

COMMUNITY COMPOSITION AND BIOGEOGRAPHY OF BEETLES AND SPIDERS
ACROSS AN ELEVATIONAL GRADIENT IN DENALI NATIONAL PARK, ALASKA

By

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Abstract

Anthropogenic climate change is rapidly altering alpine ecosystems in Alaska. Trees and woody shrubs are expanding upslope and displacing alpine tundra. As alpine tundra habitats shrink and fragment, arthropods and other animals face an increased risk of extirpation due to smaller population sizes and reduced geneflow. Arthropods—insects, spiders, and their relatives—are the most speciose component of the alpine fauna and perform key ecosystem services, such as pollination and nutrient cycling, and are food for vertebrates. Many species have responded by shifting their distribution to higher elevations, but species respond to change idiosyncratically, which could alter species interactions and disrupt communities. I compared beetle and spider communities along an elevational gradient in Denali National Park and Preserve, Alaska, an area with a complex biogeographic history and a poorly known arthropod fauna, in order to 1) examine differences in diversity, abundance, and community composition among forest, shrub, and alpine tundra habitats; 2) link the observed differences to abiotic factors relevant to climate change; and 3) test if shared habitat preferences lead to community-level patterns in geographic distribution. After three consecutive summers of sampling, I found that alpine tundra supports an unexpectedly diverse arthropod community with a high proportion of unique species and that vegetation cover and mean air temperature are strongly correlated with community composition. I therefore expect species losses among alpine tundra communities as shrubification continues. Community-level distribution patterns were not observed, but trends in the data point to a reduction of Holarctic distributions among forest-dwelling arthropods and an increased proportion of Beringian endemics among tundra species. This was the first systematic survey of Denali's terrestrial arthropods and added over 450 new park records.

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Chapter 1: General Introduction

1.1 Alpine Tundra

Alpine tundra is a treeless biome found at high elevations around the world. It is the uppermost vegetation zone and occurs between elevational treeline and the perennial snowline (Körner and Spehn 2002). The elevation of these boundaries varies by latitude, degree of continentality, and local topography, but in general it occurs at the highest elevations in the tropics and lowest in the Arctic. In the boreal mountains of Alaska, it may be found between roughly 900 – 2,000 m elevation (Grabherr et al. 2010, Roland et al. 2014). At these elevations, adiabatic cooling creates a polar climate where the mean growing season temperature does not exceed 10°C (Diaz and Eischeid 2007, Körner and Paulsen 2004), which prevents the growth of trees (Körner and Paulsen 2004, Harsch et al. 2009). Alpine plant communities are instead dominated by low-stature herbs, graminoids, dwarf shrubs, bryophytes, and lichens (Viereck et al. 1992). In Alaska, these communities can be more diverse botanically than adjacent uplands (Roland and Schmidt 2015).

Alpine tundra is among the most vulnerable biomes to climate change (Gonzalez et al. 2010; Wang et al. 2012; Pepin et al. 2015, Seddon et al. 2016). Warming is amplified at high elevations due to changes in the snow-albedo feedback mechanism (Giorgi et al. 1997, Fyfe and Flato 1999, Diaz and Eischeid 2007, Kotlarski et al. 2012). As a consequence, surface temperatures are rising, alpine glaciers are receding, and tall shrubs are expanding into open tundra ecosystems. Although currently alpine tundra covers approximately 3% of the Earth's surface, up to 80% of it is susceptible to vegetation change and biome conversion (Wang et al. 2012). In Alaska, where warming is faster than the global average (Serreze et al. 2000, Meyer et al. 2014), alpine tundra is disappearing at a rate of 5% per decade (Dial et al. 2007).

Strict elevational and climatic constraints cause alpine tundra to occur in naturally discontinuous patches on mountain peaks. Each patch acts like an “island” surrounded by a “sea” of intervening lowlands. As the climate warms, these “islands” are projected to shift upslope (Wang et al. 2012). This is already evident in the Alaska Range where the forest-tundra ecotone has advanced 150 m upslope during the last century (Lloyd and Fastie 2003). This shift will lead to decreased surface area of alpine tundra on conical mountains and an increase in the ratio of edge to core habitat (Magura et al. 2008, Elsen and Tingley 2015). It may also increase fragmentation as formerly contiguous expanses of tundra retreat up adjacent peaks (Fig. 1.1). Alpine tundra species thus face an increased risk of extirpation, or even extinction, due to smaller population sizes, reduced gene flow, and a greater vulnerability to stochastic catastrophes (MacArthur and Wilson 1963, Connor and McCoy 1979, Lande 1993, Henle et al. 2004, Habel et al. 2011).

Extinction risk is magnified for species with low dispersal potential and for habitat specialists (Henle et al. 2004, Matthews et al. 2014, Homburg et al. 2014). Habitat specialists are those species that rely exclusively on the resources or climatic conditions found in a particular habitat. Their preferred microhabitat is less likely to be represented in a smaller fragment (Henle et al. 2004), and they may be unwilling or unable to cross habitat gaps (Henle et al. 2004, Matern et al. 2009). The diversity of specialists has been shown to decrease as fragment size shrinks (Magura et al. 2008). Alpine tundra specialists are thus of conservation concern.

1.2 Alpine Arthropods

One technique for monitoring change at the ecosystem level is the use of bioindicators. Bioindicators are a species, or group of species, that reflect environmental changes that are

difficult, or impossible, to measure directly (Pearce and Venier 2006). Arthropods—insects, spiders, and their relatives—are potentially powerful bioindicators because they are diverse, ubiquitous, easy to collect, and sensitive to fine scale changes in their environment (Gerlach et al. 2013, Hansen et al. 2016). However, arthropods can be challenging to work with because many species are still undescribed, and identifying specimens requires costly expertise (Langor and Spence 2006, Gerlach et al. 2013). Nevertheless, they have proven insightful for monitoring changes in tundra environments (Rae et al. 2006, Høye and Culler 2018).

Arthropods have evolved adaptations to survive in the harsh alpine environment. Many alpine species are darkly colored to absorb heat or to protect their tissues from harmful UV radiation, which is more intense at high elevations (Mani 1968). They may have insulation in the form of bristles, setae, scales, or a waxy coating to retain heat (Mani 1968). A few—bumblebees (*Bombus*) for example—are capable of endothermic heat production (Heinrich 2004). To compensate for the short growing season, some species have an abbreviated life cycle with fewer larval instars, while others have prolonged their life cycles over multiple years through diapause (Hodkinson 2005). Aptery and brachyptery are common and may be adaptations to prevent individuals from being blown away in high winds or to conserve energy in a resource-limited environment where the advantages of flying are few (Mani 1968, Kavanaugh 1985, Roff 1990). Those that do fly have relatively large wings or beat their wings faster to compensate for the lower air density (Dillon 2006). The majority of alpine arthropods are predators or scavengers (Edwards 1987).

Most high elevation arthropods have narrow thermal niches and their metabolism has adapted to relatively low temperatures (Mani 1968). For example, the optimal temperature range of ice crawlers (*Grylloblatta*) is only 1 – 4°C (Grimaldi and Engel 2005), and they cannot survive

prolonged exposure to temperatures above 10°C (Kamp 1973). Climate warming thus threatens to push some alpine species beyond their thermotolerances. We can similarly expect negative consequences for species with an obligate cold-induced diapause in their life cycles.

Not all arthropods encountered at high elevations are true alpine inhabitants. Some low elevation species seasonally inhabit mountain tops, such as lady beetles in the genus *Hippodamia*, which over winter there in large aggregations (Fields and McMullen 1972). Others use hilltops as lekking sites (Alcock and Dodson 2008). Most common are those inadvertently carried into the alpine by strong winds. They soon die, unable to survive in the alpine environment, and provide an allochthonous food source for alpine scavengers. Diptera and Hymenoptera compose the majority of arthropod fallout in Alaska (Edwards 1987).

1.3 Effects of Climate Change on Alpine Environments and Arthropods

Climate change is altering a number of biotic and abiotic processes relevant to alpine arthropods. Alaska's alpine glaciers are shrinking due to warmer summers and reduced snowfall (Adema et al. 2007, Arendt 2002). Glaciers and perennial snowfields are frozen reservoirs that supply alpine watersheds during the warmest months and cool downstream habitats. Some insects, such as the rove beetle genus *Phlaeopterus*, are adapted to live alongside glacier-fed streams or near snowfields where they feed on the arthropod fallout that accumulates there (Mullen et al. 2018). In an extreme case, the ground beetle *Nebria praedicta* is restricted to the toe of a single rapidly receding glacier in California (Kavanaugh and Schoville 2009). The long-term survival of these species is unlikely if current climate warming trends continue.

Shrubs—primarily willow (*Salix* spp.), alder (*Alnus* spp.), and birch (*Betula* spp.)—are expanding into previously shrub-free tundra (Sturm et al. 2001b, Jia et al. 2003, Tape et al. 2006,

Dial et al. 2007). Being taller than tundra plants, they alter a broad range of ecosystem processes. Shrub thickets accumulate wind-blown snow and create deep drifts on their leeward sides (Sturm et al. 2001a). This extra insolation raises winter soil temperature (Sturm et al. 2005), which may benefit overwintering arthropods. However, drifts melt later in the spring which shortens the snow-free period and decreases the time arthropods have to gather resources and complete their life cycles (Rich et al. 2013). Late snowmelt has been correlated with smaller body size in Greenland spiders (Høye et al. 2009, Bowden et al. 2015), which may reduce fecundity (Fox and Czesak 2000, Ameline et al. 2018). Shrubs' foliar canopies may increase the diversity of web-building spiders by providing architecture for web attachment but alter epigeal communities by shading the ground (Bowden and Buddle 2010, Seibold et al. 2016). Shrubs also produce leaf litter and woody debris which can alter communities of litter-dwelling beetles, spiders, and their prey (Uetz 1979, Seibold et al. 2016).

Arthropods have responded to climate warming by changing their phenology and morphology (Miller-Struttmann et al. 2015, Pyke et al. 2016, Evans et al. 2018), but the most commonly documented response is a change in geographic distribution (e.g. Parmesan 2006, Chen et al. 2011). Short life cycles and high dispersal power allow many arthropods to quickly track their optimal climatic niches (Danks 2004). Elevational shifts have thus far been documented for spiders, dragonflies, butterflies, bees, and ground beetles (Hickling et al. 2006, Wilson et al. 2007, Chen et al. 2009, Pyke et al. 2016). However, migrating uphill is impossible for species already living on the highest local peaks. These species must either disperse to a taller mountain, disperse poleward, or be extirpated. Species loss is likely to have serious consequences for alpine communities which are thought to have low functional redundancy (Petchey et al. 1999, Inouye 2019).

1.4 Denali National Park and Preserve

National Parks and Preserves are important institutions for conservation in the United States as they represent over 300,000 km² of protected land, 66% of which lies in Alaska (National Park Service 2016). Mountains are disproportionally represented among National Park land (Perrigo et al. 2020).

Denali National Park and Preserve (DNPP) was established in 1917 as Mount McKinley National Park. Its boundaries were expanded in 1922, 1932, and in 1980 when it was combined with Denali National Monument (Pearson 1953, U.S. Congress 1980). At its present size (24,000 km²), it is the third largest US National Park and larger than any of the five smallest states. It has a subarctic climate, and temperature at park headquarters (elevation 625 m) ranges from 33°C in summer to -48°C in winter (Hooze et al. 2006). Major habitats in DNPP include spruce forests, muskeg, braided river bars, kettle ponds, scrubland, and alpine meadows. Nearly one third of the park is covered by glaciers and bare rock (Hooze et al. 2006). A single road provides access to 146 km of the northeastern section of the park (Fig. 1.2).

The most dominant topographic feature of DNPP is the Alaska Range, which roughly bisects the park from southwest to northeast (Fig. 1.2). It extends in a 650 km arc from Lake Iliamna (~350 km south west of DNPP) to the White River in Yukon, Canada (U.S. Geological Survey 2019). These relatively young mountains were uplifted six million years ago by tectonic forces along the Denali fault (Capps et al. 2016). Elevation rises from the Yentna River (67 m) to the peak of North America's tallest mountain (6,190 m) (National Park Service 2019). The range forms a barrier between two ecoregions: cold dry Interior Alaska and maritime South-central Alaska (Hammond and Yarie 1996, Chapin et al., 2006).

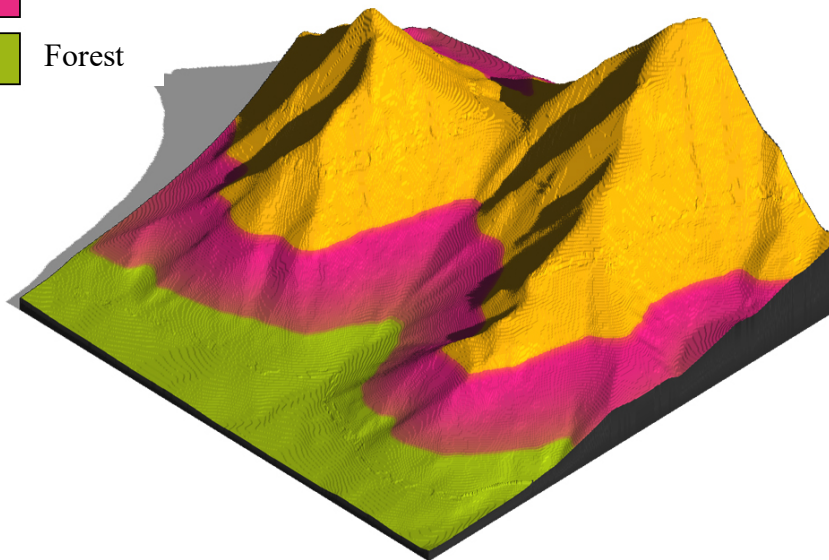
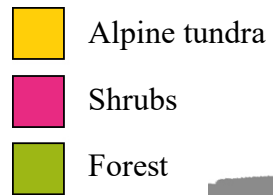
During the Pleistocene, the Alaska Range delineated the southern boundary of Beringia—an ice-free refugium connected to Eastern Siberia via the Bering Land Bridge but separated from the rest of North America by ice sheets. It spanned from the Lena River in northeastern Russia to the McKenzie River in northwestern Canada and included the northern portion of DNPP (Fig. 1.3). The biogeographic history of the region is complex. The Bering Land Bridge was alternately exposed and inundated as sea levels changed, creating conditions for both dispersal and diversification (Hopkins 1982). Climate and vegetation were spatially and temporally dynamic. Fossil evidence suggests the presence of forests, flood plains, deserts, tundra, and a xeric steppe grassland with no modern analog existed at various times (Mathews 1982, Young 1982). Beringia's legacy is a contemporary fauna replete with endemic species, inter-continental disjunctions, and unique mitochondrial lineages (Ickert-Bond 2009, Shafer et al. 2010, Sikes and Allen 2016).

Unlike DNPP's vertebrates and vascular plants, little is known about its arthropods. Past sampling documented only 354 species and genera of an anticipated 1,000+ (based on rough estimates from other regions of Alaska). Butterflies are the most thoroughly catalogued taxa with 44 recorded species (86 species are known from Alaska). Crane flies (Diptera: Tipulidae) were surveyed in 1952, and ten species were recorded, seven of which were undescribed (Alexander 1955, 1969). Stream-dwelling insects (Ephemeroptera, Plecoptera, and Trichoptera) have been surveyed as water quality indicators (e.g. Milner et al. 2006, Windsor et al. 2017), but these studies rarely identify specimens to species. The park has never been systematically sampled for beetles or spiders, and the 54 species documented prior to this study likely represent a fraction of the true biodiversity.

