number of prey remaining was significantly less than the control treatment. Perhaps in these mesocosms consumption was limited by some other variable than predator size. When prey density becomes low due to a high consumption rate, consumption rate may be limited by the predator's ability to find prey (which is only loosely related to body size), rather than their ability to manipulate and metabolize prey (which is strongly related to body size).

The best model of the number of prey remaining included a three-way interaction between assemblage composition, predator size variation, and predator biomass. The relationship is such that, while the main effect of predator biomass on the number of prey remaining was negative, for some species composition at some levels of predator body size variation, the relationship was positive. The biological meaning of these complex interactions is unclear; what is clear is that assemblage species composition, functional trait variation, functional trait identity, and their interactions all affect prey consumption.

4.6 Conclusions

Predator assemblages are changing globally and in polar communities due to elevated predator extinction risk (Estes et al. 2011) and shifting species ranges (Pöyry et al. 2009; Fossheim et al. 2015). New spiders from southern regions may join Yukon tundra assemblages, and current Yukon tundra spiders may be lost if they cannot adapt to changing climatic conditions. Furthermore, average spider body size may increase due to climate change (Høye et al. 2009).

The results of our experiments suggest suggest that these changes may affect tundra invertebrate communities. If spider diversity decreases, this could decrease spider intraguild predation, and thus decrease prey abundance. If spider body size increases, prey abundance could also decrease. Many of the prey of *Pardosa* and *Xysticus*, including springtails, are detritivorous, and changes in their abundance will affect decomposition rates (Koltz et al. 2018). Decomposition, in turn, releases greenhouse gases that drive climate change. Predicting the effect of species loss or gain on ecosystem function is an essential task of ecology in the Anthropocene. This task doubly important in climatically-sensitive polar regions. It is an appealing idea that the loss or gain of a species will have a simple and consistent effect on ecosystem functions. Our study emphasizes that the effect of species gain or loss will depend on the species involved and their relevant functional traits. To make predictions that are generalizable, we must better understand the relationships between species traits and ecosystem functions.

4.7 Permits and ethical approval

This research was permitted under the Yukon Scientists and Explorer's Act, License Number: 16-28SandE. Research activity within Tombstone Territorial Park (Sites 1 and 2) was permitted by a Research and Education Park Permit, Permit Number 15-RE-TP-02. Additionally, permission was sought and granted from the Tr'ondek Hwech'in First Nation. All applicable international, national, and institutional guidelines for the care and use of animals were followed.

4.8 Acknowledgements

Thank you to Eric Ste-Marie for his assistance in the field. This project was possible due to funding from the National Science and Engineering Research Council of Canada: A Discovery Grant and Northern Research Supplement to CMB and a Postgraduate Scholarship-Doctoral to ST. It was further supported by the W. Garfield Weston Award for Northern Research (Doctoral) from the Canadian Northern Studies Trust. **Table 4.1.** Description of the mesocosm treatment and subtreatments. The mesocosm experiment was made up of a grid of 40 mesocosms. Each mesocosm consisted of a 7.57 L heavy-duty white plastic bucket. Treatments (and subtreatments) consisted of spiders which were added to the buckets. SD is the standard deviation. The described experiment took place in the Yukon, Canada, in July 2016.

		Spid	ers added	per mesoc		Diversity	Total	Number of		
Treatment	Sub- treatment	Pardosa Iapponica	Pardosa moesta	Pardosa sodalis	Xysticus obscurus	Species richness	Phylo- genetic distance (relative)	Body mass SD (mg; mean ± SD)	predator biomass (mg; mean ± SD)	replicates
С	NA	0	0	0	0	NA			0	10
1S	NA	2	0	0	0	1	Low	4.1 ± 1.6	39.3 ± 8.0	10
25	2SM	1	1	0	0	2	Medium	2.1 ± 2.4	31.6 ± 3.6	5
	255	1	0	1	0	2	Medium	18.9 ± 6.6	59.5 ± 9.4	5
F	F1	1	0	0	1	2	High	11.9 ± 3.3	26.3 ± 3.2	5
	F4	1	0	0	4	2	High	6.2 ± 1.3	32.4 ± 6.5	5

Table 4.2. Results of prey identification feeding trials that took place in the Yukon, Canada, in July 2016. The denominator gives the number of trials in which the predator was offered the potential prey, while the numerator gives the number of individuals eaten by the predator. A "-" is given where the corresponding feeding trial did not occur.

Pote	ential prey	Predator					
Common name	Scientific name	Pardosa Iapponica	Pardosa sodalis	Pardosa moesta	Xysticus obscurus		
Groundbeetle	Carabidae	0/2	-	-	-		
Caterpillar	Lepidoptera larvae	2/5	0/2	-	-		
Centipede	Chilopoda	1/2	-	-	-		
Springtail	Collembola	9/10	-	-	2/2		
Midge	Small Nematocera	8/8	3/3	-	1/1		
Dwarf spider	Linyphiidae	5/9	2/2	-	_		
Leafhopper	Cicadellidae	6/6	3/3	1/1	1/1		
Mite	Acari	1/5	0/2	-	-		
Mosquito	Culicidae	2/2	2/2	-	-		
Wolf spider (not identified to species)	Pardosa spp.	-	2/2	-	-		
Wolf spider	Pardosa lapponica	0/10	0/1	-	0/2		
(identified to species)	Pardosa sodalis	0/1	-	-	-		
Crab spider	Xysticus obscurus	1/2	-	-	0/2		

Table 4.3. Model comparison (AICc, ΔAICc, Akaike weight, and pseudo-R²) of a mesocosm experiment performed in July 2016 in the Yukon, Canada. "Prey remaining" was measured as the number of prey extracted (Collembola, Araneae < 5mm, Diptera, and Hemiptera) from mesocosm substrate by Tullgren funnel. Control mesocosms were not included in the model dataset. "Extr. date" refers to the date which the mesocosm substrate was processed in the funnels. "Subtreatment" refers spider assemblage composition (Table 4.1). "Mass sum" is the total biomass of the spiders added to the mesocosm. "Mass SD" is the standard deviation of the mass of the spiders added to the mesocosm.

	Model	AICc	ΔAICc	weight	Pseudo-R ²
1	Prey remaining ~ Extr. date	1007.1	530.9	0	0.19
2	Prey remaining ~ Extr. date+ Subtreatment	858.8	398.9	0	0.35
3	Prey remaining ~ Extr. date+ Mass sum	997.1	520.9	0	0.2
4	Prey remaining ~ Extr. date+ Mass SD	1004.7	528.0	0	0.2
5	Prey remaining ~ Extr. date+ Subtreatment + Mass sum	973.5	497.4	0	0.52
6	Prey remaining ~ Extr. date+ Subtreatment * Mass sum	653.4	177.3	0	0.58
7	Prey remaining ~ Extr. date+ Subtreatment + Mass SD	656.6	180.4	0	0.56
8	Prey remaining ~ Extr. date+ Subtreatment * Mass SD	541.3	65.1	0	0.69
9	Prey remaining ~ Extr. date+ Mass sum + Mass SD	999.6	523.4	0	0.2
10	Prey remaining ~ Extr. date+ Mass sum * Mass SD	971.8	511.9	0	0.23
11	Prey remaining ~ Extr. date+ Subtreatment + Mass sum + Mass SD	604.5	128.3	0	0.61
12	Prey remaining ~ Extr. date+ Subtreatment * Mass sum + Mass SD	545.9	69.7	0	0.69
13	Prey remaining ~ Extr. date+ Subtreatment + Mass sum * Mass SD	589.3	129.5	0	0.63
14	Prey remaining ~ Extr. date+ Subtreatment * Mass SD + Mass sum	515.2	39.1	0	0.72
15	Prey remaining ~ Extr. date+ Subtreatment * Mass sum * Mass SD	476.2	0	1	0.88



Figure 4.1. Map of the three sites at which spiders and potential prey were collected in July 2016. The mesocosm experiment took place at Site 1. This map was created using Google Earth (Map data: Google, DigitalGlobe). Inset map from image created by Robert Klarić, distributed under a CC-BY-SA-4.0 license.



Figure 4.2. The body mass of three spiders species collected and measured alive in the Yukon, Canada, in 2016. The middle bars represent medians, the top and bottom of the boxes represent the lower and upper quartiles (25% and 75%), respectively, and the tops and bottoms of the whiskers represent the minimum and maximum values (excluding outliers), respectively. Shared letters above the bars indicated a lack of significant difference.



Figure 4.3. The relationship between spider body length and springtail consumption rate in feeding trials that took place in July 2016 in the Yukon, Canada. The dark grey line shows the fitted regression line, while the light grey polygon shows the 95% confidence interval.






Figure 4.5. The number of prey remaining in experimental mesocosms after treatments were applied, as measured by the number of prey extracted from mesocosm substrate by Tullgren funnel, varies by treatment (Table 4.1), predator biomass, and standard deviation (SD) of predator biomass. Left panels: Model fit is shown for the model Prey remaining ~ Extr. date + Subtreatment * Mass sum (Model 5 in Table 4.3). Right panels: Model fit is shown for the model Prey remaining ~ Extr. date +

refers to the date which the mesocosm substrate was processed in the funnels. The dark grey lines show the fitted regression lines, while the light grey polygons indicate the 95% confidence intervals. Note that the y-axis is logarithmic. The experiment took place in July 2016 in the Yukon, Canada.

Connecting Text:

In the experiments described in Chapter 4, I showed that predator body size is an important endogenous variable affecting the trophic structure of tundra arthropod communities. I found that predator body size mediates the relationship between predator assemblage composition and prey consumption. In this chapter, I investigate the relationship between predator body size and trophic properties, including prey body size, niche breadth, and trophic level. Previous studies have found or predicted various relationships between predator body size and trophic properties, depending on study assumptions and which ecosystem type or taxonomic group was studied. The objective of Chapter 5 is to describe the relationship between predator body size and trophic properties for terrestrial vertebrate predators (Accipitridae, Felidae, and Serpentes). By understanding the relationships between predator body size and trophic properties we can better predict the effect of predators on community structure – effects which can be profound (Estes et al. 2011). This chapter addresses the question: *How does body size of terrestrial vertebrate predators correlate to their trophic properties*?

Contributions of authors: The authors that contributed to this work are Shaun Turney¹, Gregor F. Fussmann², and Christopher M. Buddle¹. ST, GFF, and CMB conceived the ideas and designed the methodology; ST collected and analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts.