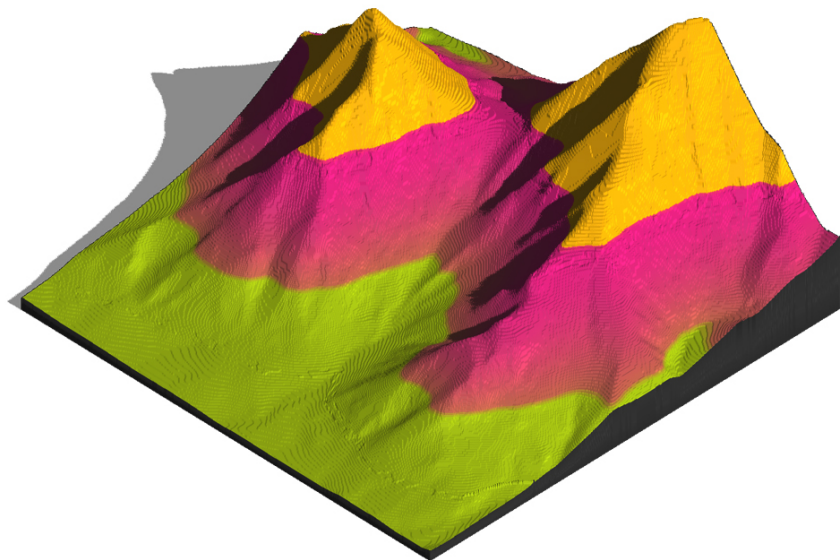
1.5 Study Goals

Understanding the response of arthropods to climate change is of the utmost importance in light of increasing evidence for global insect decline (Hallmann et al. 2017, Loboda et al. 2018, Wagner 2019). Monitoring change over time requires baseline data for comparison, which are lacking for alpine arthropods. Furthermore, no such study based in Alaska has ever been published. To address these issues, and to evaluate how alpine arthropods may respond to environmental change, I surveyed beetles and spiders across an elevational gradient in DNPP for three summers (2016 – 2018). These are two of the major representative taxa among the terrestrial alpine tundra fauna and as such play important ecological roles (Edwards 1987). As an example, wolf spiders (Lycosidae), are top predators in Alaskan tundra communities and outweigh mammalian predators, such as wolves, by orders of magnitude (Koltz et al. 2018). I coarsely divided the elevational gradient into three habitat types: forest (low-elevation), tall shrubs (mid-elevation), and alpine tundra (high-elevation) in order to (1) compare the abundance, diversity, and community composition of beetles and spiders among habitats, and (2) measure how these community metrics respond to habitat characteristics such as temperature, solar radiation, and vegetation cover. The results of Goals 1 and 2 are addressed in Chapter 2. Additionally, I wanted to place DNPP arthropods in the larger context of Beringia, so I provide a brief faunistic analysis of DNPP beetles and spiders in Chapter 3. The Appendix contains an updated checklist of DNPP's arthropods based on the specimens collected for this study, University of Alaska Museum records, and a literature review.

1.6 Figures



Current distribution



Future distribution

Figure 1.1: Upslope shift of alpine tundra leads to increased fragmentation on a hypothetical mountain. In the current distribution (left), alpine tundra forms a large contiguous patch. An upslope shift in elevation results in two small fragments of alpine tundra.

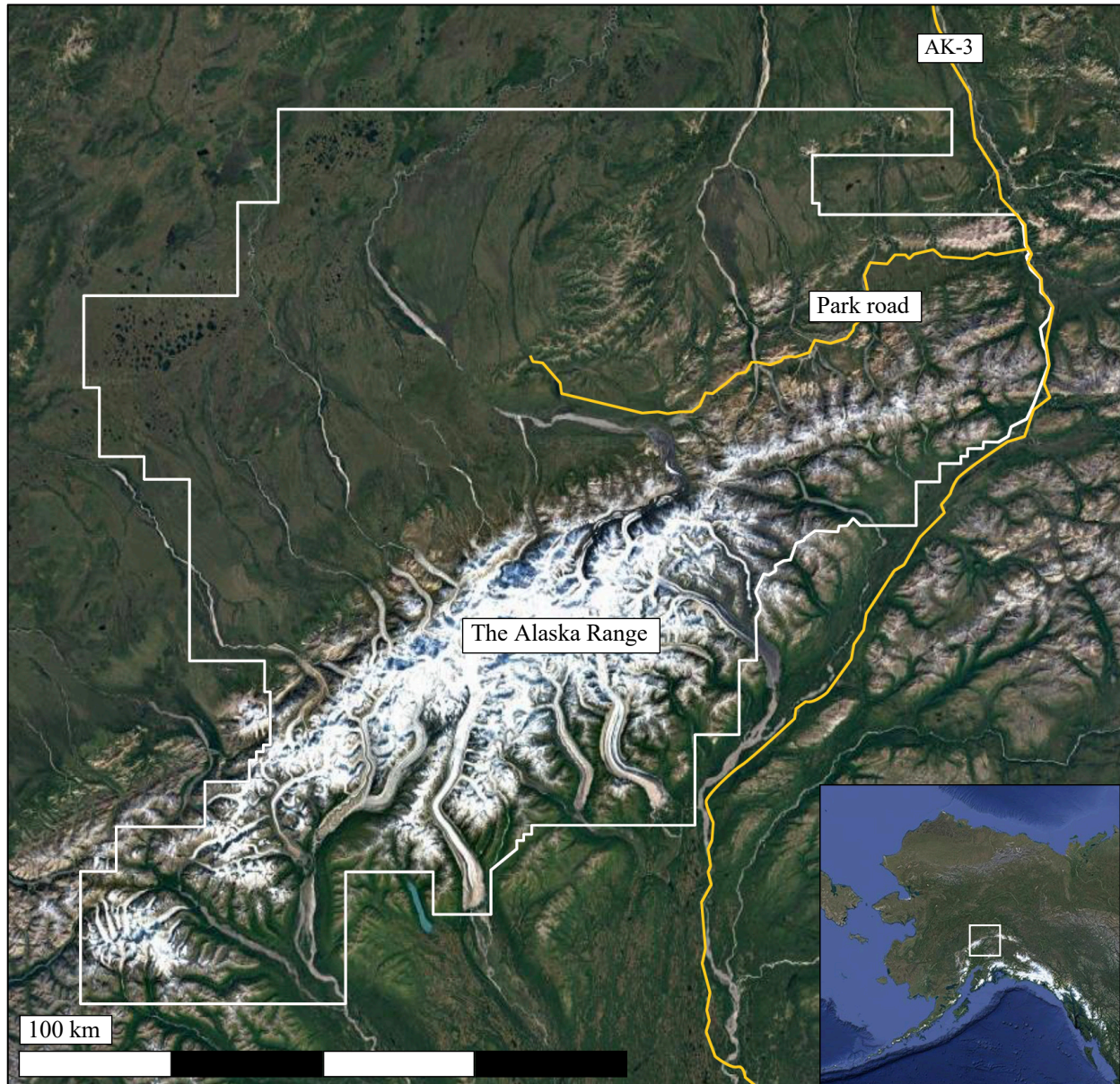


Figure 1.2: Map of Denali National Park and Preserve, Alaska. White line indicates the park boundary. Yellow lines indicate roads.



Figure 1.3: Map of Beringia. This map shows the present-day shoreline and the shoreline approximately 18,000 years ago. Denali National Park and Preserve is outlined in black. Adapted from Bond (2019).

Chapter 2: Arthropod Communities Differ Across an Elevational Gradient in Denali

National Park and Preserve, Alaska¹

2.1 Abstract

Anthropogenic climate change has caused some montane arthropods to disperse to higher elevations, which has the potential to alter community composition and function because species respond to change individualistically. We examined ground-dwelling beetle and spider communities across three elevationally stratified habitats in Denali National Park and Preserve, Alaska, a rapidly changing high-latitude environment, to describe diversity patterns and identify abiotic variables correlated with community composition. Using pitfall traps and litter sampling, we collected 25,247 adult beetles and spiders over three consecutive summers. Rove beetles (Coleoptera: Staphylinidae), wolf spiders (Araneae: Lycosidae), and sheet weaver spiders (Araneae: Linyphiidae) were abundant in all habitats and accounted for 80% of individuals collected. NMDS ordination found that alpine tundra supported a distinct arthropod community with high estimated species richness and a high proportion of unique species. Spruce forests had a unique functional guild composition with a significantly lower abundance of plant-associated beetles. Mean air temperature, solar radiation, and vegetation cover were strongly correlated with variation in community composition across the gradient. Our results suggest that climate-driven changes in vegetation cover are likely to alter beetle and spider communities and potentially decrease alpine biodiversity via the loss of alpine tundra specialists. The loss of even a few species could have cascading effects in high-elevation alpine tundra environments that are thought to have low functional redundancy.

¹ Haberski, A. Rykken, J., Sikes, D. S., 2020. Arthropod communities differ across an elevational gradient in Denali National Park and Preserve, Alaska. To be submitted for publication to journal TBD.

2.2 Introduction

Average global surface temperature has increased by 0.85°C over the last 130 years due to anthropogenic climate change (Meyer et al. 2014), and as a consequence many species have shifted their phenology or changed their geographic distribution to higher latitudes or higher elevations (Chen et al. 2011). Range shifts have been documented in a broad range of taxa including birds, insects, plants, and marine invertebrates (Parmesan 2006). However, species respond to change idiosyncratically because of differences in life history, dispersal ability, and extinction risk (Parmesan 2006). This can alter species interactions and disrupt community structure and function (Petchey et al. 1999). For example, a study of arthropod communities in Greenland found that 19 years of warming led to a reduction in detritivores and an increase in herbivores and parasitoids (Koltz et al. 2018). Examining whole communities, as opposed to a single species, is crucial for anticipating the impacts of global climate change.

Latitudinal and elevational gradients can be surrogates for studying long-term climate change (Pickett 1989). Space-for-time substitution assumes that spatial trends reflect temporal trends because temperature changes linearly along the gradient. Montane gradients are preferable because changes in climate and vegetation occur over short spatial distances. Additionally, mountains are biodiversity hotspots (Perrigo et al. 2020), and a single mountain may support numerous biomes that each harbor their own locally endemic species (Meyer et al. 2015). One such biome, alpine tundra, is among the most sensitive to climate change (Gonzalez et al. 2010, Wang et al. 2012, Pepin et al. 2015, Seddon et al. 2016).

Arthropods—insects, spiders, and their relatives—are the most abundant and diverse component of the montane fauna (Edwards 1987). They possess several traits that make them potentially powerful bioindicators on montane gradients: many high elevation species have

narrow thermal niches, and their metabolism has adapted to relatively low temperatures (Mani 1968); short life cycles and high dispersal ability allow them to closely track their optimal climatic niches (Danks 2004); and they are sensitive to fine-scale changes in vegetation cover (Hansen et al. 2016). Upslope shifts in elevational distribution have been reported for many arthropod lineages including spiders, dragonflies, butterflies, bees, and ground beetles (Hickling et al. 2006; Wilson et al. 2007, Chen et al. 2009, Pyke et al. 2016).

An increasing number of studies have reported catastrophic long-term declines in arthropod biomass (Hallmann et al. 2017, Wagner 2019). Declines are greatest in species with small geographic distributions or specialized ecological niches, such as are found on many mountains (Newbold et al. 2018, Sánchez-Bayo and Wyckhuys 2019). Many potential causes have been identified including habitat loss, pesticide use, light pollution, and climate change (Sánchez-Bayo and Wyckhuys 2019, Wagner 2019). Monitoring change over time requires baseline data for comparison, which are lacking for most arthropod populations. Long-term studies are also rare at high latitudes where warming is greatest (Meyer et al. 2014). One of the few such studies reported an 80% decline in muscid fly abundance and a shift in community composition (Loboda et al. 2018).

Denali National Park and Preserve (DNPP), Alaska, provides the opportunity to examine arthropod communities in a rapidly changing high-latitude environment. In this study, we compared ground-dwelling beetle and spider communities along an elevational gradient in DNPP. The long-term goal of this study was to determine baseline presence and distribution data and to establish a transect system that will be resampled in 10 years to directly assess changes in arthropod community structure and function. Here, we utilized the baseline data to investigate community composition among three elevationally stratified habitats: forest, tall shrubs, and

alpine tundra. Our specific research objectives were to: (1) explore the variation in biodiversity, taxonomic structure of beetle and spider communities, and functional guild structure of beetle communities among habitats; and (2) To link the observed variability to important abiotic factors, namely differences in temperature and vegetation cover. This provides the first systematic survey of terrestrial arthropods in DNPP.

2.3 Methods

2.3.1 Study area and research design

Denali National Park and Preserve encompasses over 24,000 km² and includes much of the central Alaska Range. Trees, primarily white spruce (*Picea galuca*), are abundant below 500 m and decline with elevation (Roland and Schmidt 2015). Dense stands of trees are restricted to south-facing slopes and river terraces (Roland et al. 2013). Tall shrub cover, primarily willow (*Salix* spp.), birch (*Betula* spp.), and alder (*Alnus* spp.), peaks in the subalpine zone between 800 – 950 m (Roland and Schmidt 2015). True alpine tundra vegetation extends from around 950 m to the perennial snow line near 2,000 m (Roland et al. 2014). Much of the alpine zone is inaccessible due to cliffs and talus slopes. The snow-free season at high elevation lasts from June through August. These are the warmest and wettest months with a mean temperature of 11.7°C and mean rainfall of 1.8 cm (Sousanes and Hill 2014).

We established five elevational transects along the Park Road in the northeastern portion of DNPP (Fig. 2.1). Each transect consisted of a low-elevation forest plot, a mid-elevation shrub plot, and a high-elevation alpine tundra plot, designated based on the vegetation classification system of Viereck et al. (1992) (Fig. 2.2). Transects were located where all three habitats were accessible from the road. Plots were spaced a minimum of 500 m apart and at least 100 m from

the road to minimize the influence of dust and edge effects. Plot elevation ranged from 595 – 1252 m (Table 2.1). Aspect varied from South to South-east.

2.3.2 Arthropod sampling

We collected arthropods June – August of 2016, 2017, and 2018. We used a combination of pitfall trapping and litter sampling for quantitative analyses. For inventory purposes, we also collected arthropods by hand, targeting microhabitats likely to conceal arthropods such as under rocks and logs. Sampling occurred every two weeks for a total of 11 collection periods (Table 2.1).

At each plot, four pairs of pitfall traps were deployed in a 50 m grid. This configuration has been suggested to minimize sampling bias (Engel et al. 2017). Paired traps were spaced 1 m apart, and one was randomly selected to be covered with an aluminum rainroof (a quantitative comparison of covered versus uncovered traps will be part of a future study). Each trap consisted of two yellow plastic cups, 10 cm in diameter. The cups were nested together and buried flush with the ground surface. We filled each one-third full of nontoxic Sierra-brand propylene glycol base antifreeze and added ~ 1 ml of denatonium benzoate as a bittering agent to deter curious vertebrates. The traps were emptied by straining their contents through a fine mesh cloth that was then stored in a Whirl-Pak bag inside of a crushproof plastic container for transport to the laboratory. The propylene glycol was then replaced, and the used glycol was removed from the park.

To sample litter arthropods, we collected approximately 1 m² of leaf litter haphazardly from within each plot. The litter was sifted through a sieve to remove large particles and to increase the specimen density of each sample (Guénard and Lucky 2011). The samples were

stored in a canvas bag for up to 3 days before being transferred to a Winkler or Berlese funnel for extraction. Extraction proceeded for 14 days as suggested by Owens and Carlton (2015).

Specimens were sorted to morphospecies under a dissecting microscope at the University of Alaska Museum (UAM). All adult beetles and spiders were identified to species when possible and left as morphospecies when not. Identifications were determined by the first author using dichotomous keys (e.g. Thomas 2000, Arnett et al. 2002) or by taxonomic experts. Beetles were assigned to one of eight functional guilds based on their primary feeding habits in the adult stage. The life histories of many beetles are unknown. Those species were assigned based on the predominant feeding habits of their genus or family. All specimens were vouchered into the UAM insect collection. The specimen data are available publicly through the online database Arctos, which serves data to GBIF and other online aggregators.

2.3.3 Environmental characteristics

To evaluate differences in vegetation cover among plots, we conducted vegetation surveys in the summer of 2018 at five random locations within each plot. A one-meter-square quadrat frame was laid on top of the understory vegetation and then percent cover of plant growth forms was estimated within the frame. Seventeen plant growth forms were counted: 1) evergreen trees; 2) deciduous trees; 3) evergreen tall shrubs (>150 cm); 4) deciduous tall shrubs (>150 cm); 5) evergreen low shrubs (20 – 150 cm); 6) deciduous low shrubs (20 – 150 cm); 7) evergreen dwarf shrubs (< 20 cm); 8) deciduous dwarf shrubs (< 20 cm); 9) evergreen prostrate shrubs; 10) deciduous prostrate shrubs; 11) forbs; 12) grasses; 13) sedges; 14) moss; 15) lichen; 16) bare soil; 17) rock. These variables were then reduced by principal components analysis to

create new orthogonal variables. We retained those components that explained 80% of the observed variance for downstream analysis.