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Chapter 5: Body mass predicts trophic properties of terrestrial vertebrate predators, but not always as expected

5.1 Abstract

Body mass is an important determinant of how an animal interacts with its environment, and thus plays a central role in many ecological models. We tested several hypotheses regarding relationships between body mass and trophic properties of the terrestrial vertebrate predators, Accipitridae (eagles, hawks, and their relatives), Felidae (cats), and Serpentes (snakes). We used published dietary inventories, predator and prey trait data, and phylogenetic least squares models to test hypotheses. Predators, on average, were larger than their prey. The logarithm of prey mass increased with the logarithm of predator mass with slope >1 for Accipitridae and Felidae, while it remained constant for Serpentes. Prey size breadth remained constant with predator mass; prey diversity increased with predator mass, but only for Serpentes. We found unexpected relationships between trophic level and body mass: the trophic level of Felidae decreased with their body mass, and predator-prey body mass ratio increased with trophic level for Accipitridae and Felidae. We conclude that the diet of terrestrial vertebrate predators is consistent with that of organisms in size-structured food webs, but that the same is not true for their prey; As a result, we found predator mass-trophic level relationships that were not as predicted by theory.

5.2 Introduction

The body mass of an animal is an easily measured trait that encapsulates a broad suite of life history traits, and therefore is central to many foundational (Elton 1927; Haldane 1927) and recent ecological theories (e.g., Brown et al. 2004; Loeuille & Loreau 2005; Woodward et al. 2005; Petchy et al. 2008; Alhoff et al. 2015; Welti et al. 2017). The cascading effects of body mass have the potential to explain aspects of ecosystem ecology tractable to the organismal level, providing a unifying framework across multiple scales (Brown et al. 2004). In this meta-

analysis, we test several hypotheses relating to the body mass and trophic properties of terrestrial, vertebrate predators.

Predator-prey body mass ratio (PPMR)

Predators generally eat prey smaller than themselves. Equivalently, predator-prey mass ratio (PPMR) is typically greater than 1. This general rule is an important underlying assumption in prominent food web models (e.g., Loeuille & Loreau 2005; Petchy et al. 2008; Alhoff et al. 2015) and PPMR affects food web stability (Brose et al. 2006a; Weitz and Levin 2006). Whether a specific predator species is larger than its prey depends on its ecosystem, taxonomic group, and feeding mode (Nakazawa et al. 2013). Invertebrate predators tend to consume prey of a similar size to themselves (Brose et al. 2006b), and cooperative hunters (e.g., wolves or lions) can consume prey much larger than themselves. In general, predators that are strongly gape-limited, like snakes (Shine 1991; King 2002) and fish (Jennings et al. 2001), should be most restrained in their maximum prey size.

Predator body size and niche breadth

Large predators are less mechanically constrained in their prey size than small predators, and large predators encounter a wider range of potential prey due to their larger home ranges (Jetz et al. 2004). Although large predators may be capable of consuming small prey, they may avoid these prey because they provide less energy and search cost is often greater (Werner & Hall 1974). Previous empirical studies have yielded divergent results: several studies have found that niche breadth does not change with predator body size (e.g, Shine 1991; Brandl et al. 1994; Neubert et al. 2000; Costa 2009), while many other studies have found an increase in niche breadth with body size (e.g., Cohen et al. 1993; Scharf et al. 2000; Radloff & Du Toit 2004). At least one study found a decrease in niche breadth with predator body size (Costa et al. 2008). These inconsistent findings could be because the relationship between niche breadth and body size varies between taxonomic groups or ecosystems.

The relationships between trophic level and predator body size or PPMR

The assumption that consumers are typically larger than their resource (e.g., Elton 1927; Loeuille & Loreau 2005; Petchy et al. 2008) implies a positive relationship between body size and trophic level. There is a consistent positive correlation between trophic level and body mass in fish, perhaps because gape-limited predation is common amongst fish (Jennings et al. 2001; Arim et al. 2010; Romanuk et al. 2011). The correlation between body size and trophic level is generally weaker in terrestrial food webs than aquatic food webs because terrestrial ecosystems are less size-structured, especially at low trophic levels (Shurin et al. 2006). The lack of size-structure in terrestrial ecosystems is due, in part, to nature of terrestrial plants, which are larger and less easily digested than aquatic plants. Many herbivores are much smaller than their resource, consuming only select tissues (e.g., aphids), or are much larger, with long digestive systems (e.g., deer). Terrestrial vertebrates may have no relationship between body mass and trophic level (Riede et al. 2011; Tucker & Rogers 2014), or a negative relationship (Burness et al. 2001). As predator body size increases with trophic level, the relative size of their prey has been found to increase as well (Riede et al. 2011; Tucker & Rogers 2014). PPMR typically decreases with trophic level, such that basal predators consume prey much smaller than themselves, and top predators consume prey of a similar size to themselves.

In this study, we investigated the relationship between a predator's body size and its trophic properties in three groups of terrestrial vertebrate predators: Accipitridae (hawks, eagles, and their relatives), Felidae (cats), and Serpentes (snakes). We chose these three groups because they are obligate hyper-carnivores (diet is >90% animal material), they are well-studied, and their phylogenies are available. Using a meta-analytic approach, we analyzed phylogenetic, body mass, and diet data. We hypothesized that the body size of terrestrial vertebrate predators determines how they fit into their food webs: with whom they are linked and, ultimately, their effects on community structure and dynamics. Specifically, we tested four predictions for each of the three predator groups: (1) Predators are larger than their prey (PPMR > 1). (2) Niche breadth remains constant or increases with predator body size. (3) Predator body size increases with trophic level. (4) PPMR decreases to approach 1 with trophic level. We test whether these predictions, which are supported by previous studies of other

taxa, hold true for three terrestrial vertebrate predator groups, with implications for the assumptions of widely used ecological models.

5.3 Methods

5.1.1 Prey consumption data

Using the citation database Scopus (www.scopus.com), we searched for field studies which inventoried the diet of Accipitridae, Felidae, and Serpentes species. For Accipitridae and Felidae, we included studies from 1999-2018. Appropriate Serpentes studies were rarer, so we included studies from 1980-2018. Our search terms were: "TITLE-ABS-KEY (Accipitridae OR hawk* OR eagle* OR kite*) AND TITLE (diet* OR dietary)", "TITLE-ABS-KEY (felid* OR feline*) AND TITLE (diet* OR dietary)", and "TITLE-ABS-KEY (Serpentes OR snake*) AND TITLE (diet* OR dietary)". We included in our meta-analysis all studies that reported greater than 12 prey items observed in stomach contents, feces, pellets, by camera, or by direct observation. We excluded dietary inventories of aquatic predators, which we consider to be any diet with ≥ 50% aquatic prey (fish and amphibians) by numerical frequency. Studies which described predator diet over regions larger than approximately 100,000 km² were excluded to avoid a species-area effect. Region size was not usually indicated directly in the studies and was estimated from available information. For Serpentes, we excluded studies that combined adult and juvenile diet, rather than reporting adult diet separately. We did not exclude studies that included Felidae and Accipitridae juveniles because juvenile diet is generally provided by adults in these taxa.

5.1.2 Trait data

For prey items, we identified average body mass and diet (herbivore, omnivore, or carnivore). For each predator species, we identified its average body mass and calculated its trophic level. We collected trait data from several data sources: The Encyclopedia of Life (EOL; Parr et al. 2014), PanTHERIA (Jones et al. 2009), Amniote database (Myhrvold et al. 2015), EltonTraits (Wilman et al. 2014), Amphibio (Oliveira et al. 2017), and Fishbase (Froese & Pauly 2000). To access the EOL database, we used the software *traits* (Chamberlain et al. 2017). For some species, we found multiple body size measurements across the databases, and selected median (for odd numbers of values) or mean (for even numbers of values) of the measurements. We defined herbivores as animals that never or rarely eat animals (diet is roughly \leq 10% animal material); carnivores never or rarely eat plants (roughly \geq 90% animal material); and omnivores regularly eat both plants and animals (roughly 10-90% animal material). We therefore considered insectivores to be carnivores. In addition, we made several assumptions about prey mass and diet (E.g., Insecta have a body mass of 1 g; Lagomorpha are herbivorous; Table S5.1). We searched additional literature for traits that were unidentified by the databases and assumptions.

To calculate the trophic level of the predators, we assigned herbivorous prey a trophic level of 2, omnivorous prey a trophic level of 2.5, and carnivorous prey a trophic level of 3 (following Tucker & Rogers 2014). We then combined the information on diet composition and prey trophic level, to calculate the trophic level of predator *i*:

$$TL_i = 1 + \left(\frac{\sum_{j=1}^n P_{ij} \cdot TL_j}{\sum_{j=1}^n P_{ij}}\right)$$

Where P_{ij} is the numerical proportion of each prey (*j*) in the diet of the predator (*i*). TL_j is the trophic level of prey *j*, and n is the number of prey groups consumed by predator *i*.

5.1.3 Phylogenies

Diet and body size are determined largely by evolutionary history, so any observed correlations between these variables could be due to the phylogenetic relationships between species. To control for this phylogenetic signal, we included phylogenies of Accipitridae, Felidae, and Serpentes in our analyses. The phylogenies of Accipitridae and Serpentes are not yet known with high confidence: the branch lengths (i.e., time since divergence) and relationships between some phylogenetic branches are not known with certainty. To deal with this problem, we used distributions of trees, with varying topology and branch lengths, rather than a single tree for each of the two groups. We randomly selected 1000 trees from a pseudo-posterior distribution and pruned them to contain only the study species (Accipitridae: Jetz et al. 2012; Serpentes: Tonini et al. 2016; downloaded from www.vertlife.org). Felidae phylogeny is known with higher certainty and contains no polytomies for the study species. While the relationships between branches are well known, the branch lengths are known with less certainty, so we used a distribution of trees with varying branch length but identical topology. We pruned a Carnivora phylogeny (Nyakatura & Bininda-Emonds 2012) and randomly selected 1000 trees from a pseudo-posterior distribution with varying branch length (following Kuhn et al. 2011). Branch length for Felidae was allowed to vary by an amount equal to the largest 95% confidence interval in the pruned tree.