Temperature was measured at each plot during 2018 and 2019 using HOBO Pendant 8K Data Loggers (Onset Computer Corporation, Bourne MA). The 2019 temperature data were not concurrent with arthropod sampling; however, an additional year was needed to account for annual variability. We set three loggers at the center of each plot to measure air, soil, and ground-surface temperatures. The air loggers were deployed one meter above the ground and covered with a solar radiation shield. The soil logger was buried 6 cm beneath the mineral soil. The ground surface logger was intended to measure the combination of heat and radiation available to a basking arthropod. It was covered with a tight fitting 1 mm black rubber gasket to imitate the dark surface of an arthropod and then wired to the ground. Temperature was recorded every hour. Potential direct incident radiation (PDIR), the amount of solar energy that would reach the ground surface if not obscured by clouds or vegetation, was derived from slope, aspect, and latitude using the formula provided by McCune and Keon (2002).

2.3.4 Statistical analysis

The eight pitfall traps and one litter sample from each two-week collection period were pooled into a single sample for all analyses. However, trap loss was common, and many samples included fewer than eight pitfall traps. The resulting difference in collecting effort was corrected for when necessary as described below. All analyses were conducted with the statistical software R v3.6.2 (R Core Team 2018).

For each habitat, we explored the completeness of our inventories by comparing the observed species richness (S) to the Chao 1 estimator of S, an asymptotic estimation of the

minimum expected species richness (Chao 1984), and via individual-based rarefaction curves from the iNext package (Hsieh et al. 2016). Diversity measures were assessed for each habitat. In ecology, diversity is often partitioned into regional diversity (γ), local or within-plot diversity (α), and among plot diversity (β). To measure γ - and α -diversity, we chose the Shannon diversity index, which applies equal weight to all species, and the inverse Simpson's diversity index which weighs common species more heavily. These were calculated with the SpadeR (Chao et al. 2015) and Vegan (Oksanen et al. 2018) packages in R. Beta diversity can be further broken down into turnover (the replacement of one species by another) and nestedness (species loss or gain) components. We calculated the total dissimilarity in each habitat, as well as its components, with the Betapart package (Baselga et al. 2018). We chose the Sørensen β -diversity index, which represents the proportion of shared species between two plots, because it is independent of sample size and the number of replicates (Jost et al. 2015).

We used generalized linear mixed models from the lme4 package to test for differences in diversity and abundance among habitats (Bates et al. 2015). Pitfall traps, however, do not measure true relative abundance of species because they are biased towards more active species (e.g. Topping and Sunderland 1992), and thus more accurately describe 'activity-abundance' or 'activity-density', hereafter referred to simply as "abundance". Models included elevation and habitat as fixed variables and study plot and collection date as random variables to avoid pseudoreplication. A Poisson distribution was assumed for S and abundance data, and a log normal distribution for the non-integer Chao 1 estimator, Shannon diversity index, and inverse Simpson's diversity index. The regression was weighted by the number of traps per sample to account for the difference in collection effort.

We used Non-metric Multidimensional Scaling (NMDS) ordination to explore the difference in arthropod assemblages across plots and habitats. This ordination technique uses ranked distances to visualize assemblages in two-dimensional species or environmental space. NMDS works particularly well for non-normal data, such as those found in most ecological datasets, because it does not assume a linear relationship among variables (McCune et al. 2002). Prior to ordination, rare species found in less than 5% of all samples were removed from the data set. Abundance data were then converted to presence-absence to rectify the differences in collecting effort. Because predators account for a greater proportion of beetle species at high latitudes and high elevations (Edwards 1987, Gaston et al. 1992), functional guild data were $\log(x + 1)$ transformed to down-weight the influence of the super-abundant predator guild. The ordinations were then performed using the metaMDS function in the Vegan package with random starting configurations and the Bray-Curtis dissimilarity coefficient. To test if community composition was correlated to measured environmental variables, the ordination was fit to climate and ground cover variables using the envifit function.

Finally, we performed a multivariate analysis of variance with the adonis function to test the null hypothesis of no difference among assemblages in the three habitat types. Significance tests were based on 999 permutations of the raw data, and pairwise comparison p-values were adjusted as suggested by Holm (1979). Indicator species analysis identified the species that contributed most to the observed differences in community composition. Indicator species analysis identifies those species which are significant indicators of a given habitat based on two components: specificity (the species only occurs in a particular habitat), and fidelity (the species always occurs in that habitat) (McCune et al. 2002). Significance values were generated by A

Monte Carlo test with 999 permutations. This analysis was performed using the Indicspecies package (De Cáceres and Legendre 2009).

2.4 Results

2.4.1 Environmental characteristics

Abiotic characteristics varied among plots (Table 2.2). Air temperature extremes ranged from -4.88°C to 31.06°C . Mean air temperature ($df = 2$, $F = 8.387$, $p = 0.0053$), mean soil temperature ($df = 2$, $F = 7.224$, $p = 0.0087$), and PDIR ($df = 2$, $F = 9.968$, $p = 0.0028$) differed significantly among habitats. Mean air temperature in alpine tundra plots was significantly colder than forest ($p = 0.0074$) and shrub plots ($p = 0.0156$). Soil temperature was colder in forest plots than in shrub plots ($p = 0.0071$). Forests also received less PDIR than either shrubs ($p = 0.0414$) or alpine tundra ($p = 0.0022$). There was no significant difference in mean ground surface temperature among habitats ($df = 2$, $F = 1.17$, $p = 0.345$).

Principal Components Analysis was used to reduce the 17 ground cover variables. A scree test revealed a drop in eigenvalue after the first three principle components (PCs). These PCs indicate the overall ground cover composition at each study plot and explained 80% of the variation among sites (Table 2.3). PC1, a gradient from spruce forest to open shrubs and tundra, explained 49% of the variation. PC2, a gradient of large shrubs to smaller or fewer shrubs, explained 17%, and PC3, a gradient from prostrate shrubs to an open moss and lichen understory, explained 13%. These PC scores were used in further analyses.

2.4.2 Beetle communities

We collected a total of 15,620 adult beetles, representing 186 species in 26 families (Table 2.4). Ptiliids from all three years (82 individuals) and aleocharine staphylinids from 2017

and 2018 (5,952) were unable to be identified to morphospecies and were thus included in abundance measures but excluded from diversity estimates and functional guild comparisons. The family Staphylinidae was the most speciose and abundant family and contributed more individuals than all other families combined. The six most abundant species collectively accounted for approximately 25% of the total catch: *Eucnecosum brunnescens* (8%), *Pterostichus brevicornis* (4%), *Acidota quadrata* (4%), *Olophrum latum* (3%), *Eucnecosum brachypterum* (3%), *Agoliinus piceatus* (3%). Inventory completeness ranged from 73 – 84% (Table 2.5). Individual-based rarefaction curves show that shrub was the most thoroughly sampled habitat and that sampling effort in alpine tundra needs to be double to collect the estimate species total (Fig. 2.3). There was no linear relationship between abundance and elevation ($df = 12$, $z = -0.38$, $p = 0.705$), nor any difference in mean beetle abundance among habitats ($df = 2$, $\chi^2 = 0.332$, $p = 0.8471$) (Fig. 2.4a).

Observed and expected species richnesses were higher in alpine tundra than in other habitats, and alpine tundra had the highest proportion of unique species (Table 2.5). In contrast, γ -diversity was highest in shrubs. Visual inspection of rank-abundance curves revealed similar evenness among all three habitats (Fig. 2.5). We found no significant difference in α -diversity among habitats (S: $df = 2$, $\chi^2 = 1.52$, $p = 0.4672$; Chao 1: $df = 2$, $\chi^2 = 1.52$, $p = 0.4672$; Shannon: $df = 2$, $\chi^2 = 2.03$, $p = 0.3621$; Inverse Simpson's: $df = 2$, $\chi^2 = 3.13$, $p = 0.2093$) (Fig. 2.4) and no linear relationship between α -diversity and elevation (S: $df = 12$, $z = 0.17$, $p = 0.867$; Chao 1: $df = 12$, $t = -0.06$, $p = 0.957$; Shannon: $df = 12$, $z = -0.40$, $p = 0.698$; Inverse Simpson's: $df = 12$, $t = -0.25$, $p = 0.807$). Beta diversity was primarily the result of species turnover (Table 2.5).

An NMDS ordination of community composition resulted in a three-axes solution with a final stress of 0.086 after 20 iterations (Fig. 2.6). Beetle communities differed by habitat ($df = 2$,

$F = 3$, $p = 0.001$). Specifically, alpine tundra communities were significantly different from forest and shrub communities ($p = 0.021$), which were more similar to each other. The ordination also revealed that beetle community structure was correlated with mean air temperature ($r^2 = 0.64$, $p = 0.003$), elevation ($r^2 = 0.61$, $p = 0.004$), ground cover PC1 ($r^2 = 0.46$, $p = 0.023$), and PDIR ($r^2 = 0.38$, $p = 0.047$). Indicator species analysis identified 41 species as significant indicators of habitat (Table 2.6).

Functional guild composition also differed by habitat ($df = 2$, $F = 3.25$, $p = 0.001$). An NMDS ordination of functional guilds resulted in a three-dimensional solution with a final stress of 0.067 after 20 iterations (Fig. 2.7). The NMDS axes were correlated with ground cover PC1 ($r^2 = 0.55$, $p = 0.008$), elevation ($r^2 = 0.41$, $p = 0.038$), and PDIR ($r^2 = 0.39$, $p = 0.044$). All three communities were dominated by predators (Fig. 2.8). Detritivores ($z = 2.354$, $p = 0.0487$), and phytophages ($z = 2.703$, $p = 0.0189$) were less abundant in forests than in alpine tundra, and florivores were less abundant in forests than in either shrubs ($z = 4.009$, $p = 0.0002$) or alpine tundra ($z = 3.109$, $p = 0.0053$).

2.4.3 Spider communities

We collected 9,627 adult spiders representing 182 species in 16 families (Table 2.7). The families Linyphiidae and Lycosidae were most abundant, accounting for roughly 41% of abundance each. Species diversity was dominated by the Linyphiidae, which accounted for over half of all species. The three most abundant species were all lycosids and accounted for 30% of the total catch: *Pardosa lapponica* (15%), *Pardosa uintana* (8%), and *Alopecosa aculeata* (7%). Inventory completeness ranged from 61 – 80% (Table 2.8, Fig. 2.9). Mean spider abundance differed among habitats ($df = 2$, $\chi^2 = 11.96$, $p = 0.0025$) (Fig. 2.10a) but was not linearly related

to elevation ($df = 12$, $z = 0.61$, $p = 0.541$). The incidence of unique species was high among spiders with 46% of species collected in a single habitat (Table 2.8) compared to only 38% of species among beetles (Table 2.5). Alpine tundra had the highest observed species richness and was estimated to contain 25% more species than other habitats. Similar to beetles, γ -diversity was highest in shrubs. Visual inspection of rank-abundance curves revealed similar evenness among all three habitats (Fig. 2.11). We found significant differences in Simpson's diversity ($df = 2$, $\chi^2 = 6.79$, $p = 0.0336$) (Fig. 2.10). Shannon's diversity ($df = 12$, $t = -2.65$, $p = 0.0201$). Simpson diversity ($df = 12$, $t = -3.357$, $p = 0.0051$) decreased linearly with elevation, but there was no significant relationship between elevation and species richness (S: $df = 12$, $z = -1.70$, $p = 0.0888$; Chao 1: $df = 12$, $t = -1.91$, $p = 0.0801$). Beta diversity was primarily the result of species turnover (Table 2.8).

An NMDS ordination of community composition resulted in a three-axes solution with a final stress of 0.054 after 20 iterations (Fig. 2.12). Spider communities in all three habitats were significantly different ($df = 2$, $F = 5.65$, $p = 0.001$). The environmental variables elevation ($r^2 = 0.68$, $p = 0.001$), mean air temperature ($r^2 = 0.64$, $p = 0.006$), PDIR ($r^2 = 0.64$, $p = 0.001$), mean soil temperature ($r^2 = 0.55$, $p = 0.015$), and ground cover PC1 ($r^2 = 0.42$, $p = 0.042$) were significantly correlated with the NMDS axes. Indicator species analysis identified 82 species as significant indicators of habitat (Table 2.9).

2.5 Discussion

2.5.1. Elevational patterns

High latitudes are warming faster than the global average (Meyer et al. 2014). Interior Alaska warmed by 1.7 °C between 1949 and 2012 and is projected to warm a further 3 – 7 °C by

the end of the century (Walsh et al. 2008, Bieniek et al. 2014). As a consequence, treeline is advancing upslope (Lloyd and Fastie 2003), and tall shrubs are expanding into high-elevation alpine tundra (Dial et al. 2007). We compared ground-dwelling beetle and spider communities across an elevational gradient in DNPP to identify patterns of diversity and community composition and to assess how arthropod communities may respond to climate-driven changes in temperature and vegetation cover. This was the first effort to systematically document ground-dwelling arthropods in DNPP, and it yielded 375 new species and genus records for the park.

We found a consistent gradient of beetle and spider composition from forests, through shrubs, to tundra communities. Compositional differences were due to both changes in the abundance of widespread species, such as *Eunecosum brachypterum* and *Acidota crenata*, and by the turnover of unique species (Table 2.6 & 2.9). Additionally, vegetation cover (PC1) was an important predictor of both community and functional guild composition. This habitat gradient represents the presumed chronological succession of high-elevation vegetation in response to warming. We therefore expect climate-driven shifts in vegetation cover will alter alpine arthropod communities. This could lead to a loss of γ -diversity because alpine tundra supported the most distinct and diverse community of the habitats examined. In total, 21% of species were unique to, or significantly associated with, alpine tundra and may represent specialists with specific habitat requirements or narrow thermal niches. However, behavioral plasticity could allow these species to persist in suitable microclimates even after habitat change (Sunday et al. 2014).

Functional guild composition also displayed a strong elevational pattern, but via a different mechanism. While species composition was unique at high elevations due, in part, to the addition of alpine specialists, functional guild composition was unique at low elevation due

to a lack of plant-feeding beetles (Fig. 2.7). We found the forest floor supported fewer phytophages, florivores, and detritivores than either shrubs or alpine tundra (Fig. 2.8), and no florivores, phloeophages, or detritivores were significant indicators of forest (Table 2.6). The majority of forest phytophages (80%) and detritivores (53%) were collected at plot 1F, the only forest plot that contained deciduous trees, namely aspen (*Populus tremuloides*). All other forest plots were homogenous stands of white spruce. In Alaska, spruce trees are known to support a lower biomass of phytophagous insects than deciduous trees (Chapin et al. 2006) and our results indicate the same is true of the spruce understory.

Beetles experience different trophic interactions with mammalian herbivores among habitats. Exclosure experiments have shown that moose (*Alces alces*) and snowshoe hare (*Lepus americanus*) increase the abundance of silphids, which feed on vertebrate carrion, and carabids, many of which prey on insects that feed on carrion or dung, but decreased the abundance of phytophagous Curculionidae, probably via competition for a shared food plant (Suominen et al. 1999). Snowshoe hare were abundant in our forest and shrub plots. Their populations follow a decadal cycle (Krebs et al. 2001) and were at or near their peak during our study. If beetle communities fluctuate in response to hare populations, then our results may not represent beetle communities in low hare years. In contrast, the primary vertebrate herbivore we observed in alpine tundra plots were arctic ground squirrels (*Spermophilus parryii*), which have more stable populations (Hik et al. 2001). Their colonies supported large numbers of *Agoliinus piceatus* which feed on their dung (Rice 2010).

Ernst and Buddle (2015) found that functional guild assemblages across a latitudinal gradient in Canada were strongly correlated with temperature. We found no significant correlation between temperature and functional guild composition. This was surprising because

mean air temperature significantly differed among habitats, and it was the most highly correlated environmental variable for beetle community composition. It may be that at smaller spatial scales, like those encountered on a mountain, habitat-level temperature may be less important than microclimate.

Arthropod species richness is generally thought to decrease with elevation (Werenkraut and Ruggiero 2011), but we observed the opposite pattern; estimated species richness was roughly 20% greater in the alpine tundra, our highest elevation biome (Tables 3 & 9). The same pattern has been observed in DNPP's vascular plants (Roland and Schmidt 2015). This may be the result of greater microclimate heterogeneity in the alpine tundra. At high latitudes, microclimates on north- and south-facing slopes receive different radiation loads and support different plant and invertebrate communities (Armbruster et al. 2007). This effect is mitigated by canopy shading (Frey et al. 2016, W. S. Armbruster personal communication). Small variations in topography thus have a greater impact on microclimate, and by extension arthropod communities, in the open tundra than in enclosed forests or shrubs. This is supported by the high correlation we found between PDIR and community composition (Fig. 2.6, 2.7, & 2.12).

2.5.2 Beetles

One peculiarity of our results was the predominance of the beetle family Staphylinidae. The staphylinids, or rove beetles, compose the most speciose animal family with over 63,000 described species (Irmeler et al. 2018). Evolutionary and ecological lability have allowed them to fill a wide variety of microhabitats and ecological niches, primarily in leaf litter (Mckenna et al. 2015). They are present in nearly every biome (Thomas 2000, Irmeler et al. 2018). Staphylinids accounted for 78.5% of DNPP beetles by abundance and 37.6% of beetle species richness (Table

2.4). Our results cannot be attributed to a single, or even a few, super-abundant species; twelve of the 15 most abundant species were staphylinids. Nearly 6,000 specimens of the subfamily Aleocharinae have yet to be identified to species and will no doubt further increase staphylinid species richness. To the best of our knowledge, they have never before been reported in such high relative abundance in North America. Most studies at similar latitudes have reported a comparatively lower abundance of staphylinids and a higher abundance of carabids. A study of ground-dwelling beetle communities in Nunavut, Canada reported that staphylinids accounted for only 2.2% of individuals, and a Canada-wide study reported 9.6% of individuals (Ernst and Buddle 2013, Ernst and Buddle 2015). In alpine northern Norway, Rae et al. (2006) collected two staphylinid species compared to 11 carabid species, although abundances were not reported. High densities of staphylinids are known from Russia and western Europe. Russian and Slovakian spruce forests support densities between 30 and 187 individuals per m², and densities in alder (*Alnus* spp.) forest could reach 783 individuals per m² (Bohac 1999). Alder shrubs were common in our study area. Staphylinids, especially aleocharines, have been largely avoided by ecological studies in North America because they are small and difficult to identify (although see Klimaszewski et al. 2018). Most studies instead focus on the taxonomically well-known carabids (Rainio and Niemela 2003, Langor and Spence 2006, Pearce and Venier 2006). Our results highlight the ecological importance of staphylinids in montane Alaska and their potential as bioindicators.

2.5.3 Spiders

Spider communities differed among every habitat because a majority of species showed strong habitat preferences. Sixty-two species (34%) were significant habitat indicators (Table

2.9), and an additional 69 (38%) were collected only in a single habitat (Table 2.8)—although some of these species were rare and we cannot say with confidence that they would not be found elsewhere with increased sampling effort. High rates of habitat specialization for ground-dwelling spiders have now been reported in several disparate biomes across North America (Mallis and Hurd 2005, Meyer et al. 2015).

Spider species richness has been previously found to be highest at sites with greater structural complexity (forest and shrubs), and spider abundance was greatest at open sites (tundra) where pitfall traps collect large numbers of lycosids (Bowden and Buddle 2010, Rich et al. 2013). We observed the opposite pattern; spider abundance was greatest at shrub plots, including many lycosids (Fig. 2.10), and estimated species richness was greatest at open alpine tundra plots (Table 2.8). Spiders have strict micro-habitat requirements for shelter, humidity, and architecture to support web building (Samu 1999). It is possible that DNPP spiders are responding to an unmeasured variable, such as humidity, and further study is needed to explain the observed pattern.

2.5.4 Solar Radiation

Vegetation can shape arthropod communities indirectly by modifying the available solar radiation (shading). Muff et al. (2009) found that vegetation variables related to light—namely tree density, branch distance from ground, and proportion of visible sky—explained the majority of environment-induced variation in spider communities. We used ground temperature loggers to capture the effect of shading on DNPP communities. Contrary to our expectations, we observed no trends in ground temperature, and mean ground temperature was not correlated with beetle, spider, nor functional guild composition. Instead we found PDIR, which does not account for

shading and is strongly influenced by slope, to be among the most important predictors. There are two possible explanations for this. First, we only deployed one ground logger per site and always placed it in the center of the plot, so our data may not be representative of the surrounding habitat. Second, mobile arthropods may move to unobstructed surfaces to maximize solar radiation while basking.

2.5.5 Conclusion

We compared the diversity of ground-dwelling beetles and spiders across an elevational gradient in DNPP to (1) explore the variation in biodiversity, taxonomic structure of beetle and spider communities, and functional guild structure of beetle communities among habitats; and (2) to link the observed variability to important abiotic factors, namely differences in temperature and vegetation cover. We found strong elevational gradients of both community and functional guild composition, and that alpine tundra supported a unique community assemblage with higher than expected species richness of both beetles and spiders. Our study has also provided the baseline population data necessary for monitoring long-term changes in arthropod communities.

Alpine communities harbor a diverse species pool of arthropods, including a high proportion of species found nowhere else in the park and that are unlikely to thrive in woody vegetation. Alaska's alpine tundra is being replaced by shrubs at the rate of 5% per decade (Dial et al. 2007). These species therefore face increased risk of extirpation or extinction due to smaller population sizes and reduced gene flow as their habitat shrinks and fragments (MacArthur and Wilson 1963; Lande 1993; Henle et al. 2004). Arthropods perform key ecosystem services, such as pollination and nutrient cycling and the loss of even a few species could disrupt tundra

interaction webs, which are believed to have low functional redundancy (Petchey et al. 1999, Inouye 2019).

2.6 References

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2.7 Figures

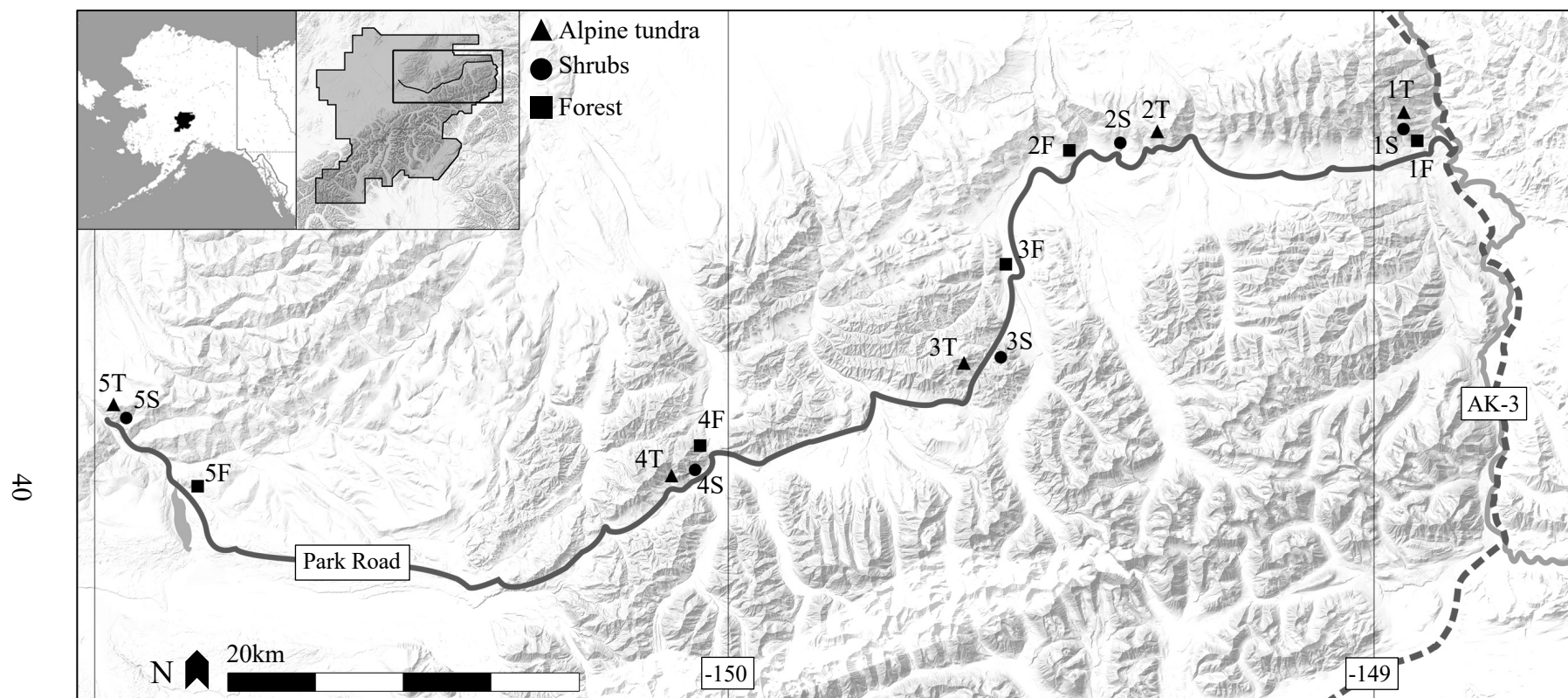


Figure 2.1: The study area in Denali National Park and Preserve, Alaska. We sampled along five elevational transects, each containing a forest (low-elevation), shrub (mid-elevation), and alpine tundra (high-elevation) plot.



Figure 2.2: Examples of study habitats: forest (a), tall shrubs (b), and alpine tundra (c).

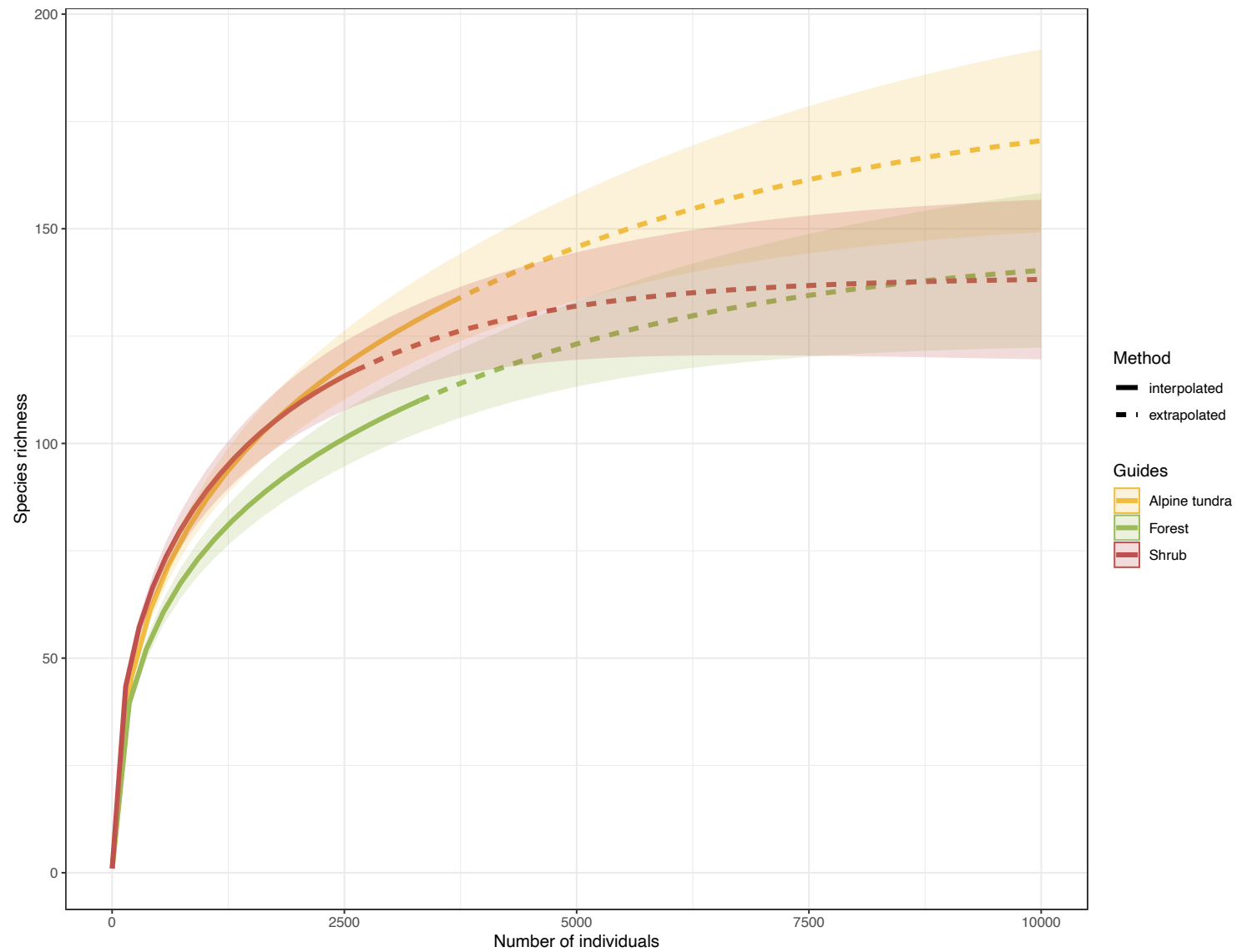


Figure 2.3: Individual-based rarefaction curves for beetles in three habitats in Denali National Park and Preserve, Alaska. Solid lines indicate observed species richness, dashed lines indicate estimated species richness, and shaded region indicates 95% confidence intervals.

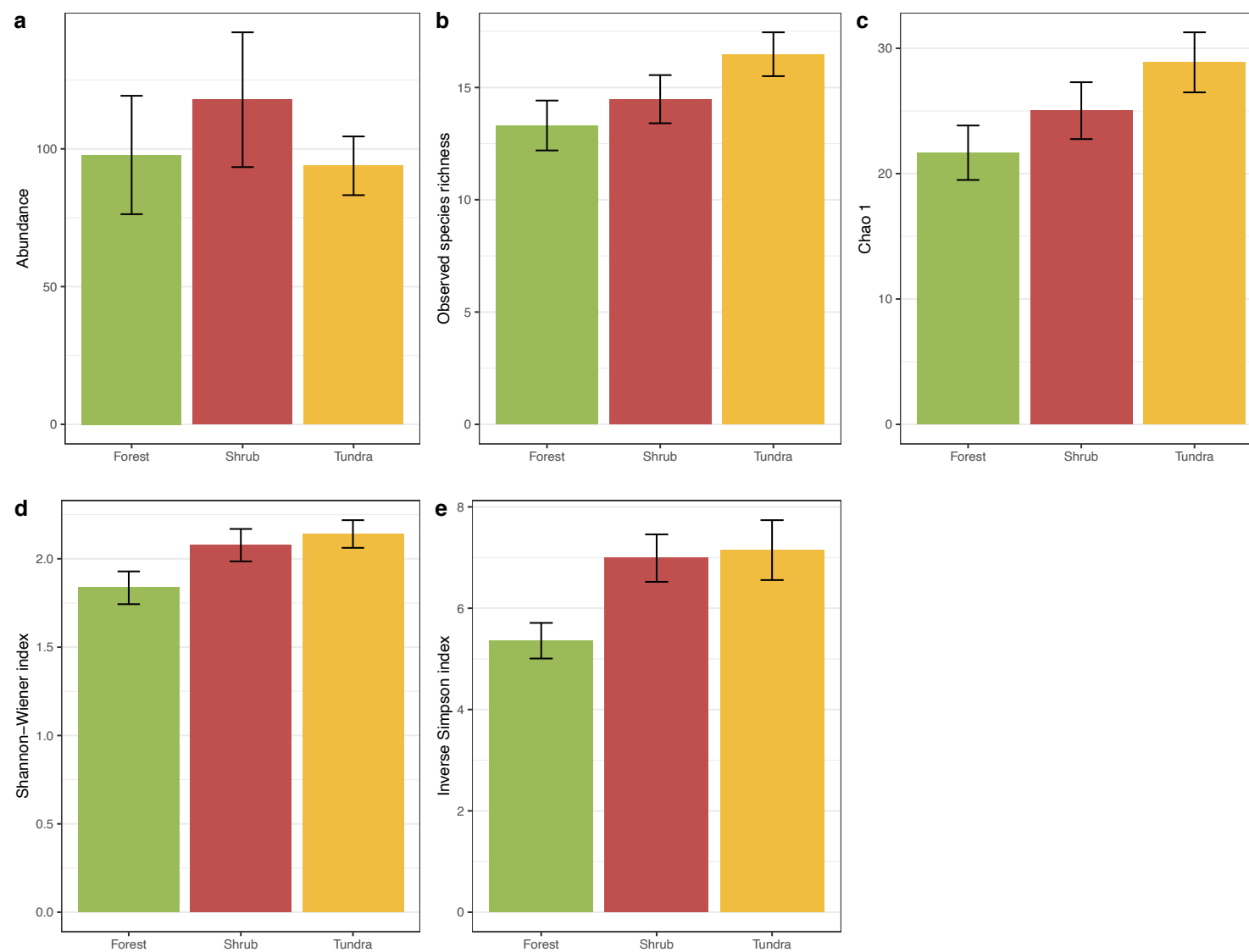


Figure 2.4: Mean beetle abundance and diversity measures among three habitats in Denali National Park and Preserve, Alaska. Error bars represent standard error. Differences were not significant at $\alpha = 0.05$.