5.3.4 Data analysis

To test if predators were larger than their prey, we determined if log (PPMR) > 0, and therefore if PPMR > 1. We used base 10 for all logarithmic transformations. We calculated the PPMR as the predator mass over the average prey mass. We calculated the average prey mass as the geometric mean of prey masses, weighted by the relative frequency of the prey items. Geometric mean is closer to the median than an arithmetic mean for most log-normal distributions and is calculated as the arithmetic mean of the log (prey mass), converted back to a base 10 number. To determine whether log (PPMR) > 0, we used a phylogenetic least squares model (PGLS; using *qls* in *nlme*; Pinheiro et al. 2018) containing only an intercept (β_0). β_0 was an estimate of log (PPMR), and therefore if $\beta_0 > 0$, then PPMR > 1. PGLS is a phylogenetic comparative method to test for correlations between species' traits while accounting for nonindependence generated by evolutionary relationships between species. We selected a Brownian correlation structure with a value of Pagel's λ optimized by restricted maximum likelihood (using *corPagel* in *ape*; Paradis et al. 2004). Pagel's λ is measure of phylogenetic signal, where $\lambda = 0$ indicates no effect of phylogeny and $\lambda = 1$ indicates that species' traits covary in proportion to shared evolutionary history (Pagel 1999; Freckleton et al. 2002). λ is usually between 0 and 1, but $\lambda > 1$ suggests the rate of evolution is greater at the base of the tree than at the tips and $\lambda < 0$ suggests that related species are more dissimilar than expected under phylogenetic independence. For each predator taxa, we repeated the PGLS for each of the 1000 sampled trees and then averaged the 1000 models (following Garamszegi 2014). Each model contained an estimate of the β_0 and λ , which varied due to the slightly different phylogeny used in each model. We calculated the model-averaged estimate of β_0 and its 95% confidence interval (using AlCcmodavg; Mazerolle 2017), to test if $\beta_0 > 0$. For all PGLS

regressions, we considered a value to be significantly different from 0 when its confidence interval did not overlap with 0. We used the *R* statistical environment to carry out all analyses (R Core Team, 2018).

To test for correlations between predator and prey mass, we used three measures of prey mass: average, minimum, and maximum prey mass. The minimum and maximum prey masses were simply the mass of the lightest and heaviest prey items, respectively. For each of the three measures of prey mass, we calculated the model-averaged slope (β_1) for PGLS models of log (prey mass) with log (predator mass) as the explanatory variable. In these models and the following models, β_1 is the slope of the relationship between the two variables, when accounting for phylogeny. If β_1 is significantly > 0, this indicates the relationship is positive, and if β_1 is significantly < 0, this indicates the relationship is negative.

To test for relationships between predator body mass and niche width, we measured niche width in terms of prey mass breadth. We calculated prey mass breadth as log (maximum prey mass) – log (minimum prey mass). We also measured niche width in terms of prey taxonomic diversity using two measures: Levins niche breadth and rarefied family richness. Levins niche breadth is the reciprocal of Simpson's index of diversity, or $1/\Sigma p_i^2$, where p_i is the proportion of prey items belonging to category *i* (Levins 1968 as cited in Krebs 1999). Rarefied family richness was calculated as the number of prey families expected in a dietary sample with 13 items (calculated using *vegan*; Oksanen et al. 2018). For each of the niche width measures and each of the predator taxa, we calculated the model-averaged slope (β_1) of PGLS models for niche width with log (predator mass) as the explanatory variable.

Next, to test for correlations between predator body mass and trophic level, we calculated the model-averaged slope (β_1) of PGLS models for trophic level, with log (predator mass) as the explanatory variable. Finally, we tested for relationships between PPMR and trophic level. For each predator taxon, we calculated the model-averaged slope (β_1) of PGLS models for log (PPMR) with trophic level as the explanatory variable.

For predator species described by multiple studies, we averaged the trophic characteristics (trophic level, prey mass, niche breadth) across the studies and used these averaged values for

all PGLS analyses. Dietary inventories for which the body mass of < 50% of prey were known (by numerical frequency) were excluded from this averaging for prey mass variables. Likewise, predators for which the diet of < 50% of prey were known were excluded from this averaging for trophic level.

5.4 Results

Our Scopus search for Accipitridae yielded 284 studies, of which we included 26 studies (Table S5.2; Table S5.3). Our Scopus search for Felidae yielded 385 studies, of which we included 36 studies. Our Scopus search for Serpentes yielded 366 studies, of which we included 17 studies. Some studies described the diet of > 1 predator species (2 Accipitridae studies, 8 Felidae studies, and 1 Serpentes study) and the diets of some species were described in > 1 study (6 Accipitridae species, 10 Felidae species, and 1 Serpentes species). In total, the 79 studies yielded 95 dietary inventories of 55 predator species: 21 Accipitridae, 17 Felidae, and 17 Serpentes species.

The dietary inventory of each predator included, on average, 297.5 prey items (SD = 485.5) identified into 15.7 taxonomic groups (SD = 11.7). These taxonomic groups were most often prey species or genera. We were able to assign body mass to 84.6% of prey taxa, and to assign diet to 79.2% of prey taxa. Only one dietary inventory (of *Leopardus tigrinus*) was excluded for having < 50% of prey mass known, and two dietary inventories (of *Leopardus wiedii* and *Felis catus*) for having < 50% of prey diet known. All three of these species were described by multiple studies and were therefore still present in the PGLS analyses.

In agreement with our first prediction, all three predator groups were larger in body mass than their average prey (Fig. 5.1). Accipitridae predators had a greater mean body mass than their prey ($\beta_0 = 1 \pm 0.61$; $\lambda = 0.898 \pm 0.004$), with a geometric mean PPMR of 7.15 (geometric standard deviation = $\sigma_g = 2.64$). The geometric mean of Accipitridae body mass was 867 g ($\sigma_g = 3$), while the geometric mean of average prey body mass was 121 g ($\sigma_g = 6$). The PPMR for the smallest Accipitridae prey was, on average, 104.1 ($\sigma_g = 3.6$), while the PPMR for the largest prey was 0.4 ($\sigma_g = 6.3$). Felidae had a greater mean body mass than their prey ($\beta_0 = 1.46 \pm 1.04$; $\lambda = 1.09 \pm 0$), with a geometric mean PPMR of 20.7 ($\sigma_g = 5.9$). The geometric mean of Felidae body

mass was 14,486 g ($\sigma_g = 4$), while the geometric mean of average prey body mass was 698 g ($\sigma_g = 22$). The PPMR for the smallest Felidae prey was 283.8 ($\sigma_g = 7.2$), while the PPMR for the largest prey was 1.13 ($\sigma_g = 7.11$). Serpentes had a greater mean body mass than their prey ($\beta_0 = 1.33 \pm 0.37$; $\lambda = 0.006 \pm 0.002$), with a geometric mean PPMR of 21.2 ($\sigma_g = 5.7$). The geometric mean of Serpentes body mass was 407 g ($\sigma_g = 4$), while the geometric mean of average prey body mass was 19 g ($\sigma_g = 4$). The PPMR for the smallest Serpentes prey was 117.4 ($\sigma_g = 6$), while the PPMR for the largest prey was 2.3 ($\sigma_g = 8.2$).

Average prey mass increased with predator mass (Fig. 5.1) for Accipitridae ($\beta_1 = 1.56 \pm 0.41$; $\lambda = 0.835 \pm 0.005$) and Felidae ($\beta_1 = 2.11 \pm 0.43$; $\lambda = 0.358 \pm 0.002$). For Serpentes, there was no significant relationship between prey and predator mass ($\beta_1 = 0.21 \pm 0.33$; $\lambda = -0.175 \pm 0.004$).

In agreement with our second prediction, niche width increased or did not change with predator body mass, depending on the predator taxon and niche width measure. There was no change in prey mass breadth for Accipitridae ($\beta_1 = 0.68 \pm 0.96$; $\lambda = 0.181 \pm 0.004$), Felidae ($\beta_1 = -0.16 \pm 1.35$; $\lambda = 0.675 \pm 0.002$), or Serpentes ($\beta_1 = 0.49 \pm 0.63$; $\lambda = -0.21 \pm 0.019$). For Accipitridae and Felidae, prey mass breadth remained constant because minimum and maximum prey mass increased equally (Fig. 5.1). For Serpentes, prey mass breadth remained constant because minimum and maximum prey mass both remained constant. In contrast, Levins niche breadth ($\beta_1 = 1.17 \pm 0.9$; $\lambda = -0.236 \pm 0.006$) and rarefied family richness ($\beta_1 = 1.54 \pm 0.86$; $\lambda = -0.208 \pm 0.005$; Fig 5.2) increased with predator body mass for Serpentes. Levins niche breadth did not change with predator body mass for Accipitridae ($\beta_1 = -1.57 \pm 1.84$; $\lambda = 1.042 \pm 0.002$) or Felidae ($\beta_1 = -0.17 \pm 0.35$; $\lambda = -0.415 \pm -0.002$). Nor did rarefied family richness change with predator body mass for Accipitridae ($\beta_1 = -1.57 \pm 1.84$; $\lambda = 1.042 \pm 0.002$) or Felidae ($\beta_1 = -0.17 \pm 0.35$; $\lambda = -0.415 \pm -0.002$). Nor did rarefied family richness ($\beta_1 = -0.024 \pm 0.004$) or Felidae ($\beta_1 = -0.17 \pm 0.35$; $\lambda = -0.415 \pm -0.002$). Nor did rarefied family richness ($\beta_1 = -0.024 \pm 0.004$) or Felidae ($\beta_1 = -0.024 \pm 0.004$).

Contrary to our third prediction, Felidae trophic level decreased with predator body mass ($\beta_1 = -0.18 \pm 0.04$; $\lambda = -0.541 \pm 0.007$; Fig 5.3). Trophic level did not change with predator body mass for Accipitridae ($\beta_1 = -0.18 \pm 0.27$; $\lambda = 0.558 \pm 0.003$) or Serpentes ($\beta_1 = -0.2 \pm 0.24$; $\lambda = 0.45 \pm 0.003$).

Contrary to our fourth prediction, PPMR increased with predator trophic level (Fig. 5.4) for Accipitridae ($\beta_1 = 1.08 \pm 0.61$; $\lambda = 0.002 \pm 0.001$) and Felidae ($\beta_1 = 2.31 \pm 1.35$; $\lambda = 0.593 \pm 0.001$). For Serpentes, there was no significant relationship between PPMR and trophic level ($\beta_1 = -0.2 \pm 1.22$; $\lambda = 0.052 \pm 0.002$).

5.4.1 Diet composition

In all three predator taxa, Mammalia were the most frequently consumed prey class (Table 5.1). The diet of Accipitridae, regardless of their body mass, was composed of about half Mammalia, while Aves and Reptilia composed most of the rest of their diet. The most widely consumed prey families for large Accipitridae (\geq 800 g; n = 10 species) were Columbidae (pigeons and doves; consumed by n = 9 Accipitridae species), Phasianidae (pheasants, partridges, and their relatives; n = 8), Corvidae (crows, rooks, and their relatives; n = 8), and Leporidae (rabbits; n = 7). The most widely consumed prey families for small Accipitridae (< 800 g; n = 11) were Muridae (mice and rats; n = 9), Cricetidae (hamsters, voles, and their relatives; n = 5), Sturnidae (medium-sized passerine birds; n = 4), and Columbidae (n = 4).