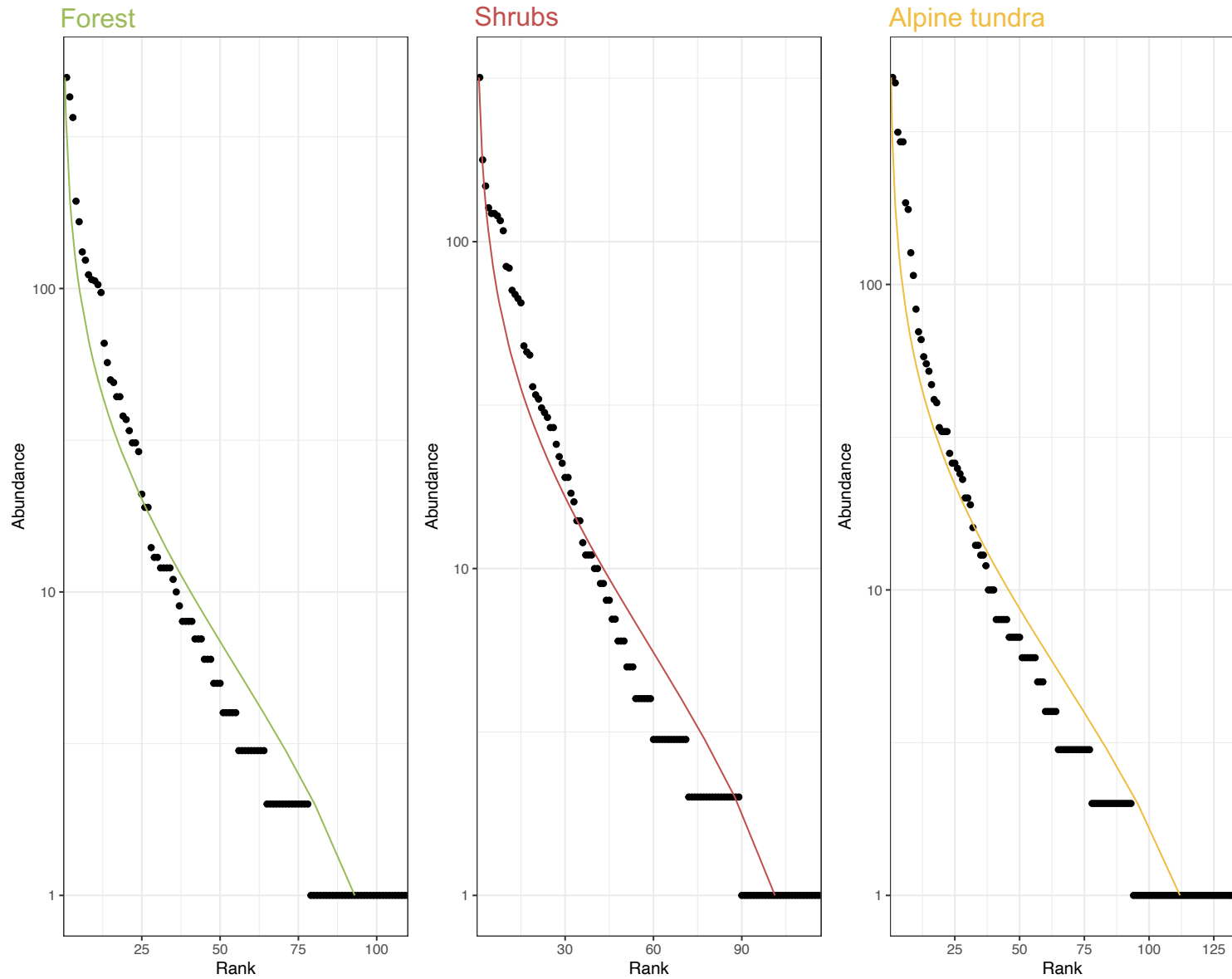


Figure 2.5: Rank abundance plots of beetles in three habitats in Denali National Park and Preserve, Alaska. The slopes of the log-normal curves are an indication of relative evenness; habitats with steeper slopes are less even than those with shallow slopes.

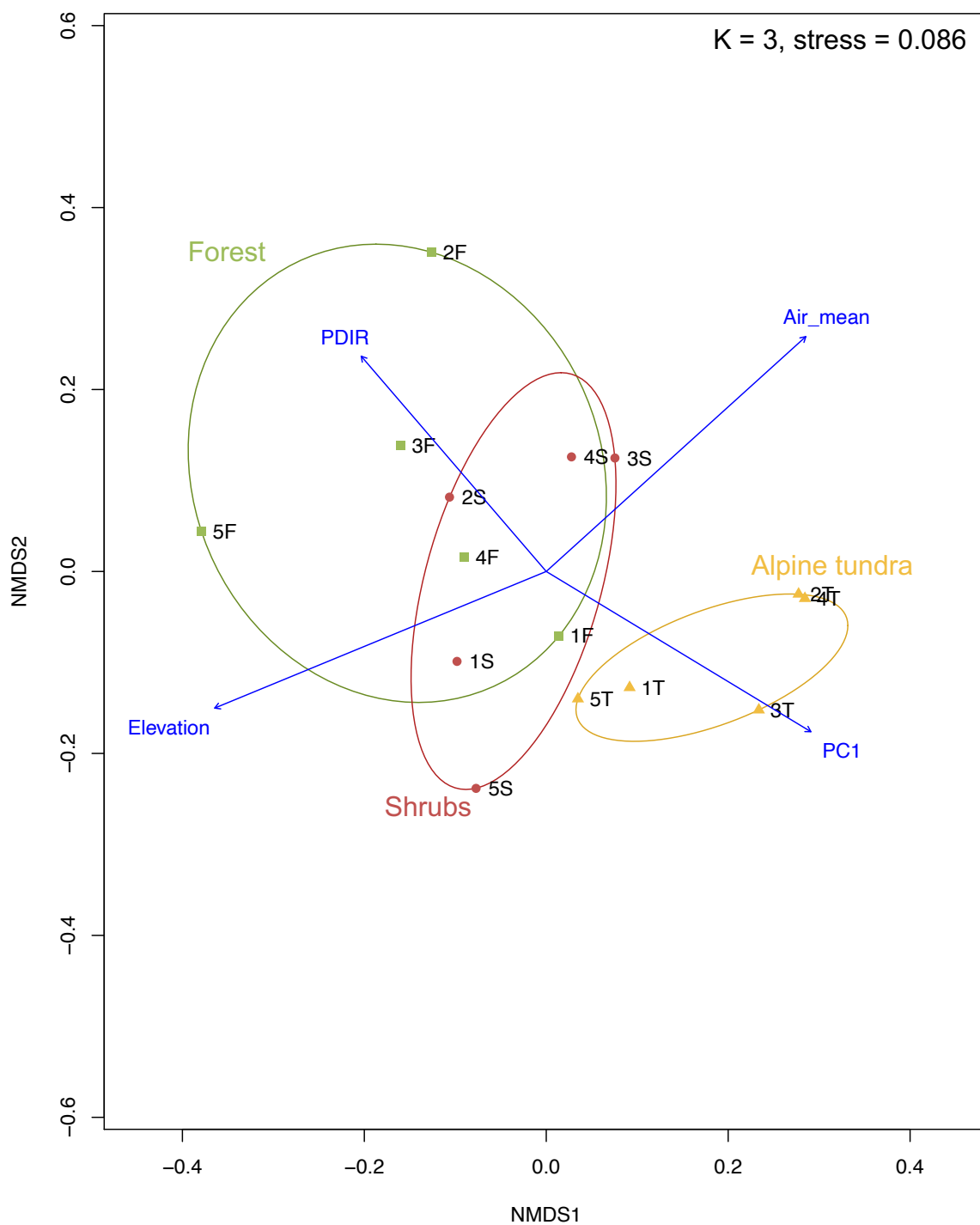


Figure 2.6: NMDS ordination of beetle communities in Denali National Park and Preserve, Alaska. Each point represents the community composition at a single study plot in forest (green square), shrubs (red circles), and alpine tundra (yellow triangles). Elevation, mean air temperature, potential direct incidence radiation (PDIR) and ground cover PC1 (a gradient from spruce forest to open shrubs) are overlain as correlated vectors. Community composition significantly differed by habitat ($df = 2$, $F = 3$, $p = 0.001$).

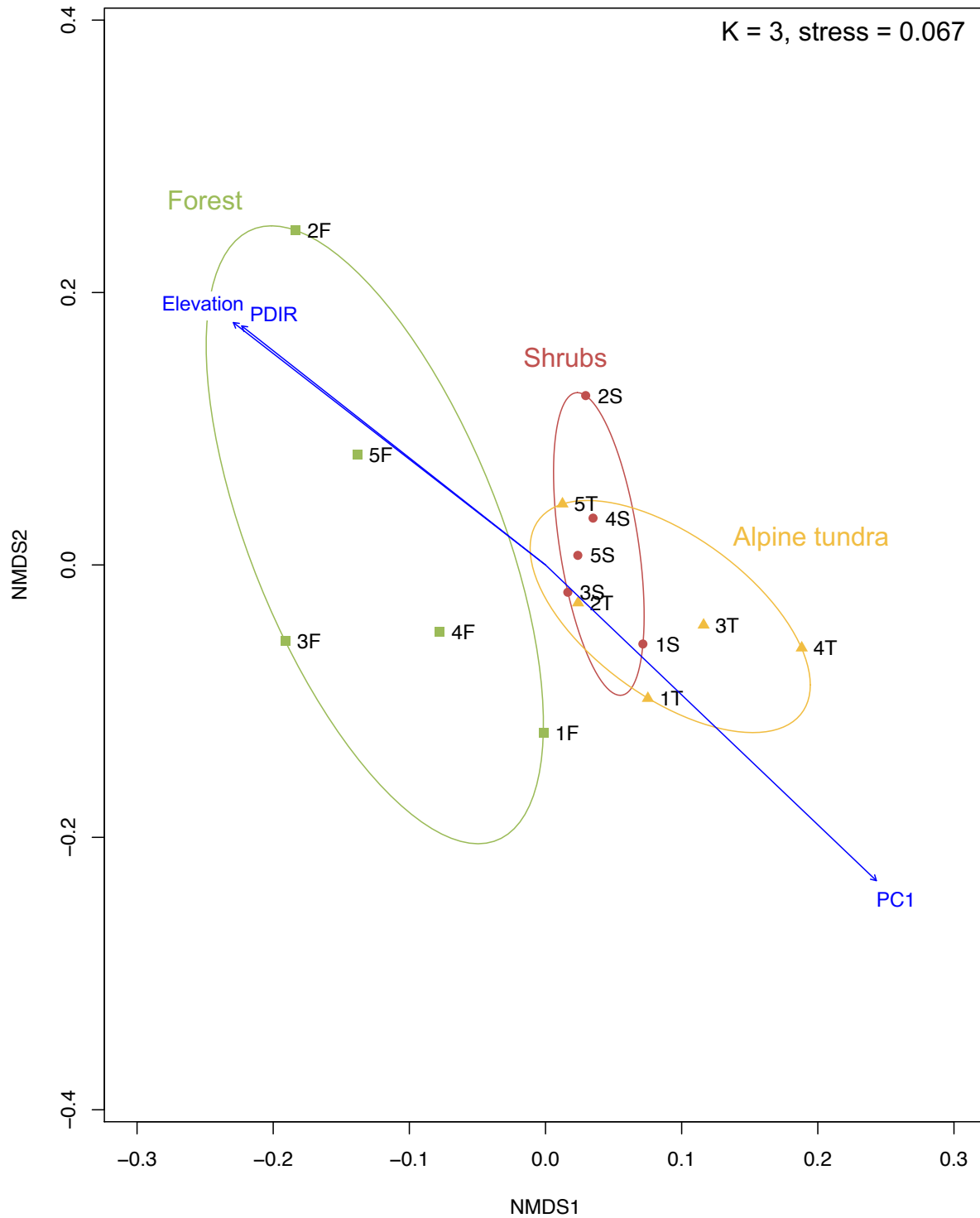


Figure 2.7: NMDS ordination of beetle functional guilds in Denali National Park and Preserve, Alaska. Each point represents the functional guild composition at a single study plot in forest (green square), shrubs (red circles), and alpine tundra (yellow triangles). PC1 (a gradient from spruce forest to open shrubs), elevation, and PDIR are overlain as correlated vectors. Functional guild composition differed by habitat ($df = 2$, $F = 3.25$, $p = 0.001$).

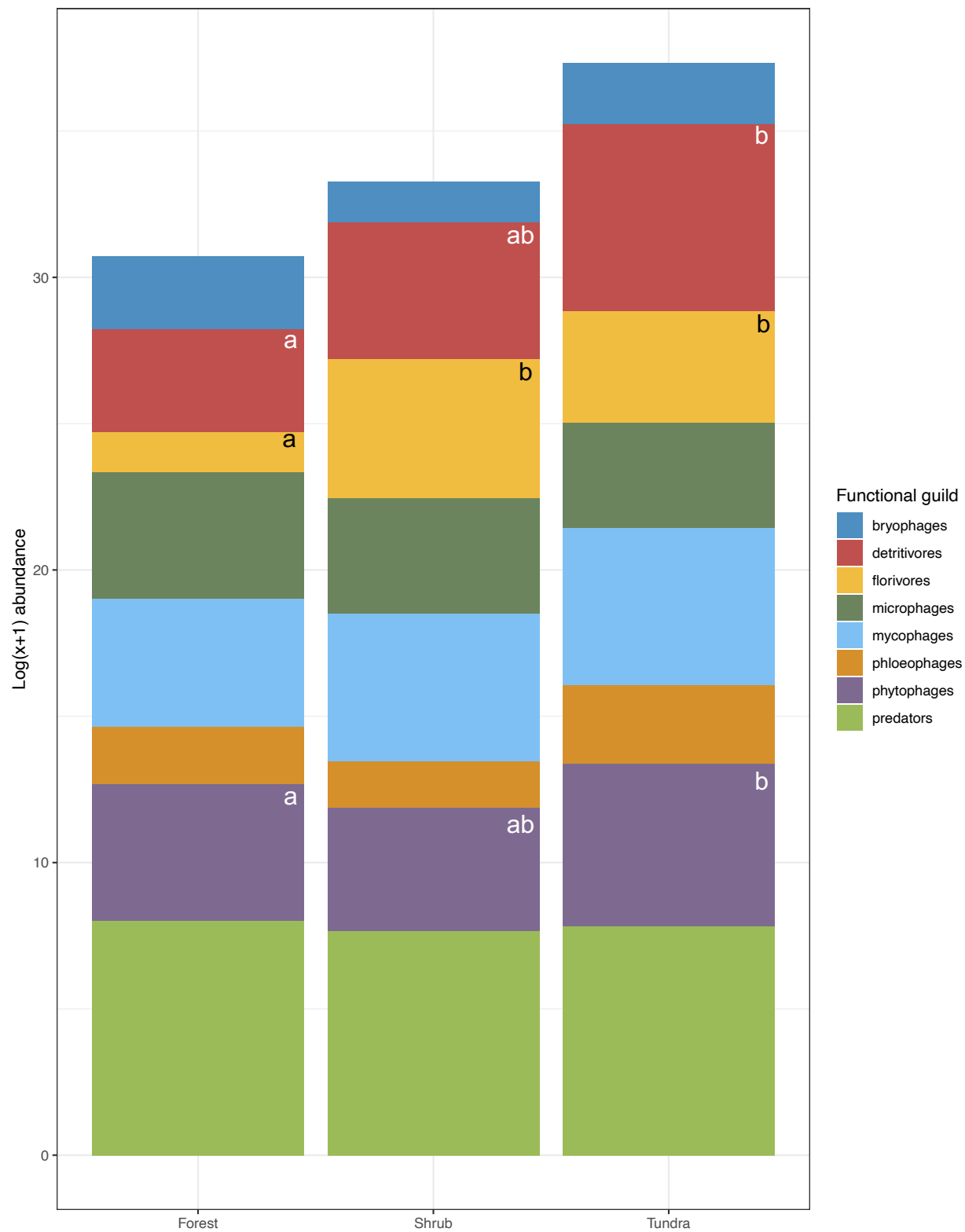


Figure 2.8: Log(x+1) transformed abundance of functional guilds in three habitats in Denali National Park and Preserve, Alaska. Data were log (x+1) transformed to down-weight the influence of the super-abundant predator guild. Letters indicate significantly different groups at $\alpha = 0.005$.