On average, large Felidae (\geq 10 kg; n = 9 Felidae species) consumed almost exclusively Mammalia, while the diet of small Felidae (< 10 kg; n = 8 species) also included Aves or other prey classes. The most widely consumed prey families for large Felidae were Bovidae (bison, goats, and their relatives; n =7), Cervidae (elk, deer, and their relatives; n = 6), and Muridae (n = 6). The most widely consumed prey families for small Felidae were Cricetidae (n = 7), Muridae (n = 6), Lacertidae (wall lizards; n = 4), and Leporidae (n = 4).

On average, small Serpentes (< 500 g; n = 9) consumed almost exclusively Mammalia and Reptilia, while large Serpentes (\geq 500 g; n = 8) consumed a more varied diet of Mammalia, Insecta, Reptilia, Amphibia, and Aves. The most widely consumed prey families for large Serpentes were Leporidae (n = 4), Muridae (n = 3), Teiidae (whiptail lizards; n = 3), and Cricetidae (n = 3). The most widely consumed prey families for small Serpentes were Cricetidae (n = 6), Muridae (n = 4), and Soricidae (shrews; n = 4).

5.5 Discussion

The goal of this research was to determine the relationship between the body size and trophic properties of terrestrial vertebrate predators. We achieved this by testing the validity of several hypotheses relating to predator body mass for three groups: Accipitridae, Felidae, and Serpentes. The patterns we observed for these three taxa were largely in agreement with theory and with previous work on other predator taxa, with some strong exceptions. While Accipitridae, Felidae, and Serpentes are size-structured in their prey choice, they exist in food webs that are not size-structured. As a result, trophic level did not respond to predator body mass as predicted.

The predator-prey body mass ratio (PPMR) is greater than 1

Predators were larger than their prey, on average, and this has implications for community structure. Accipitridae, Felidae, and Serpentes typically consumed prey that were a fraction of their own body mass, with PPMRs of 7.15, 20.7, and 21.2, respectively (Fig. 5.1). When predators are larger than their prey, this contributes to food web stability (Brose et al. 2006a) because the predator is less likely to be out-competed by an invading competitor (Weitz and Levin 2006). While the PPMR of Accipitridae, Felidae, and Serpentes were greater than one, they were lower than values that Brose et al. (2006b) found in an extensive food web analysis (2006b), which found an average PPMR of 812.8 for terrestrial endotherms and 120.2 for terrestrial ectotherms. The difference is likely due to the low rate of insectivory amongst the studied predators (Table 5.1), which raises the question of why these species rarely consume insects. Due to their relatively low PPMR, Accipitridae, Felidae, and Serpentes may have high trophic efficiency (Anderson et al. 2009), and interaction intensity (Brose et al. 2005), both variables that are predicted to be greater when PPMR is close to 1.

Predators were larger than their average prey but it was common for predators to also consume prey larger than themselves. The largest prey of the average Accipitridae species was about twice its own mass (PPMR = 0.4) and the largest prey of the average Felidae species was about the same mass as itself (PPMR = 1.13). In contrast, the average Serpentes species almost exclusively consumed prey much smaller than itself (largest prey of the average Serpentes

species had PPMR = 2.3). Many of the cases in which PPMR > 1 were probably instances of scavenging. For example, six Accipitridae species consumed adult Bovidae (large, ruminant mammals), much more likely accomplished by scavenging than predation; but the two types of prey uptake cannot be distinguished by examining pellets or stomach contents. Scavenging is very common amongst predators and has ecosystem effects profoundly different from predation (Garvey & Whiles 2016) but is rarely considered in food web models (Wilson & Wolkovich 2011). In other cases, predators likely truly preyed upon large animals, such as for consumption of Bovidae by large Felidae. Cases where predators are larger than their prey are rarely studied (Nakazawa et al. 2013) and assumed by many theoretical models to not exist (e.g., Loeuille & Loreau 2005; Petchy et al. 2008), and so the consequences of PPMR > 1 for food web dynamics and topology are not well understood. Overall, PPMR varies strongly within and between species due to variation in prey preference and availability. As a result, even within species the effect of a predator on food web structure and topology will vary spatially and temporally.

Average prey body mass increased with predator body mass for Accipitridae and Felidae, and the slope of the log-log regression was greater than unity (Fig. 5.1). In other words, PPMR decreased with predator body mass such that small predators consumed prey much smaller than themselves and large predators consumed prey of a similar size to themselves. This finding agrees with the food web analysis of Cohen et al. (1993) but contrasts with the findings of Brose et al. (2006b), who calculated the slope to be less than unity. Brose et al. (2006b) attributed their finding to an increase in prey mass breadth with predator mass, which we did not observe for our studied predators. While globally the log-log relationship between predator and prey body mass has a slope greater than one, the relationship differs between predator phyla and classes and is sometimes less than one (Naisbit et al. 2011). We found that the predator-prey body mass relationship was not strongly correlated to phylogeny within the predator taxa ($\lambda < 0.4$ for all groups), but that, in contrast to Accipitridae and Felidae, the loglog regression slope for Serpentes was less than one and not significantly greater than 0 (Fig. 5.1). The average size of Serpentes' prey remained constant with Serpentes size. Consequently, PPMR increased with Serpentes body mass: small Serpentes taxa consumed prey similar in size

to themselves and large Serpentes taxa consumed prey much smaller than themselves. For example, the largest Serpentes in our analyses, the Boa constrictor (10.6 kg) consumed Ameiva *bifrontata* (32 g) most frequently, and the smallest Serpentes, the Cerastes vipera (16 g) consumed Acanthodactylus scutellatus (75 g) most frequently. These findings contrast with previous studies, which have consistently found that prey mass increases with Serpentes head or gape size (e.g. Shine 1991; King 2002). Jaw size increases with body mass in Serpentes (King 2002), but perhaps this correlation is not strong enough to detect a signal between predator and prey body mass. More likely, we did not detect any relationship because we averaged predator and prey mass. Using species averages rather than the mass of individual predators and prey in specific encounters will obscure true PPMR when there is high intraspecific variation in body mass (Jennings et al. 2001; Nakazawa et al. 2011). Although we excluded juvenile Serpentes, Serpentes (unlike Accipitridae and Felidae) continue to grow throughout their lives, leading to high level of variation in adult body mass. Our results indicate that prey body mass preference varies little between species, despite probable variation within species. This interspecific relationship may be because large Serpentes species avoid large prey because they are less abundant than small prey or are more difficult to subdue. Another trait which differentiates Serpentes species is their lack of limbs for prey handling. Serpentes taxa overcome this limitation generally by employing one of two strategies: venom and constriction (Lillywhite 2014). If the ability to subdue prey, rather than gape size, sets the upper prey size limit in some constrictors, then prey size will be limited both by predator size and by handling strategy.

Niche breadth remains constant or increases with predator body size

Prey mass breadth remained constant with predator mass for all three groups (Fig. 5.1). Our findings were consistent with the prediction that large Accipitridae and Felidae avoided small prey. Many large Accipitridae and Felidae did consume the small rodents and other small animals preferred by their smaller relatives, but the bulk of their diet was composed of larger animals (Table 5.1), presumably because the energetic cost of hunting small animals is not usually worth the payoff. Note that while the difference between minimum and maximum PPMR remained constant, the absolute difference between maximum and minimum prey mass

increased. Therefore, prey mass breadth might be considered to have increased or not, depending on how it is measured. Serpentes prey mass breadth (whether prey mass was measured as a relative or absolute value) remained constant with predator mass, but it was because both the maximum and minimum prey size remained constant with predator mass. Large Serpentes consumed different prey than small Serpentes (Table 5.1), but on average their prey was the same size. Again, this finding is likely due to averaging of predator and prey mass, and avoidance of large prey by large Serpentes. Constant niche breadth size is inconsistent with the cascade food web model (Pimm et al. 1991), but consistent with the niche food web model (Williams and Martinez 2000) and some previous observations (Brandl et al. 1994; Neubert et al. 2000; Costa 2009). Accipitridae, Felidae, and Serpentes consume prey smaller than themselves, but, like the niche model, the prey fall within a certain limited range of PPMR.

Niche breadth, as measured by prey diversity, increased with predator body mass for Serpentes, but not for Accipitridae or Felidae (Fig 5.2). Small Serpentes consumed almost exclusively mammals and reptiles, while large Serpentes typically consumed a more diverse diet of mammals, birds, reptiles, insects, and amphibians (Table 5.1). Prey diversity increased with Serpentes body mass even after rarefaction, so the effect is not due to large Serpentes eating a greater number of prey items. Serpentes home range size increases with body mass (Reed, 2003). Due to a species-area effect, larger Serpentes will therefore encounter a greater diversity of potential prey. More precisely, if a predator is a generalist, consuming individuals as it randomly encounters them, then its prey species richness should increase with its body mass according to a power law, where the exponent of the relationship is equal to the species-area curve exponent multiplied by the home range-body size exponent. Home range size also increases with body mass for birds and mammals (Haskell et al. 2002), so it is unclear why Felidae and Accipitridae prey diversity did not increase with predator body mass. It does not seem to be because Felidae and Accipitridae are more specialized than Serpentes, since average prey diversity was similar across the three groups. Our measures of prey diversity must be interpreted with caution because we were unable to control for the size of the study region. Predator body size increases with trophic level and PPMR decreases to 1 with trophic level

Contrary to our predictions, PPMR increased with predator trophic level for Accipitridae and Felidae (Fig. 5.4). That is, predators at low trophic levels were similar size to their prey and predators at high trophic levels were much larger than their prey. We found no relationship between PPMR and trophic level for Serpentes. These findings contrast with previous findings that PPMR decreases to approach unity with increasing predator trophic level (Riede et al. 2011; Tucker & Rogers, 2014). Related, we also found that trophic level decreased with predator body mass (although only significantly for Felidae; Fig 5.3), a relationship which seems not to have previously been observed within a predator taxon. In a size-structured food web, large animals have higher trophic levels than small animals, and therefore predators that consume large prey will have high trophic levels. Terrestrial food webs are minimally sizestructured compared to pelagic food webs (Shurin et al. 2006). In fact, herbivorous terrestrial vertebrates are generally larger than carnivorous terrestrial vertebrates (Burness et al. 2001; Tucker & Rogers 2014), perhaps due to the gut length required to digest terrestrial plant matter or the large amount of food available for most terrestrial herbivores. Insects and spiders provide an abundant source of suitably small animal prey for small terrestrial vertebrates, allowing small carnivorous (insectivorous) vertebrates to consume a high-trophic-level diet in terrestrial environments. Interestingly, Tucker and Rogers (2014) observed a negative relationship between PPMR and trophic level for terrestrial mammalian predators despite the prevalence of insectivory among mammals and the tendency for terrestrial mammal herbivores to be large. Ultimately, the relationships amongst predator mass, prey mass, and predator trophic level are driven by the relationship between prey mass and prey trophic level (Layman et al. 2005). Prey size increased with predator size for Accipitridae and Felidae, and their large prey are mostly herbivorous. This pattern is most evident for large Felidae, whose diets were composed mostly of large, herbivorous ungulates, while small Felidae typically consumed small, omnivorous rodents (Table 5.1). Prey body mass did not change with Serpentes body mass, so Serpentes trophic level was not affected by any relationship between its prey body mass and trophic level.

Conclusions

The body mass of predators like Accipitridae, Felidae, and Serpentes can be used to predict their trophic characteristics, including prey size, niche breadth, and trophic level. By advancing our understanding of the effects of predator body mass, we will be able to make more accurate food web models. Much of current food web theory assumes that food webs are size-structured even at low trophic levels, which is not true of terrestrial food webs (Shurin et al. 2006). We found that all three predator groups consumed resources smaller than themselves, as is seen in size-structured food webs. Their prey however, do not follow this same rule, and consequently many of our results were the inverse of our predictions. Further study is required to understand the role of body mass in terrestrial food webs. Research on the role of predators in communities is pressing because large apex predators have elevated extinction risk compared to other species, and their loss has cascading effects on communities (Estes et al. 2011; Ripple et al. 2014). By better understanding the role of predator body mass in food webs, we may be able to predict the role of specific predators in their communities and therefore prevent their loss or anticipate its effects.

5.6 Acknowledgements

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Table 5.1. The mean relative numerical frequency of prey classes (% of diet) for large and small Accipitridae, Felidae, and Serpentes species (standard deviation is given in brackets), with examples of widely consumed prey families. Images are copyright-free images from PhyloPic (phylopic.org).

Predator taxon	Size class	Number of predator species	Mean relative frequency of prey class (SD)						Examples of
			Mammalia	Aves	Reptilia	Insecta	Amphibia	Actinopteri	widely consumed prey families
Accipitridae	≥ 800 g	10	48 (26)	35 (20)	12 (24)	0 (1)	1 (2)	5 (13)	Columbidae 🔪 Leporidae 为
	< 800 g	11	52 (34)	25 (30)	11 (17)	6 (10)	4 (8)	1 (3)	Muridae 📌 Cricetidae 룊
Felidae	≥ 10 kg	9	96 (6)	2 (3)	2 (3)	0 (1)	0 (0)	0 (0)	Cervidae 🖮 Bovidae 🏹
	< 10 kg	8	75 (11)	14 (8)	5 (4)	5 (8)	0 (1)	0 (0)	Muridae 📌
Serpentes	≥ 500 g	8	39 (34)	11 (13)	15 (16)	16 (29)	15 (20)	0 (0)	Leporidae 🦒 Teiidae
	< 500 g	9	64 (39)	3 (7)	26 (36)	1 (2)	5 (16)	0 (0)	Cricetidae 🛸 Muridae 📌



Figure 5.1. The relationship between prey and predator mass (g) for Accipitridae, Felidae, and Serpentes species. Each point represents one predator species. The dashed lines indicate where predator and prey mass are equal (PPMR = 1). The solid lines represent the PGLS model fit for average prey mass ("NS" indicates a non-significant slope). The upper and lower delineations of the grey polygons represent the PGLS model fit for maximum and minimum prey size, respectively.



Figure 5.2. The relationship between the rarefied family richness of the prey (a measure of taxonomic diversity) and predator body mass (g) for Accipitridae, Felidae, and Serpentes species. Each point represents one predator species. The solid lines represent the PGLS model fit ("NS" indicates a non-significant slope).



Figure 5.3. The relationship between predator trophic level and body mass (g) for Accipitridae, Felidae, and Serpentes species. Each point represents one predator species. The solid lines represent the PGLS model fit ("NS" indicates a non-significant slope).



Figure 5.4. The relationship between predator-prey body mass ratio (PPMR) and predator trophic level for Accipitridae, Felidae, and Serpentes species. Each point represents one predator species. The dashed lines indicate where predator and prey mass are equal (PPMR = 1). The solid lines represent the PGLS model fit ("NS" indicates a non-significant slope).

Chapter 6: Discussion and Conclusions

Community structure is determined by endogenous variables, including body size, community composition, centrality, and diversity. Community structure is also determined by exogenous variables including latitude, ecosystem type, temperature, and human disturbance. Additionally, the structure of any described community will also be affected by the methodology used to describe it. In this final chapter, I summarize the endogenous and exogenous determinants of trophic structure. I discuss potential interactions between variables and the effects of global change. I conclude by suggesting future avenues of research and summarizing my findings.

6.1 Determinants of community structure

All ecological communities are generated by natural laws, and the consequences of these laws generate patterns that are observed across many or all communities. Energy is lost at each trophic level in a community, and this often generates a pyramidal trophic structure - a classic "textbook" generality. Communities typically have more organisms at basal trophic levels than top trophic levels, whether that "more" is measured in abundance, productivity, biomass, or diversity. In my meta-analysis of published food webs (Chapter 2), I found that species richness decreased with trophic level, on average, resulting in pyramids of species richness (Fig 2.1). I found that large published food webs were more predator-poor, prey-rich, and hierarchical than equivalent random, niche, or cascade models. Communities must always conform to a pyramid of energy but can have non-pyramidal trophic structure by other measures (biomass, diversity, abundance, etc.), depending on the effects of endogenous and exogenous variables. The body size of an organism determines much of its behaviour, and the body size distribution of a community determines much of its trophic structure (Trebilco et al. 2013). I found that in the Yukon tundra there was, on average, a higher abundance of high trophic level macroinvertebrates (parasitoids and carnivores) than low trophic level macroinvertebrates (herbivores and detritivores; Table 3.2). The macroinvertebrate assemblage of the Yukon tundra does not conform to a pyramid of numbers, likely because of the body size distribution

of the community. A single tundra plant can feed numerous herbivorous macroinvertebrates, and a single animal host can feed numerous immature parasitoids. Small organisms can reach greater density than large organisms, so if consumers are sufficiently smaller than their resource, they can be more abundant, despite that less energy is available at higher trophic levels.

I demonstrated that spider body size was an important variable determining their prey consumption as individuals and as assemblages (Chapter 4). Spider body size affected its diet, energy requirements, and its interactions with other spiders. These variables, in turn, affected community trophic structure. When the spider assemblages had high biomass or high size variance, we observed a decrease in the abundance of arthropods at lower trophic levels (Fig 4.5).

Predator body size is predicted to affect many of its trophic properties, but the body size relationships observed by empirical studies differ depending on the taxonomic group, ecosystem, and methodology. I investigated the relationship between predator body size and trophic properties for three terrestrial predator taxa: Accipitridae, Felidae, and Serpentes (Chapter 5). These predators behaved as hypothesized of predators in size-structured food webs (Fig 5.1 and 5.2). In contrast, the communities to which they belonged were not size-structured, and as a result, predator mass-trophic level relationships were not as predicted by theory (Fig 5.3 and 5.4). As with the tundra spiders, the body size of these predators affects community trophic structure. For instance, large Felidae consume biomass at lower trophic levels than small Felidae, with possible consequences for pyramids of biomass.

Body size is just one of several endogenous variables that affect trophic structure. Trophic structure is correlated to centrality, such that the trophic diversity structure of food webs with more generalist species (high in-reach centrality) tended to have a stronger pyramid structure (Chapter 2). Phylogeny also affects trophic structure because an organism's requirements, constraints, and capabilities depend on its evolutionary history. Macroinvertebrate and soil prokaryote communities respond in different ways to their shared environment on the Yukon tundra (Chapter 3). I had hypothesized that macroinvertebrates would respond to variation at a

larger spatial scale than soil prokaryotes. Instead, I found that both taxonomic groups responded to variation at multiple scales, but not always to the same variation.

The relationships between body size and trophic properties differed between Accipitridae, Felidae, and Serpentes (Chapter 5). Serpentes of all sizes consumed prey of a constant size, while prey size increased with Felidae and Accipitridae size. The taxonomic composition of experimental spider assemblages determined the amount of prey they consumed (Chapter 4). The composition of a community is closely tied to another endogenous variable that affects trophic structure: diversity. I had predicted that prey consumption would increase with spider diversity because of niche complementarity and sampling effects. Instead, I found that there was intraguild predation and little niche complementarity, resulting in the least diverse assemblage consuming the most prey (Fig 4.4). The log-linear relationship between predator and prey species richness for stream food webs had a slope less than unity (Chapter 2; Fig 2.3; β = 0.75). The slope of $\frac{3}{4}$ suggests a possible relationship to metabolic scaling and means that less diverse stream communities have a larger predator: prey species richness ratio than more diverse communities.

Variation in community structure is also caused by exogenous variables. Latitude is correlated to climatic variables, including solar energy intensity, seasonality, and temperature. These variables affect trophic variables including primary productivity and biotic interaction intensity. Trophic diversity structure of large published food webs changed with latitude (Chapter 2). More polar food webs tended to have a strong pyramid structure, while more equatorial food webs tended to have species richness more uniformly distributed across trophic levels (Fig 2.4). This may be because biotic interaction intensity decreases with latitude (Schemske et al. 2009; Roslin et al. 2017; Hargreaves et al. 2018), decreasing the efficiency of energy transfer across trophic levels. Macroinvertebrate and soil prokaryote community composition changed along a latitudinal biome transition (Chapter 3; Fig 3.3). The abundance of herbivores relative to carnivores increased with latitude (Fig 3.5), which is suggestive of an increasingly strong pyramid of numbers. Again, this may be due to a decrease in biotic interaction intensity with latitude.

In addition to latitude, I found that ecosystem type was also important in determining trophic diversity structure of published food webs (Chapter 2). Aquatic food webs were more pyramidal than terrestrial food webs (Fig 2.4), in agreement with previous research showing that aquatic and terrestrial communities differ in their trophic structure (Shurin et al. 2006). Similarly, terrestrial predators had different relationships between body size and trophic properties than what previous authors have found for aquatic predators (Chapter 5). Terrestrial food webs, unlike aquatic food webs, are typically not size-structured, and this generates important trophic structural differences. Communities may respond to countless other environmental variables: On the Yukon tundra, the soil prokaryote community responded to active layer depth (related to annual temperature), and the macroinvertebrate community responded to a source of human disturbance, the Dempster Highway (Chapter 3).