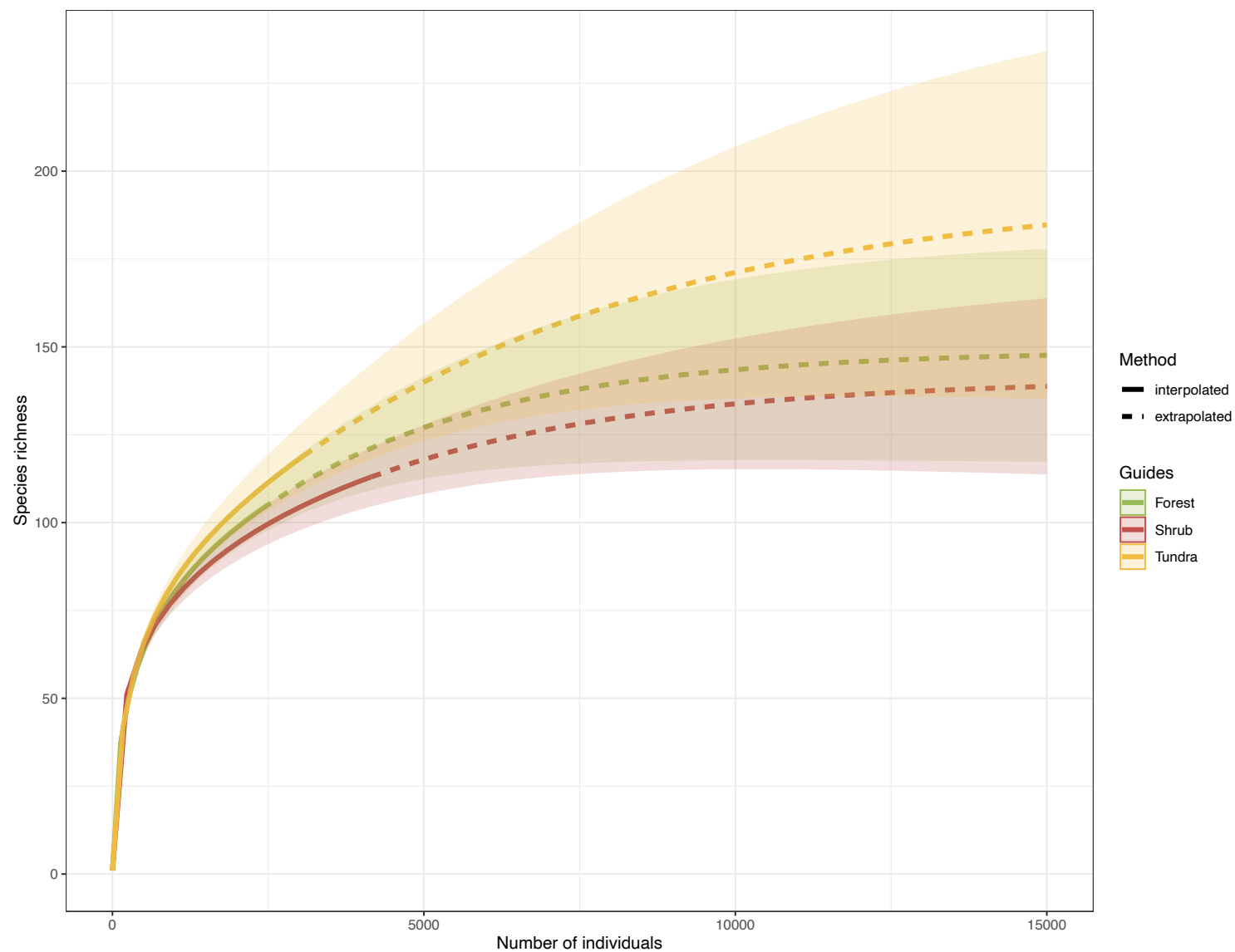


Figure 2.9: Individual-based rarefaction curves for spiders in three habitats in Denali National Park and Preserve, Alaska. Solid lines indicate observed species richness, dashed lines indicate estimated species richness, and shaded region indicates 95% confidence intervals.

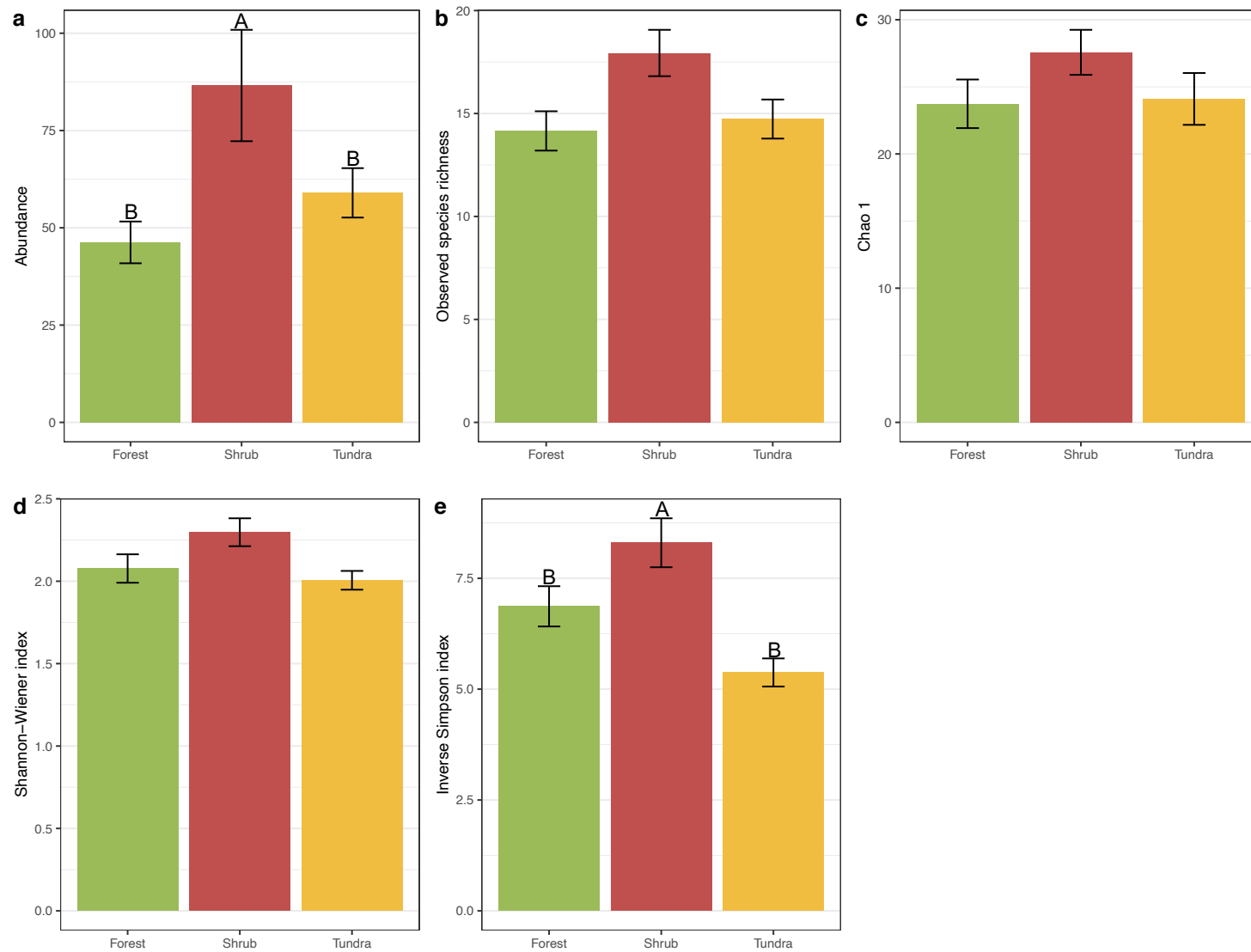


Figure 2.10: Mean spider abundance and diversity measures among three habitats in Denali National Park and Preserve, Alaska. Error bars represent standard error. Capital letters indicate significantly different means at $\alpha = 0.05$. Observed species richness, Chao 1 estimator, and Shannon-wiener index were not significantly different.

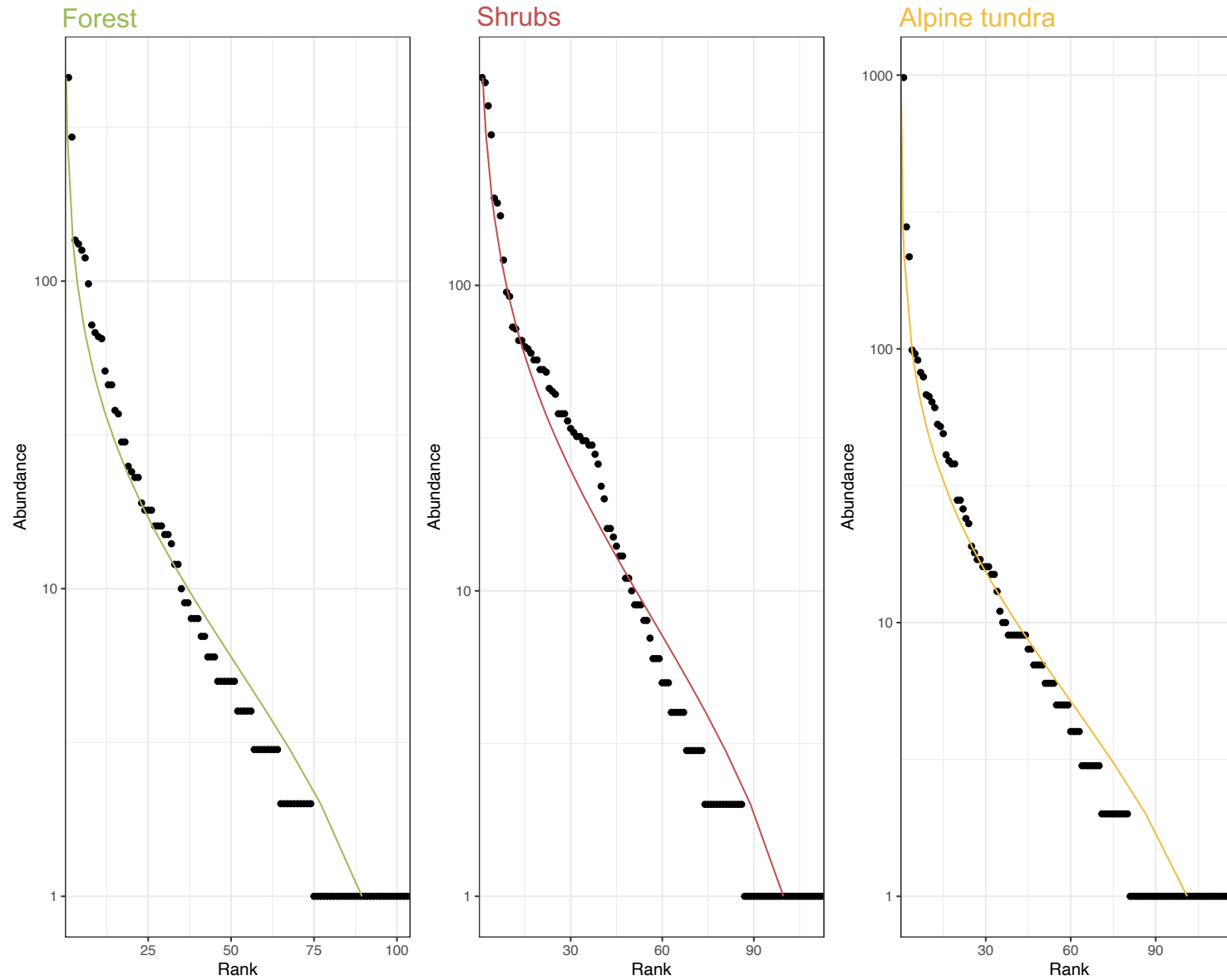


Figure 2.11: Rank abundance plots of spiders in three habitats in Denali National Park and Preserve, Alaska. The slopes of the log-normal curves are an indication of relative evenness; habitats with steeper slopes are less even than those with shallow slopes.

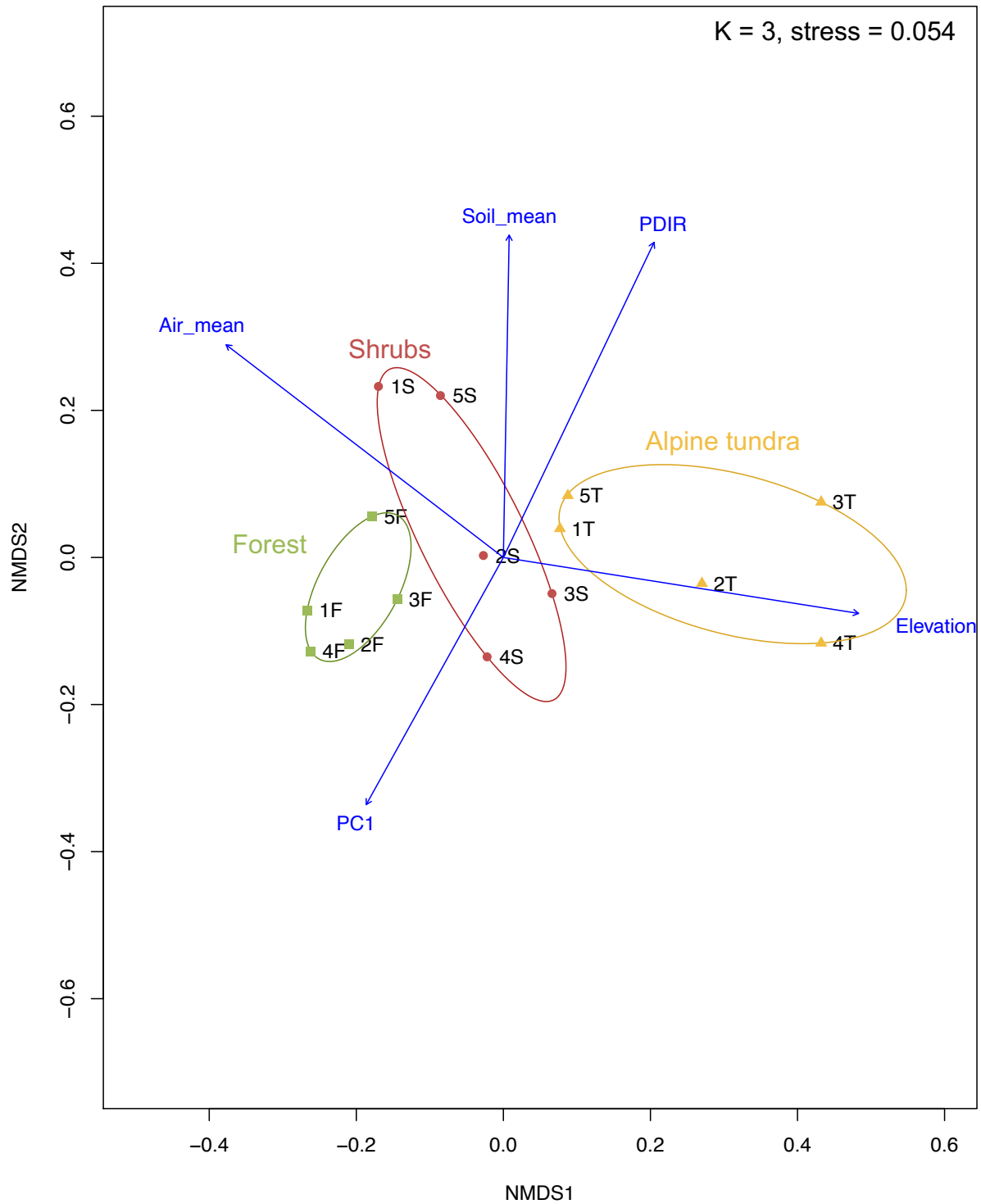


Figure 2.12: NMDS ordination of spider communities in Denali National Park and Preserve, Alaska. Each point represents the community composition at a single study plot in forest (green square), shrubs (red circles), and alpine tundra (yellow triangles). Elevation, mean air temperature, mean soil temperature, potential direct incidence radiation (PDIR) and ground cover PC1 (a gradient from spruce forest to open shrubs) are overlain as correlated vectors. Community composition significantly differed by habitat ($df = 2$, $F = 5.65$, $p = 0.001$)

2.8 Tables

Table 2.1: Location and sampling period of study plots.