No human worker can describe an ecological community completely and without error. The act of describing a community will always introduce error, and this error is often biased and can affect trophic structure (Hodkinson & Coulson 2004). Methodological bias is not a determinant of trophic or community structure, but it introduces bias into our measures of structure. The trophic diversity structure of published food webs is predicted best by the study identity, suggesting that food webs produced by shared methods will produce similar structure (Chapter 2). While the effect of methodological bias was studied explicitly only in Chapter 2, it is implicitly present in all my thesis chapters because methodological bias is an unavoidable fact of empirical ecology. For example, in Chapter 3, I did not assign diet to some taxa due to a lack of accessible keys and/or available dietary information (Table 3.2). In Chapter 5, diet inventories could not distinguish predation from scavenging, although the two types of consumption are very different in terms of their energetic pathways. I took measures to decrease bias in this thesis, such as only including large food webs (>50 species) in Chapter 2 because large food webs presumably have fewer missing dominant species. I rarefied taxonomic richness in Chapters 3 and 5 to reduce the effect of sample size on diversity. I included Tullgren extraction date as a variable in Chapter 4 to reduce the effect of Tullgren funnel methods on the sampled invertebrates. Trophic theory can only be as strong as the

empirical evidence it is tested against, so it is important to minimize and account for methodological bias.

Endogenous, exogenous, and methodological variables interact with one another, resulting in difficult-to-predict and diverse trophic structures. Methodology likely interacts with organism phylogeny and body size, biasing described trophic structure. Preferred sampling methods differ between phylogenetic groups (e.g., transects for trees, pan traps for arthropods), and these methods inevitably differ in their efficiency. Large organisms are usually more easily observed than small organisms. Phylogenetic groups and organism size are distributed non-randomly across trophic levels, and, as a result, sampling efficiency is unequal across trophic levels. Depending on the ecosystem, some trophic levels will be described with more missing species, aggregated species, and missing consumer-resource links than others. This methodology-trophic level effect most likely influenced the trophic diversity structure we observed for large published food webs (Chapter 2). For instance, plants are often easier to sample than animals, given the stationary nature of terrestrial and benthic plants, which may have contributed to the pyramidal structure of the food webs.

The Yukon tundra is a high latitude biome with defining environmental conditions, such as acidic soil, permafrost, and an absence of trees. If the observations and experiments of Chapter 3 and 4 were repeated in other regions of the world, we might expect different results. The impact of a road on macroinvertebrate communities may be less in regions where human activity is more frequent and widespread. Prey consumption may increase with spider diversity in regions where spiders are more specialized. Specialists may be more common in the tropics (MacArthur 1972), and tropical spiders may niche partition more finely than temperate spiders (Cardoso et al. 2011).

Predator size interacts with predator phylogeny because phylogenetic groups develop predation strategies depending on their evolutionary history, and the effect of body size will depend on strategy. For example, Serpentes are gape-limited and therefore have an inflexible upper limit on prey size, whereas Felidae and Accipitridae may consume indefinitely large prey given the right strategy or circumstances (e.g., cooperative hunting, injured prey). Endogenous,

exogenous, and methodological variables intervene simultaneously at all scales of trophic ecology, affecting variation in trophic structure.

6.2 The implications of global change

Many of the variables that determine community structure are changing due to human activity. Global temperature is rising, biodiversity is being lost, land cover is being altered, and energetic and nutrient cycles are being disrupted. All these changes are part of the current geological epoch, the Anthropocene. Understanding which variables control community structure will allow us to better predict how communities will change in the Anthropocene. Ecologists have observed several consistent latitudinal gradients, including the biodiversity gradient and the biotic interaction intensity gradient. I observed a latitudinal gradient in trophic diversity structure, such that polar food webs were more pyramidal than equatorial food webs. To the extent that latitudinal gradients are generated by temperature, we can expect them to change with global warming. We might expect these gradients to shift, so that the conditions which were observed at a more equatorial site will be observed at a more polar site. Equating latitude with time (a space-for-time substitution) may be a useful way to predict some effects of climate change (Pickett et al. 1989).

The Arctic is more sensitive to the effects of global change than the rest of the world (Ford et al. 2006; McGuire et al. 2009). Increased temperature has allowed shrubs to spread and increase density in the Subarctic and Arctic tundra (Myers-Smith et al. 2015). The patterns and relationships I described in the grassy tundra of the Subarctic Yukon (Chapters 3 and 4) may change as the assemblage of primary producers changes with shrub encroachment. Soil prokaryote communities changed with active layer depth (Figs 3.3 and 3.7), which will increase as permafrost melts. Macroinvertebrate communities changed with road proximity (3.3), and similar disturbance may increase as infrastructural development and resource exploitation continues. Both macroinvertebrate and prokaryote communities changed with latitude, and supposing a space-for-time substitution, we may expect the future state of northern sites to resemble the current state of southern sites. For instance, the abundance of herbivores relative to carnivores may decrease (Fig 3.5).

Due largely to human activities, the Earth is currently undergoing the beginning of a sixth mass extinction (Barnosky et al. 2011). Biodiversity loss is changing many aspects of ecosystems, including trophic structure and ecosystem function. If spider diversity decreases on the Yukon tussock tundra, we can expect that prey consumption may increase due to a decrease in intraguild predation (Chapter 4). Predicting the effects of biodiversity loss on an ecosystem function in a specific assemblage requires an understanding of the relevant functional traits, such as body mass. Extinction risk is not evenly distributed across communities: large predators, including many Accipitridae, Felidae, and Serpentes (Chapter 6), are at a higher risk of extinction than other species (Estes et al. 2011; Ripple et al. 2014). Losses at top trophic levels have cascading effects on lower trophic levels: Predators exert top-down control that maintains prey diversity and affects prey productivity, abundance, and size distribution (Estes et al. 2011). Extinction of predators also entails extinction of scavengers because most apex predators are also scavengers (Devault et al. 2003; Garvey and Whiles 2016), which will affect the trophic structure of detrital food webs. Understanding the role of body size as a predator functional trait allows us to better predict the effect of predator loss on community structure (Chapter 5).

6.3 Future work, summary, and conclusions

A complete and unbiased understanding of community structure requires that research is balanced across trophic levels, taxa, and ecosystems. Research on detritivores, scavengers, and the detrital web, especially, have been neglected (Martinson et al. 2008; Wilson & Wolkovich 2011). Detrital food webs are enmeshed with living food webs, and the structure and dynamics of one cannot be understood without the other. In the soil of the Yukon tundra we observed a high relative abundance of mites and springtails, which are often detritivorous organisms. Future work may continue to study the interactions between detrital invertebrates and microbes in tundra soil. The actions of these organisms will release or store greenhouse gasses, including methane and carbon dioxide, with implications for global climate change. Trophic ecological research has also been biased towards large organisms, including vertebrates and macrophytes, perhaps because these organisms are most easily observed and identified. Future research should continue to illuminate the role of small organisms in food webs, from arthropods to microbes. By biomass, most consumers are unicellular, and most animals are arthropods (Bar-On et al. 2018). Rapid advancements in arthropod and microbial ecology are already occurring due to developments in genetic technologies. Finally, because of the Arctic's sensitivity to the effects of global change, research must continue in the North, to predict, monitor, and respond to changes in ecological communities.

The objective of this thesis has been to investigate the determinants of community structure, with a focus on trophic structure and Yukon tundra communities. In Chapter 1, I reviewed the concept and trophic structure and variables which affect it, including latitude, body size, ecosystem type, taxonomic group, and biodiversity loss. In Chapter 2, for the first time in several decades, I systematically described the average trophic diversity structure of large published food webs. I tested which variables were correlated to trophic diversity structure. In Chapter 3, I described how macroinvertebrate and soil prokaryote communities responded together and separately to environmental variables in the Yukon. I addressed questions that had not previously been explored in a forest-tundra ecotone. In Chapter 4, I returned to the Yukon tundra to investigate the relationship between two trophic variables: predator assemblage composition and prey consumption. I explored the role of predator body size in this relationship, which few have addressed. In Chapter 5, I tested hypotheses regarding the relationship between body size and trophic properties of terrestrial vertebrate predators. These hypotheses had not previously been tested for Accipitridae, Felidae, and Serpentes.

Community structure, including the distribution of biodiversity across trophic levels, affects ecosystem functions (Duffy et al. 2007). Biodiversity loss, rising global temperature, and other anthropogenic effects are changing the structure of ecological communities. These structural changes have consequences for ecosystem functions that affect human well-being. It is therefore imperative that we continue to study the determinants of community structure, especially those which may be influenced by global change.

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- Zou, K., Thébault, E., Lacroix, G., Barot, S. (2016). Interactions between the green and brown food web determine ecosystem functioning. *Funct Ecol*, 30, 1454-1465.

Appendix

Table S2.1. Literature references for the food webs used in the food web meta-analysis (Chapter 2). The food webs were downloaded from the online database, University of Canberra's GlobalWeb (University of Canberra 2015). Data file of variables describing the food webs is available on Dryad: <u>https://doi.org/10.5061/dryad.22hn1.2</u>.