Plot	Habitat	Locality	Latitude	Longitude	Elev. (m)	2016	2017	2018	Samples
1F	forest	Mt. Healy	63.73478	-148.92911	595	2 Jul – 16 Aug	13 Jun – 8 Aug	5 Jun – 31 Jul	11
1S	shrub	Mt. Healy	63.74016	-148.95346	927	2 Jul – 16 Aug	13 Jun – 8 Aug	5 Jun – 31 Jul	11
1T	alpine tundra	Mt. Healy	63.75095	-148.96071	1183	2 Jul – 16 Aug	13 Jun – 8 Aug	5 Jun – 31 Jul	11
2F	forest	Wright Mountain	63.71967	-149.48056	772	2 Jul – 17 Aug	16 Jun – 11 Aug	8 Jun – 3 Aug	11
2S	shrub	Primrose Ridge	63.72686	-149.40852	883	2 Jul – 17 Aug	16 Jun – 11 Aug	8 Jun – 3 Aug	11
2T	alpine tundra	Primrose Ridge	63.74163	-149.35381	1252	2 Jul – 17 Aug	16 Jun – 11 Aug	8 Jun – 3 Aug	11
3F	forest	Teklanika River	63.64261	-149.57181	833	2 Jul – 17 Aug	15 Jun – 9 Aug	6 Jun – 1 Aug	11
3S	shrub	Igloo Canyon	63.59455	-149.60834	970	2 Jul – 17 Aug	15 Jun – 9 Aug	6 Jun – 1 Aug	11
3T	alpine tundra	Igloo Canyon	63.57143	-149.64784	1200	2 Jul – 17 Aug	15 Jun – 9 Aug	6 Jun – 1 Aug	11
4F	forest	Toklat Road Camp	63.52373	-150.04829	960	2 Jul – 18 Aug	15 Jun – 9 Aug	6 Jun – 1 Aug	11
4S	shrub	Toklat River	63.50232	-150.06764	1047	2 Jul – 18 Aug	15 Jun – 9 Aug	6 Jun – 1 Aug	11
4T	alpine tundra	Toklat River	63.49723	-150.10019	1179	2 Jul – 18 Aug	15 Jun – 9 Aug	6 Jun – 1 Aug	11
5F	forest	Wonder Lake	63.48534	-150.86235	674	-	15 Jun – 10 Aug	7 Jun – 2 Aug	8
5S	shrub	Wickersham Dome	63.54800	-150.97749	811	-	15 Jun – 10 Aug	7 Jun – 2 Aug	8
5T	alpine tundra	Wickersham Dome	63.55630	-150.97755	977	-	15 Jun – 10 Aug	7 Jun – 2 Aug	8

Table 2.2: Abiotic characteristics of study plots. Temperatures are mean daily values $\pm$ Standard Error. Potential direct incident radiation (PDIR) was calculated with the formula of McCune and Keon (2002) based on latitude, slope, and aspect.

Plot	Elevation (m)	PDIR	Air ($^{\circ}\text{C}$)	Ground ($^{\circ}\text{C}$)	Soil ($^{\circ}\text{C}$)
1F	595	0.33	12.84 ± 0.1	12.84 ± 0.1	7.17 ± 0.2
1S	927	15.67	11.93 ± 0.1	13.13 ± 0.1	10.94 ± 0.2
1T	1183	20	10.01 ± 0.1	11.84 ± 0.1	7.86 ± 0.2
2F	772	13.33	11.74 ± 0.1	12.02 ± 0.1	7.26 ± 0.2
2S	883	8.33	11.97 ± 0.1	13.37 ± 0.1	8.97 ± 0.3
2T	1252	17.33	9.72 ± 0.1	13.18 ± 0.2	7.64 ± 0.2
3F	833	0	11.7 ± 0.1	13.44 ± 0.2	6.59 ± 0.2
3S	970	6.33	11.35 ± 0.1	13.47 ± 0.1	9.42 ± 0.3
3T	1047	26	10.41 ± 0.1	11.9 ± 0.1	9.91 ± 0.2
4F	960	5	11.41 ± 0.1	12.61 ± 0.1	8.3 ± 0.2
4S	1047	2.67	11.24 ± 0.1	12.63 ± 0.1	8.9 ± 0.2
4T	1179	6.67	10.36 ± 0.1	13.35 ± 0.2	6.61 ± 0.3
5F	674	7.67	11.51 ± 0.1	13.52 ± 0.1	6.78 ± 0.1
5S	811	27.67	12.92 ± 0.1	12.94 ± 0.2	7.43 ± 0.0
5T	977	10	12.98 ± 0.1	18.47 ± 0.2	11.4 ± 0.2

Table 2.3: Principle component loadings of ground cover types. The first 3 principle components explained 80% of the variation among sites collectively. The most influential eigenvalues are in bold.

Species Scores	PC1	PC2	PC3
Evergreen trees	3.54	-1.01	-0.04
Deciduous tree	0.25	-0.91	-0.47
Evergreen tall shrubs (>1 m)	0.41	-0.04	0.03
Deciduous tall shrubs (>1 m)	-0.61	-0.45	-0.53
Evergreen low shrubs	0.10	-0.01	0.01
Deciduous low shrubs	-1.21	5.16	-2.31
Evergreen dwarf shrubs	0.37	-0.18	0.11
Deciduous dwarf shrubs	-1.75	0.70	-1.12
Evergreen prostrate shrubs	-0.06	0.35	0.13
Deciduous prostrate shrubs	-0.67	-1.48	-0.10
Forbs	0.15	-0.21	-0.16
Grass	-0.40	-0.23	-0.35
Sedge	0.38	-0.02	0.14
Moss	9.33	1.63	0.60
Lichen	-2.27	2.26	4.73
Bare soil	-0.04	-0.03	0.01
Rock	-0.23	-0.16	-0.24

Table 2.4: Summary of beetle families.

Family	Subfamily	Species		Individuals	
Brentidae		1	(0.5%)	58	(0.4%)
Buprestidae		1	(0.5%)	1	(< 0.1%)
Byrrhidae		5	(2.7%)	22	(0.1%)
Cantharidae		1	(0.5%)	20	(0.1%)
Carabidae		30	(16.1%)	1515	(9.7%)
	Broscinae	1		4	
	Carabinae	2		163	
	Elaphrinae	1		1	
	Harpalinae	20		1313	
	Nebriinae	3		28	
	Scaritinae	1		3	
	Trechinae	1		2	
Chrysomelidae		4	(2.2%)	7	(< 0.1%)
Ciidae		1	(0.5%)	4	(< 0.1%)
Coccinellidae		5	(2.7%)	17	(0.1%)
Cryptophagidae		12	(6.5%)	160	(1%)
Curculionidae		14	(7.5%)	294	(1.9%)
Dytiscidae		1	(0.5%)	1	(< 0.1%)
Elateridae		8	(4.3%)	74	(0.5%)
Eucinetidae		1	(0.5%)	7	(< 0.1%)
Hydrophilidae		1	(0.5%)	3	(< 0.1%)
Lampyridae		1	(0.5%)	3	(< 0.1%)
Latridiidae		11	(5.9%)	319	(2%)
Leiodidae		9	(4.8%)	133	(0.9%)
Mordellidae		2	(1%)	2	(< 0.1%)
Nitidulidae		3	(1.6%)	20	(0.1%)
Ptiliidae		-	-	82	(0.5%)
Ptinidae		1	(0.5%)	11	(0.1%)
Scarabaeidae		2	(1%)	485	(3.1%)
Silphidae		2	(1%)	122	(0.8%)
Staphylinidae		70	(37.6%)	12260	(78.5%)
	Aleocharinae	18		6290	
	Micropeplinae	1		56	
	Omaliinae	12		3307	
	Oxytlinae	2		4	
	Proteininae	3		301	
	Scaphidiinae	1		20	
	scydmaeninae	4		178	
	Staphylininae	8		561	
	Steninae	2		45	
	Tachyporinae	19		1498	
Total		186		15620	

Table 2.5: γ -diversity and β -diversity of ground-dwelling beetles in three habitat types. γ -diversity measures ($\pm$ 95% confidence interval) are observed species richness (S), estimated species richness (Chao1), Shannon diversity index, and inverse Simpson's index. Completeness is the percentage of estimated species collected. Sørensen index values of β -diversity equal the proportion of shared species between two plots.

	Forest	Shrub	Alpine tundra	Total
Samples	52	48	52	152
Abundance	5084	5656	4880	15620
S	110	117	133	186
Unique species	18	16	37	71
Chao1	147 $\pm$ 33.9	139 $\pm$ 21.1	183 $\pm$ 41.9	
Completeness	75%	84%	73%	
Shannon diversity	26.2 $\pm$ 1.0	8.2 $\pm$ 1.7	28.8 $\pm$ 1.2	
Inverse Simpson's diversity	14.8 $\pm$ 0.8	23.6 $\pm$ 1.3	15.9 $\pm$ 0.8	
β -diversity	0.64	0.66	0.67	
Turnover	0.56	0.55	0.50	
Nestedness	0.08	0.11	0.17	

Table 2.6: Significant beetle indicator species of forest, shrub, and alpine tundra habitats. Component A is the proportion of individuals collected in the given habitat (specificity) and Component B is the proportion of sites belonging to that habitat that contained the species (fidelity).

	Abundance	Guild	A	B	stat	P
Forest						
1. <i>Tachinus basalis</i>	141	predator	0.65	0.46	0.55	0.001
2. <i>Pterostichus pinguedineus</i>	104	predator	0.94	0.35	0.57	0.001
3. <i>Pterostichus</i> DNP #1	46	predator	0.70	0.37	0.50	0.001
4. <i>Megarthrhus angulicollis</i>	23	mycophage	0.77	0.21	0.40	0.001
5. <i>Olophrum latum</i>	526	predator	0.49	0.56	0.52	0.004
6. <i>Ischnosoma splendidum</i>	13	predator	0.82	0.17	0.38	0.004
7. <i>Stenus austini</i>	44	predator	0.67	0.25	0.41	0.006
8. <i>Pterostichus brevicornis</i>	688	predator	0.42	0.79	0.57	0.01
9. <i>Dorytomus frostii</i>	8	phytophage	1.00	0.10	0.31	0.011
10. <i>Cryptophagus bidentatus</i>	28	microphage	0.64	0.21	0.37	0.013
11. <i>Pterostichus</i> DNP #2	13	predator	1.00	0.10	0.31	0.013
12. <i>Notiophilus borealis</i>	16	predator	0.69	0.17	0.35	0.017
13. <i>Quedius frigidus</i>	19	predator	0.65	0.19	0.35	0.02
14. <i>Pseudanostirus ochreipennis</i>	4	phytophage	1.00	0.08	0.28	0.037
Shrubs						
1. <i>Amara brunnea</i>	88	florivore	0.83	0.38	0.56	0.001
2. <i>Catops alpinus</i>	54	detritivore	0.60	0.38	0.47	0.001
3. <i>Amara hyperborea</i>	32	florivore	0.87	0.25	0.47	0.001
4. <i>Lordithon fungicola</i>	319	predator	0.61	0.40	0.49	0.002
5. <i>Atomaria kamtschatica</i>	5	microphage	1.00	0.10	0.32	0.002
6. <i>Orthocis punctatus</i>	4	mycophage	1.00	0.08	0.29	0.007
7. <i>Proteinus parvulus</i>	262	predator	0.51	0.42	0.46	0.012
8. <i>Ischnosoma fimbriatum</i>	68	predator	0.49	0.44	0.46	0.016
9. <i>Tachinus quebecensis</i>	213	predator	0.61	0.21	0.36	0.02
10. <i>Nycteus</i> DNP #1	7	mycophage	1.00	0.06	0.25	0.027
11. <i>Bolitobius cingulatus</i>	3	predator	1.00	0.06	0.25	0.031
Alpine tundra						
1. <i>Agoliinus piceatus</i>	483	detritivore	0.95	0.37	0.59	0.001
2. <i>Tachinus elongatus</i>	291	predator	0.50	0.52	0.51	0.001
3. <i>Corticaria</i> DNP #1	162	mycophage	0.60	0.62	0.61	0.001
4. <i>Carabus truncaticollis</i>	127	predator	1.00	0.27	0.52	0.001
5. <i>Hypera diversipunctata</i>	63	phytophage	0.62	0.46	0.54	0.001
6. <i>Loborhynchapion cyanitinctum</i>	58	phytophage	1.00	0.37	0.60	0.001
7. <i>Tachinus instabilis</i>	51	predator	0.92	0.21	0.44	0.001
8. <i>Carabus chamissonis</i>	36	predator	0.76	0.33	0.50	0.001
9. <i>Amara alpina</i>	34	florivore	1.00	0.29	0.54	0.001
10. <i>Omalium</i> DNP #3	28	predator	0.80	0.25	0.45	0.001
11. <i>Bryophacis smetanai</i>	25	predator	0.72	0.25	0.42	0.001
12. <i>Tachyporus rulomus</i>	20	predator	0.90	0.17	0.40	0.001
13. <i>Acidota quadrata</i>	579	predator	0.42	0.88	0.61	0.002
14. <i>Eucnecosum brachypterum</i>	522	predator	0.51	0.52	0.51	0.003
15. <i>Quedius fellmani</i>	263	predator	0.48	0.58	0.53	0.004

Table 2.6: Continued

16. <i>Colon liebecki</i>	19	mycophage	0.81	0.17	0.37	0.005
17. <i>Epuraea DNP #1</i>	18	phloeophage	0.70	0.19	0.37	0.005
18. <i>Ascoliocerus sanborni</i>	7	phytophage	1.00	0.12	0.34	0.005
19. <i>Cymindis unicolor</i>	12	predator	0.79	0.15	0.35	0.006
20. <i>Olophrum consimile</i>	302	predator	0.66	0.19	0.36	0.012
21. <i>Lepidophorus lineaticollis</i>	154	phytophage	0.49	0.48	0.48	0.013
22. <i>Tachyporus nimbicola</i>	27	predator	0.65	0.19	0.35	0.02
23. <i>Veraphis DNP #2</i>	143	predator	0.46	0.44	0.45	0.022
24. <i>Corticarina DNP #1</i>	15	mycophage	0.76	0.13	0.32	0.024
25. <i>Neohypdonus restrictulus</i>	36	phytophage	0.83	0.10	0.28	0.036
26. <i>Caenocara scymnoides</i>	11	detritivore	0.69	0.13	0.30	0.041

Table 2.7: Summary of spider families.

Family	Species		Individuals	
Agelenidae	1	(0.6%)	5	(0.1%)
Amaurobiidae	1	(0.6%)	49	(0.5%)
Araneidae	1	(0.6%)	11	(0.1%)
Clubionidae	3	(1.7%)	17	(0.2%)
Dictynidae	7	(3.9%)	84	(0.9%)
Gnaphosidae	13	(7.1%)	854	(8.8%)
Hahniidae	2	(1%)	89	(0.9%)
Linyphiidae	103	(56.7%)	4026	(41.8%)
Liocranidae	1	(0.6%)	2	(< 0.1%)
Lycosidae	20	(11%)	3956	(41.1%)
Philodromidae	4	(2.2%)	71	(0.7%)
Salticidae	7	(3.9%)	28	(0.3%)
Theridiidae	6	(3.3%)	8	(0.1%)
Thomisidae	11	(6%)	351	(3.7%)
Titanoecidae	2	(1%)	76	(0.8%)
Total	182		9627	

Table 2.8: γ -diversity and β -diversity of ground-dwelling spiders in three habitat types. γ -diversity measures ($\pm$ 95% confidence interval) are observed species richness (S), estimated species richness (Chao1), Shannon diversity index, and inverse Simpson's index. Completeness is the percentage of estimated species collected. Sørensen index values of β -diversity equal the proportion of shared species between two plots.

	Forest	Shrub	Alpine tundra	Total
Samples	52	48	52	152
Abundance	2405	4155	3067	9627
S	104	113	119	182
Unique species	26	27	30	83
Chao1	149 $\pm$ 22.7	141 $\pm$ 14.3	195 $\pm$ 35.3	
Completeness	70%	80%	61%	
Shannon diversity	28 $\pm$ 0.8	34.1 $\pm$ 0.6	22.5 $\pm$ 0.7	
Inverse Simpson's diversity	14.1 $\pm$ 0.6	19.4 $\pm$ 0.4	8.1 $\pm$ 0.4	
β -diversity	0.64	0.60	0.60	
Turnover	0.53	0.52	0.56	
Nestedness	0.11	0.08	0.03	

Table 2.9: Significant spider indicator species of forest, shrub, and alpine tundra habitats. Component A is the proportion of individuals collected in the given habitat (specificity) and Component B is the proportion of sites belonging to that habitat that contained the species (fidelity).