Web ID	Reference							
foodweb123.csv	Harris, L.D. and Paur, L. (1972). A quantitative food web analysis of a shortgrass community, Technical Report No. 154,							
	Grassland Biome. (U.S. International Biological Program).							
foodweb167.csv	Askew, R.R. (1961). On the biology of the inhabitants of oak galls of Cynipidae (Hymenoptera) in Britain. Trans. Soc. Brit.							
	Entomol. 14:237-268.							
foodweb181.csv	H.E. Savely Jr. (1939). Ecological Relations of Certain Animals in Dead Pine and Oak Logs. Ecological Monographs. 9(3), pp. 321-385.							
foodweb182.csv	H.E. Savely Jr. (1939). Ecological Relations of Certain Animals in Dead Pine and Oak Logs. Ecological Monographs. 9(3), pp. 321-385.							
foodweb187.csv	B.W. Cornaby. (1974). Carrion Reduction by Animals in Contrasting Tropical Habitats. Biotropica. 6(1), pp. 51-63.							
foodweb210.csv	E. Percival and H. Whitehead (1929). A Quantitative Study of the Fauna of Some Types of Stream-Bed. Journal of Ecology. 17(2), pp. 282-314.							
foodweb214.csv	R.M. Thompson and C.R. Townsend. (2003). Impacts on Stream Food Webs of Native and Exotic Forest: An Intercontine							
foodweb215.csv	Comparison. Ecology. 84(1), pp. 145-161.							
foodweb216.csv								
foodweb217.csv								
foodweb218.csv	R.M. Thompson and C.R. Townsend. (2004). Land-use influences on New Zealand stream communities: effects of species							
foodweb219.csv	composition, functional organisation, and food-web structure. New Zealand Journal of Marine and Freshwater Researc							
foodweb220.csv	pp. 595-608.							
foodweb221.csv								
foodweb222.csv								
foodweb223.csv								
foodweb224.csv								

foodweb225.csv	
foodweb226.csv	
foodweb227.csv	R.M. Thompson and C.R. Townsend. (2004). Land-use influences on New Zealand stream communities: effects of species
foodweb228.csv	composition, functional organisation, and food-web structure. New Zealand Journal of Marine and Freshwater Research. 38,
foodweb229.csv	pp. 595-608.
foodweb230.csv	
foodweb231.csv	
foodweb232.csv	
foodweb233.csv	
foodweb234.csv	
foodweb235.csv	
foodweb236.csv	
foodweb237.csv	
foodweb238.csv	
foodweb239.csv	
foodweb240.csv	
foodweb241.csv	
foodweb242.csv	
foodweb244.csv	
foodweb245.csv	
foodweb246.csv	
foodweb248.csv	R.M. Thompson, K.N. Mouritsen and R. Poulin. (2005). Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. Journal of Animal Ecology. 74, pp. 77-85.
foodweb263.csv	Schneider, D.W. (1997). Predation and Food Web Structure along a Habitat Duration Gradient. Oecologia. 110, pp. 567-575.
foodweb271.csv	Amundsen, P-A., Lafferty, K.D., Knudsen, R., Primicerio, R., Kristofferson, R., Klemetesen, A., and Kuris, A.M. (2013). New parasites and predators follow the introduction of two fish species to a subarctic lake: implications for food-web structure and functioning. Oecologia, 171, pp. 993-1002. See also: Amundsen, P-A., Lafferty, K.D., Knudsen, R., Primicerio, R., Klemetesen, A., and Kuris, A.M. (2009). Food web topology and parasites in the pelagic zone of a subarctic lake. Journal of Animal Ecology. 78, pp. 563-572.
foodweb273.csv	Parker, S.M., and Huryn, A.D. (2006). Food web structure and function in two arctic streams with contrasting disturbance
foodweb274.csv	regimes. Freshwater Biology. 51, pp. 1249-1263.

foodweb275.csv									
foodweb276.csv									
foodweb295.csv	Preston, D.L., Orlofske, S.A., McLaughlin, J.P., and Johnson, P.T.J. (2012). Food web including infectious agents for a California freshwater pond. Ecology. 93(7), pp. 1760.								
foodweb307.csv	Closs, G.P., and Lake, P.S. (1994). Spatial and Temporal Variation in the Structure of an Intermittent-Stream Food Web.								
foodweb308.csv	Ecological Monographs. 64, pp. 1-21.								
foodweb311.csv	Memmott, J. Martinez, N.D., and Cohen, J.E. (2000). Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. Journal of Animal Ecology. 69, pp. 1-15.								
foodweb312.csv	Kaiser-Bunbury, C.N., Memmott, J., and Muller, C.B. (2009). Community structure of pollination webs of Mauritian								
foodweb313.csv	heathland habitats. Perspectives in Plant Ecology, Evolution and Systematics. 11, pp. 241-254.								
foodweb314.csv									
foodweb315.csv									
foodweb316.csv									
foodweb317.csv									
foodweb318.csv									
foodweb319.csv									
foodweb320.csv	Ruzicka, J.J., Brodeur, R.D., Emmett, R.L., Steele, J.H., Zamon, J.E., Morgan, C.A., Thomas, A.C., and Wainwright, T.C. (2012).								
foodweb321.csv	Interannual variability in the Northern California Current food web structure: Changes in energy flow pathways and the of forage fish, euphausiids, and jellyfish. Progress in Oceanography. 102, pp. 19-41.								
foodweb322.csv									
foodweb323.csv									
foodweb324.csv									
foodweb325.csv	Lewis, O.T., Memmott, J., Lasalle, J., Lyal, C.H.C., Whitefoord, C., and Godfray, C.J. (2002). Structure of a Diverse Tropical								
foodweb326.csv	Forest Insect-Parasitoid Community. Journal of Animal Ecology. 71, pp. 855-873.								
foodweb327.csv	Kelleway, J., Mazumder, D., Wilson, G.G., Saintilan, N., Knowles, L., Iles, J., and Kobayashi, T. (2010). Trophic structure of								
foodweb328.csv	benthic resources and consumers varies across a regulated floodplain wetland. Marine and Freshwater Research. 61, pp.								
foodweb329.csv	430-440.								
foodweb333.csv	Link, J. (2002). Does food web theory work for marine ecosystems?. Marine Ecology Progress Series. 230, pp. 1-9.								
foodweb342.csv	Hopkins, T.L., Ainley, D.G., Torres, J.J., and Lancraft, T.M. (1993). Trophic structure in open waters of the marginal ice zone in the Scotia-Weddell confluence region during spring (1983). Polar Biol. 13, pp. 389-397.								
foodweb346.csv	Rayner, T.S., Pusey, B.J., Pearson, R.G., and Godfrey, P.C. (2010). Food web dynamics in an Australian Wet Tropics river. Marine and Freshwater Research. 61, pp. 909-917.								

foodweb347.csv	Motta, R.L., and Uieda, V.S. (2005). Food web structure in a tropical stream ecosystem. Austral Ecology. 30, pp. 58-73.							
foodweb359.csv	Baiser, B., Gotelli, N.J., Buckley, H.L., Miller, T.E., and Ellison. A.M. (2012). Geographic variation in network structure of a							
	nearctic aquatic food web. Global Ecology and Biogeography. 21, pp. 579-591.							

Table S5.1. Assumptions regarding the mass and diet of Accipitridae, Felidae, and Serpentesprey. These statements were assumed to be true unless otherwise indicated in the sourcestudies.

Assumption #	Assumption							
1	Insecta, Myriapoda, Armadillidiidae, and Araneae weigh 1 g.							
2	Juvenile Amphibia weigh 2 g and Mature Anura weigh 20 g.							
3 Lagomorpha, Bovidae, Camelidae, Cervidae, Giraffidae, Moschida								
	Lepidoptera, Diprodontia, juvenile Anura, Equidae, Cicadidae,							
	Hystricognathi (Ctenomyidae and Echimyidae), Columbidae, Phasmatodea,							
	and Curculionidae are herbivores.							
4 Felidae, Serpentes (Colubridae, Boidae, Dipsadidae, Elapidae,								
Lamprophiidae, and Xenodermidae), Falconiformes, Strigiforme								
Arachnida, mature Amphibia, Salamandridae, Ambystomatidae,								
	Spheniscidae, Ardeidae, Chilopoda, Scolopacidae, Lacertidae, Anguidae,							
	Soricidae, Cephalopoda, Procellariidae, Odonata are carnivores.							
5	Juveniles are half the mass of adults of the same species.							
6	Lacertidae weigh 10 g.							

Table S5.2. Literature references for the food webs used in the predator trophic properties meta-analysis (Chapter 5).

Study ID	Reference
1A	Ponce, C., Carevic, F.S., Carmona, E.R. (2017). Seasonal diet by a generalist raptor: the case of the variable hawk
	(Geranoaetus polyosoma) at Atacama Desert, northern Chile. New Zealand Journal of Zoology, ,1-9.
3A	Goodman, S.M., Razakaratrimo, S.V.J., Roland, LA.R. (2016). An analysis of Bat Hawk Macheiramphus alcinus diet in
	the Melaky Region of lowland western Madagascar. Ostrich, 87,77-80.
4A	Hussain, T., Ashraf, I., Ahmed, I., Ruby, T., Rafay, M., Abdullah, M., Siddiqa, N., Nawaz, S., Akhtar, S. (2016).
	Comparison of diet analysis of eurasian sparrowhawk, accipiter nisus and black kite, milvus migrans (accipitridae:
	Accipitriformes) from southern punjab, Pakistan. Pakistan Journal of Zoology, 48,789-794.
5A	Sándor, A.D., Alexe, V., Marinov, M., Doroşencu, A., Domşa, C., Kiss, B.J. (2015). Nest-site selection, breeding success,
	and diet of white-tailed eagles (Haliaeetus albicilla) in the Danube Delta, Romania. Turkish Journal of Zoology, 39,300-
	307.
6A	Resano-Mayor, J., Hernández-Matías, A., Real, J., Parés, F., Inger, R., Bearhop, S. (2014). Comparing pellet and stable
	isotope analyses of nestling Bonelli's Eagle Aquila fasciata diet. Ibis, 156,176-188.
7A	Manaa, A., Souttou, K., Sekour, M., Bendjoudi, D., Guezoul, O., Baziz-Neffah, F., Doumandji, S., Stoetzel, E., Denys, C.
	(2013). Diet of Black-shouldered Kite Elanus caeruleus in a farmland area near Algiers, Algeria. Ostrich, 84,113-117.
8A	Olsen, J., Judge, D., Fuentes, E., Rose, A.B., Debus, S.J.S. (2010). Diets of Wedge-tailed Eagles (Aquila audax) and Little
	Eagles (Hieraaetus morphnoides) breeding near Canberra, Australia. Journal of Raptor Research, 44,50-61.
9A	Woolaver, L.G., Nichols, R.K., Morton, E.S., Stutchbury, B.J.M. (2013). Feeding ecology and specialist diet of critically
	endangered Ridgway's Hawks. Journal of Field Ornithology, 84,138-146.
10A	Cava, J.A., Stewart, A.C., Rosenfield, R.N. (2012). Introduced species dominate the diet of breeding urban Cooper's
	Hawks in British Columbia. Wilson Journal of Ornithology, 124,775-782.
11A	Travaini, A., Santillán, M.A., Zapata, S.C. (2012). Diet of the Red-backed Hawk (Buteo polyosoma) in two
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Table S5.3. Data used in the predator trophic properties meta-analysis (Chapter 5). Each row represents data for one species from one study. Study ID corresponds to the Study ID in Table S2. N Items indicates the number of prey items in the dietary inventory. Lat and Long indicate the latitude and longitude of the field study location. Predator mass indicates the average mass of an individual belonging to the predator species. Ave prey mass indicates the weighted geometric average mass of the prey items. Smallest prey indicates the mass of the lightest prey item. Largest prey indicates the mass of the heaviest prey item. Levins indicates the Levins niche breadth of the dietary inventory. TL indicates the predator trophic level.

STUDY ID	PREDATOR SPECIES	N ITEMS	LAT	DNOT	PREDATOR MASS (G)	AVE PREY MASS (G)	SMALLEST PREY (G)	LARGEST PREY (G)	LEVINS	RAREFIED FAM RICHNESS	Ę
1A	Buteo polyosoma	52	-20.2	-69.4	783	45	2	100	2.57	3.09	3.29
3A	Macheiramphus alcinus	36	-17.5	44.1	650	13	3	147	6.31	7.60	3.91
4A	Accipiter nisus	920	29.3	71.9	212	34	1	250	6.58	6.25	3.31
4A	Milvus migrans	900	29.3	71.9	829	53	1	250	3.96	4.83	3.47
5A	Haliaeetus albicilla	260	45.2	29.3	4793	2159	82	306000	5.87	6.62	3.57
6A	Aquila fasciata	2254	41.3	1.5	2000	401	25	2000	5.18	5.88	3.15
7A	Elanus caeruleus	282	36.7	3.3	248	19	8	123	1.79	3.32	3.56
8A	Aquila audax	1421	-35.3	149	3466	1374	1	309321	8.28	7.74	3.22
8A	Hieraaetus morphnoides	192	-35.3	149	791	253	1	41455	5.97	7.55	3.22
9A	Buteo ridgwayi	362	19	-71	866	66	10	2000	4.64	5.66	3.90
10A	Accipiter cooperii	3268	48.4	-123.4	452	64	10	1500	3.79	4.47	3.35
11A	Buteo polyosoma	423	-47.7	-68	783	32	1	3000	4.70	5.99	3.09
12A	Aquila heliaca	177	31	37	3262	3403	40	30000	3.51	5.16	3.27

13A	Elanus leucurus	1062	-36.1	-63.8	312	16	1	338	1.06	1.39	3.14
14A	Aquila chrysaetos	99	2.5	37.8	4383	876	10	92500	2.77	4.71	3.21
15A	Aquila audax	111	-37.7	144.5	3466	1431	100	4000	1.12	1.70	3.01
16A	Elanus leucurus	343	-36.8	-73	312	24	1	158	1.12	1.70	3.50
17A	Spizaetus nipalensis	118	22.6	120.8	3000	676	9	3016	1.87	3.91	3.27
18A	Elanus scriptus	225	-25.1	135.5	316	36	10	58	1.12	1.56	3.49
20A	Aquila chrysaetos	469	69	25	4383	1261	188	101250	2.93	4.84	3.11
21A	Aquila audax	192	-31.1	141.7	3466	799	400	5000	2.77	3.43	3.22
22A	Accipiter cooperii	18	39.4	-87.4	452	62	20	355	4.27	6.03	3.20
23A	Buteo polyosoma	213	-38	-57.6	783	30	15	147	1.64	2.51	3.27
24A	Buteo jamaicensis	478	35.9	-122	1126	246	8	57000	4.65	5.50	3.37
25A	Accipiter cooperii	57	39.5	-87.4	452	115	28	355	2.15	2.71	3.31
26A	Accipiter gentilis	233	53.6	10	989	190	75	2000	3.70	4.60	3.33
27A	Accipiter gentilis	55	65	23.5	989	826	241	3028	3.69	3.86	3.07
28A	Geranospiza caerulescens	227	17.2	-89.6	303	30	5	1599	4.55	5.61	3.60
29A	Buteo magnirostris	140	17.2	-89.7	269	11	1	250	3.65	5.31	3.87
30A	Polyboroides radiatus	63	-25	46.3	570	35	1	3588	6.71	7.45	3.51
2F	Panthera onca	55	21.3	-87.4	81150	6385	170	65320	7.86	7.35	3.48
2F	Puma concolor	49	21.3	-87.4	48000	12158	2230	65320	4.47	5.23	3.36
3F	Felis catus	233	21.5	-158	4573	6	1	200	3.57	4.83	3.42
4F	Acinonyx jubatus	57	-22.2	29	50578	66161	2775	320000	1.20	2.04	3.00
5F	Felis silvestris	21	42.7	11.2	5037	43	21	425	2.34	4.15	3.47
6F	Panthera pardus	64	-21.5	30.1	53075	35859	1375	320000	1.95	3.93	3.10
6F	Panthera leo	89	-21.5	30.1	149062	90275	1867	830000	1.92	3.78	3.10
7F	Panthera pardus	77	-22.5	30	53075	14186	1067	160000	2.67	3.57	3.08
8F	Panthera uncia	125	35.9	71.9	44167	3376	17	583500	4.82	5.75	3.17
9F	Felis catus	201	35.9	12.9	4573	132	1	500	3.75	4.23	3.38
13F	Prionailurus bengalensis	126	1.4	104.1	4150	27	1	400	2.26	3.84	3.58
14F	Panthera pardus	131	19	74.5	53075	9207	500	40000	4.03	4.99	3.66
15F	Leptailurus serval	248	-29.5	29.9	12000	67	1	58000	1.67	3.51	3.30
16F	Felis catus	175	28.3	129.3	4573	80	1	2295	1.43	2.64	3.19

17F	Panthera pardus	1052	34.5	73.6	53075	4800	17	800000	5.94	6.43	3.04
18F	Felis catus	203	-23.5	138.5	4573	18	1	150	1.65	2.71	3.47
19F	Leopardus colocolo	248	-11	-76	2950	39	20	1236	1.33	2.40	3.15
20F	Panthera onca	23	22	-99.5	81150	6979	1031	65320	4.68	6.05	3.48
20F	Puma concolor	30	22	-99.5	48000	8239	510	65320	4.33	5.77	3.42
21F	Panthera pardus	67	37	57.7	53075	25376	250	45000	2.37	3.87	3.20
23F	Panthera tigris	103	27.5	76.3	128800	96780	9000	180000	1.81	2.23	3.00
23F	Panthera pardus	112	27.5	76.3	53075	58324	2197	180000	2.46	4.24	3.04
24F	Panthera tigris	1125	11.6	76.5	128800	71369	1432	700000	1.45	2.77	3.02
24F	Panthera pardus	519	11.6	76.5	53075	39647	1060	700000	1.72	3.39	3.03
25F	Panthera pardus	120	-33.9	22.5	53075	5557	40	120000	2.48	4.07	3.11
26F	Panthera leo	21	-20.1	32.1	149062	88336	17851	350000	1.50	3.10	3.02
26F	Panthera pardus	64	-20.1	32.1	53075	40434	1036	350000	1.80	3.02	3.09
27F	Puma concolor	292	-47.7	-68.2	48000	11562	1500	95500	3.29	4.00	3.15
28F	Leopardus tigrinus	85	-25.4	-49.6	2250	41	21	120	1.41	2.43	3.47
28F	Puma yagouaroundi	125	-25.4	-49.6	7000	36	20	120	1.48	2.64	3.49
28F	Leopardus pardalis	66	-25.4	-49.6	10500	37	20	237	1.17	1.91	3.51
29F	Panthera leo	325	21	71	149062	79769	5000	180000	2.29	3.06	3.05
30F	Felis catus	974	-22	144	4573	6	1	500	9.76	8.11	3.80
31F	Panthera pardus	127	-32.5	19.5	53075	7904	1600	30000	3.05	4.38	3.06
32F	Leopardus wiedii	55	-19	-40.1	3600	69	10	934	2.79	3.89	3.52
33F	Otocolobus manul	249	47.8	106	3050	52	1	25000	4.14	4.92	3.15
34F	Felis catus	595	-51.8	-61.3	4573	85	1	409	3.30	3.90	3.40
38F	Prionailurus bengalensis	96	5.2	118.6	4150	53	1	400	1.64	3.29	3.60
39F	Felis catus	1610	32.9	-118.5	4573	4	1	123	8.13	6.99	3.62
40F	Panthera leo	360	-33.3	26	149062	65018	1036	575000	1.53	2.85	3.03
41F	Puma concolor	117	9.2	-79.9	48000	3859	15	23000	8.79	7.67	3.19
41F	Leopardus pardalis	248	9.2	-79.9	10500	1024	10	23000	8.99	7.60	3.23
42F	Leopardus pardalis	17	-23.3	-45.1	10500	65	25	3963	5.28	7.99	3.60
42F	Leopardus wiedii	20	-23.3	-45.1	3600	125	20	4000	5.69	7.57	3.47
42F	Leopardus tigrinus	24	-23.3	-45.1	2250	52	20	934	4.94	5.51	3.52

43F	Puma concolor	62	-40	-71	48000	1958	23	100000	3.17	3.73	3.11
44F	Felis catus	288	-49.5	69.8	4573	443	17	6500	3.16	4.03	3.46
25	Bitis arietans	24	-25.38	28.31	2381	30	9	123	4.80	6.98	3.82
4S	Crotalus horridus	40	36.92	-76.3	1000	184	20	600	2.77	3.47	3.18
6S	Crotalus willardi	103	31.3	-108.78	100	8	1	186	4.77	5.59	3.95
10S	Agkistrodon contortrix	15	34.17	-95.19	950	2	1	20	2.97	6.00	3.27
14S	Cerastes vipera	24	31.2	35	16	7	5	10	1.65	2.53	4.00
15S	Coronella austriaca	226	50.73	2.13	196	9	4	165	2.86	3.76	3.95
18S	Vipera aspis	794	42.42	12.11	161	21	2	93	2.41	3.11	3.59
19S	Crotalus polystictus	337	19.8	-101.1	160	21	1	75	1.36	2.29	3.29
35S	Rhinechis scalaris	86	36.92	-3.5	1587	22	2	180	3.39	4.66	3.37
40S	Natrix natrix	55	42	12.9	96	36	10	165	3.43	4.21	3.58
43S	Philodryas patagoniensis	71	-29.72	-53.7	1306	20	1	1306	5.94	6.33	4.00
45S	Boa constrictor	52	12.51	-70	10592	60	15	1850	4.73	6.38	3.23
62S	Crotalus viridis	32	50.17	-110.5	393	32	28	39	1.20	1.80	3.00
63S	Crotalus enyo	20	26.37	-105.78	250	23	1	2800	1.53	3.19	3.06
67S	Agkistrodon bilineatus	13	10.85	-85.7	500	27	2	1034	6.09	6.93	3.30
71S	Pituophis catenifer	54	42.8	-115.8	202	55	17	760	2.70	4.76	3.37
71S	Crotalus viridis	150	42.8	-115.8	393	119	13	760	2.60	3.76	3.46
75S	Opheodrys aestivus	443	35.3	-91.6	601	1	1	1	3.41	4.51	3.45