	Abundance	A	B	stat	P
Forest					
1. <i>Pardosa uintana</i>	778	0.50	0.73	0.60	0.001
2. <i>Hilaira herniosa</i>	528	0.66	0.71	0.69	0.001
3. <i>Zornella armata</i>	201	0.62	0.67	0.65	0.001
4. <i>Sisicottus montanus</i>	164	0.75	0.69	0.72	0.001
5. <i>Impropantes complicatus</i>	104	0.54	0.56	0.55	0.001
6. <i>Scotinotylus sacer</i>	90	0.57	0.48	0.52	0.001
7. <i>Bathypantes eumenis</i>	83	0.77	0.52	0.63	0.001
8. <i>Semljicola obtusus</i>	25	0.93	0.25	0.48	0.001
9. <i>Acanthoneta aggressa</i>	12	1.00	0.17	0.42	0.001
10. <i>Ceraticelus fissiceps</i>	67	0.60	0.37	0.47	0.002
11. <i>Sisicus apertus</i>	20	0.91	0.19	0.42	0.002
12. <i>Lepthyphantes alpinus</i>	225	0.48	0.63	0.55	0.003
13. <i>Microneta viaria</i>	76	0.67	0.25	0.41	0.005
14. <i>Semljicola lapponicus</i>	5	1.00	0.10	0.31	0.008
15. <i>Walckenaeria karpinskii</i>	70	0.53	0.38	0.45	0.009
16. <i>Hahnina glacialis</i>	39	0.62	0.23	0.38	0.01
17. <i>Walckenaeria atrotibialis</i>	85	0.51	0.42	0.46	0.014
18. <i>Diplocentria rectangulata</i>	58	0.56	0.29	0.40	0.029
19. <i>Sisis rotundus</i>	16	1.00	0.08	0.28	0.034
20. <i>Oreonetides vaginatus</i>	34	0.58	0.19	0.33	0.047
Shrubs					
1. <i>Alopecosa aculeata</i>	715	0.51	0.79	0.64	0.001
2. <i>Pardosa moesta</i>	435	0.61	0.75	0.68	0.001
3. <i>Gnaphosa microps</i>	258	0.54	0.69	0.61	0.001
4. <i>Pardosa furcifera</i>	201	0.84	0.31	0.51	0.001
5. <i>Micaria tripunctata</i>	83	0.62	0.38	0.48	0.001
6. <i>Cnephalocotes obscurus</i>	75	0.92	0.46	0.65	0.001
7. <i>Titanoeca nivalis</i>	73	1.00	0.25	0.50	0.001
8. <i>Ivielum sibiricum</i>	66	0.65	0.35	0.48	0.001
9. <i>Micaria aenea</i>	58	0.94	0.29	0.52	0.001
10. <i>Zelotes sula</i>	29	0.92	0.23	0.46	0.001
11. <i>Haplodrassus hiemalis</i>	137	0.57	0.48	0.52	0.003
12. <i>Xysticus luctuosus</i>	7	1.00	0.08	0.29	0.004
13. <i>Pardosa mackenziana</i>	33	1.00	0.10	0.32	0.005
14. <i>Gnaphosa muscorum</i>	25	0.71	0.19	0.37	0.009
15. <i>Pocadicnemis occidentalis</i>	66	0.62	0.25	0.39	0.012
16. <i>Hackmania prominula</i>	53	0.61	0.27	0.41	0.013
17. <i>Hypselistes jacksoni</i>	6	1.00	0.08	0.29	0.013
18. <i>Ceraticelus crassiceps</i>	39	0.59	0.25	0.38	0.019
19. <i>Ozyptila sincera</i>	21	0.64	0.21	0.37	0.02
20. <i>Hahnina ononidum</i>	50	0.56	0.29	0.40	0.021
21. <i>Gonatium crassipalpus</i>	145	0.50	0.42	0.46	0.023
22. <i>Ceraticelus laticeps</i>	4	1.00	0.06	0.25	0.028

Table 2.9: Continued

23. <i>Hilaira gibbosa</i>	52	0.65	0.15	0.309	0.034
Alpine tundra					
1. <i>Pardosa lapponica</i>	1413	0.59	1.00	0.77	0.001
2. <i>Tiso aestivus</i>	317	0.73	0.56	0.64	0.001
3. <i>Horcotes strandi</i>	100	0.87	0.54	0.68	0.001
4. <i>Pardosa podhorskii</i>	93	0.91	0.44	0.64	0.001
5. <i>Ozyptila arctica</i>	93	0.58	0.54	0.56	0.001
6. <i>Xysticus emertoni</i>	85	0.67	0.46	0.56	0.001
7. <i>Thanatus arcticus</i>	66	0.76	0.40	0.56	0.001
8. <i>Pardosa palustris</i>	64	1.00	0.17	0.42	0.001
9. <i>Gnaphosa orites</i>	39	1.00	0.38	0.62	0.001
10. <i>Arctella lapponica</i>	25	0.87	0.27	0.48	0.001
11. <i>Agyneta jacksoni</i>	24	1.00	0.27	0.52	0.001
12. <i>Hypsosinga groenlandica</i>	11	1.00	0.15	0.39	0.001
13. <i>Micaria alpina</i>	72	0.62	0.35	0.47	0.004
14. <i>Gnaphosa borea</i>	141	0.53	0.37	0.44	0.009
15. <i>Alopecosa pictilis</i>	15	1.00	0.08	0.28	0.031
16. <i>Agyneta allosubtilis</i>	21	0.62	0.15	0.31	0.033
17. <i>Diplocephalus barbiger</i>	8	0.83	0.10	0.28	0.033
18. <i>Tapinocyba bicarinata</i>	29	0.57	0.21	0.35	0.034
19. <i>Walckenaeria clavicornis</i>	6	0.83	0.10	0.28	0.034

Chapter 3: Community-level Patterns of Beringian Dispersal Among Ground-dwelling Beetles and Spiders in Denali National Park and Preserve, Alaska²

3.1 Abstract

The glacial cycles of the Pleistocene shaped the contemporary geographic distribution of Alaskan beetles (Coleoptera) and spiders (Araneae). At that time, Denali National Park and Preserve was part of Beringia, an ice-free refugium connected to eastern Asia via the Bering Land bridge. The land bridge allowed for biotic exchange between continents, but its primarily steppe-tundra environment prevented the dispersal of forest-dwelling species. At the end of the Pleistocene, the boreal forest spread rapidly across North America, while tundra became restricted to the alpine zone. Species with similar habitat requirements likely experienced the same barriers to dispersal, so we expect that there are community-level patterns of geographic distribution. We tested two hypotheses: 1) alpine tundra communities support a relatively greater richness of Beringian species because it acts as a refugium for previously widespread tundra species, and 2) forest communities support relatively fewer Holarctic species because they were unable to disperse across the Bering Land Bridge. Here, we summarized the distribution patterns of 257 ground-dwelling beetles and spider species. Most species had a North American or Holarctic distribution, and Beringian distributions were relatively uncommon. A chi-squared test did not detect a significant relationship between habitat preference and geographic distribution, and neither hypothesis was supported. However, the overall trend was that alpine tundra contained the highest proportion of Beringian species. Additionally, DNA sequence data suggest that several Holarctic species contain distinct Palearctic and Nearctic populations that are likely separate species, consistent with hypothesis two. Community-level distribution patterns may be

² Haberski, A. Sikes, D. S., 2020. Community-level patterns of Beringian dispersal among ground-dwelling beetles and spiders in Denali National Park and Preserve, Alaska. To be submitted to journal TBD.

difficult to detect because the Bering Land Bridge environment was spatially and temporally dynamic. Nevertheless, taxonomic revisions and more complete distribution data may reveal these patterns and improve our understanding of Pleistocene dispersal.

3.2 Introduction

Large-scale patterns of biodiversity reflect historical processes such as orogeny, plate tectonics, and climate fluctuations. The glacial cycles of the Pleistocene were one of the most important influences on the geographic distribution of Alaska's arthropod fauna. During the last glacial maximum, much of Canada and Alaska was overlaid by ice sheets and alpine glaciers. Arthropod species either survived south of the ice sheets or in ice-free refugia. Beringia, the largest northern refugium, spanned from the McKenzie River in Yukon, Canada, to the Lena River, Russia, and included most of interior Alaska (Hopkins 1967). Fossil and phylogenetic evidence show that Beringia supported a richness of plants, mammals, and insects and was a major source for postglacial recolonization (Elias and Crocker 2008, Shafer et al. 2010, Eidesen et al. 2013). Dispersal within, and ultimately out of, Beringia gave rise to divergent distributional patterns which include local endemics, intercontinental disjunctions, and pairs of vicariant taxa on opposite sides of the Bering Strait (Ickert-Bond et al. 2009, Sikes and Allen 2016).

The Bering Land Bridge (BLB) afforded a corridor for biotic exchange between eastern and western Beringia (Hoffecker 1993). However, the BLB's environment acted as a filter that slowed or prevented the dispersal of some arthropods. For example, the leaf beetle *Phaedon armoraciae* (Chrysomelidae) colonized both sides of the Bering Strait while its congeners, *P. concinnus* and *P. cyanescens*, were relegated to the western and eastern sides, respectively (Elias and Crocker 2008). A xeric steppe-tundra prevailed on the BLB during the last glacial maximum

(Young 1982). This facilitated the east-west dispersal of tundra insects (Vila et al. 2011) but prohibited the spread of obligate forest-dwellers. Indeed, recent revisions of supposedly Holarctic forest insects in several taxa have found that most were in fact sister species with distinct Palearctic and Nearctic distributions (Kimsey and Carpenter 2012, Sikes et al. 2016, Brunke et al. 2019). The boreal forest expanded rapidly after glaciation and provided forest arthropods an unbroken dispersal corridor across North America (Payette et al. 2002). At the same time, many steppe-tundra species became relegated to small refugia on south facing bluffs or in the alpine zone (Bishop and Armbruster 1999, Roland and Schmidt 2015, Edwards et al. 2018).

Here, we summarize the geographical distributional patterns of beetle and spider assemblages in Denali National Park and Preserve (DNPP), Alaska. DNPP is uniquely positioned at the southern border of Beringia. Park land north of the Alaska Range was unglaciated, while the mountains and land to the south were covered by alpine glaciers and the Cordilleran ice sheet (Kaufman et al. 2011) (Fig. 3.1). Graminoid tundra predominated in DNPP lowlands prior to the establishment of conifer forests around 6500 ya (Elias et al. 1996). Similar conditions persist today in alpine tundra, which is believed to be a refugium for previously widespread Beringian vascular plants (Roland and Schmidt 2015, Edwards et al. 2018). Based on previous results (see Chapter 2), indicating community-level assemblages related to habitat preference (forest, shrub, and alpine tundra), we evaluated arthropods based on their geographic distributions to see if there were community-level patterns. We tested two hypotheses: 1) forest communities support relatively fewer Holarctic species because they were unable to cross the BLB, and 2) alpine tundra communities support a relatively greater richness of Amphi-Beringian species and

Alaska–Yukon endemics because they were unable to disperse out of Beringia at the end of the Pleistocene.

3.3 Methods

We collected beetles and spiders from 15 localities in the northeast foothills of the Alaska Range in DNPP (Fig. 3.1). Sites were classified as forest, tall shrubs, or alpine tundra based on elevation and dominant vegetation cover. Arthropod sampling took place during the summers of 2016 – 2018 using a combination of pitfall traps, litter samples processed via Winkler funnels, and hand collecting. A more detailed description of our study design and collecting methods can be found in Chapter 2.

Geographic distribution records were downloaded from the Global Biodiversity Information Facility (GBIF) (GBIF.org 2020), which aggregates records from institutions around the world, including the University of Alaska Museum Insect Collection. We filtered the results to include only records based on preserved specimens to eliminate fossils and unverifiable determinations. We then visually classified the resulting distribution maps into one of five categories (Fig. 3.2):

- 1) Alaska–Yukon endemic: species restricted to Alaska and Yukon Territory, Canada.
- 2) North American: species restricted to North America.
- 3) Amphi-Beringian: species that are well established on both sides of the Bering Strait but do not have complete Holarctic distributions.
- 4) Holarctic: species widely distributed across both North America and Eurasia.
- 5) Data deficient: species with no GBIF records outside of this project. Data deficient species were excluded from analyses.

There are acknowledged data limitations. Digitizing natural history collections is an ongoing effort and many records are not yet available in GBIF. Furthermore, much of the Arctic is under-sampled because of its remote and rugged terrain. Where sampling has occurred, a species may not have been collected even if present because of biased sampling methods, phenology, or random chance. Lastly, many taxa are in need of revision and could represent multiple cryptic or over-split species. Therefore, the distributions presented here are undoubtedly incomplete.

We used a chi-squared test of independence to investigate the relationship between geographic distribution and habitat preference (forest, shrub, and alpine tundra as defined in Chapter 2). Species were considered to prefer a habitat if at least 75% of all specimens were collected in the same habitat; otherwise, they were categorized as a generalist. Singletons, species represented by a single individual, were removed to avoid mis-categorizing transients. The chi-squared test p-value was calculated using a Monte Carlo simulation with 2,000 replicates because of the small sample size. Because chi-squared test results can be inaccurate when the expected values are small, we also used Fisher's exact test to verify our results (Kim 2017). Analyses were performed with the statistical software R and the MASS package (Venables and Ripley 2002, R Core Team 2018).

3.4 Results

We collected 155 beetle species and 179 spider species. Sufficient GBIF occurrence data were available for all but eight species (Table 3.1 & 3.2). North American and Holarctic distributions were the most common and accounted for 55% (180 species) and 32% (104) of species, respectively. Only 6% (19) of species had an Amphi-Beringian distribution, and 7% (24)

were Alaska–Yukon endemics. Proportions were similar between beetles and spiders, with the notable exception that beetles were twice as likely to be Alaska–Yukon endemics (11% versus 5%).

We assessed habitat preference for the 257 non-singleton species (Table 3.3) with a chi-square test of independence and found no significant relationship between habitat preference and geographic distribution of beetles and spiders ($\chi^2 = 8.612$, $p = 0.4668$). Fisher’s exact test also failed to reject the null hypothesis of no relationship ($p = 0.5149$).

3.5 Discussion

The steppe-tundra environment of the BLB was a biological filter that blocked the dispersal of some arthropods. It stands to reason that species with similar habitat requirements experienced similar barriers to dispersal. We were unable to detect a significant relationship between habitat preference and geographic distribution for ground-dwelling arthropods in DNPP (Table 3.3). However, it should be noted that the imperfect nature of GBIF data and the unresolved taxonomy of most arthropods contributed error, and trends in the data were consistent with both hypotheses.

We predicted forest communities would contain fewer Holarctic species. The forests of North American and Eurasian have not been contiguous since the opening of the Bering Strait ~4.8 mya and are today separated by 1400 km (Payette et al. 2002). Forest species are therefore unlikely to be able to maintain gene flow between continents and avoid allopatric speciation (Brunke et al. 2019). Nevertheless, we recorded 10 forest species with a Holarctic distribution (Table 2.1 & 2.2). However, DNA barcode sequences available in the Barcode of Life Database (Ratnasingham and Hebert 2007) indicate that at least three of these species, *Microneta viaria*,

Tachinus basalis, and *Dryocoestes autographus*, have distinct Palearctic and Nearctic populations that may be distinct species. *Dryocoestes autographus* is interesting because it feeds and reproduces in the phloem layer of spruce trees (*Piceae* sp.) and is a clear forest obligate (Bright 1963). They are strong fliers known to disperse up to 171 km beyond the northern spruce limit, but this represents only one-eighth of the distance required to disperse between continents (Nilssen 1984). After accounting for these species, we see a trend towards fewer Holarctic species among forest communities. Additionally, our collection methods were inadequate for sampling arthropods that live on or inside of trees. Presumably, obligate tree-associates are the least-likely members of the forest community to have dispersed across the BLB, and we have therefore likely underestimated the proportion of NAM species in forest communities. Correcting for this would likely further strengthen the trend.

Alpine tundra had the greatest proportion of Alaska–Yukon endemics, consistent with the hypothesis that the alpine zone is a refugium for Beringian species (Roland and Schmidt 2015; Edwards et al. 2018). Other potential refugia are the small patches of subarctic steppe that persist on south facing bluffs. Elsewhere in Alaska, these patches are known to harbor locally endemic Beringian insects (Edwards et al. 2018). Steppe is uncommon in DNPP and restricted to the warmest and driest slopes (Hooge et al. 2006). This relict habitat may better represent BLB environmental conditions than alpine tundra.

Both hypotheses were based on the assumption that the BLB environment was homogenous tundra, but the BLB covered an area of 1.5 million km² and almost certainly comprised a mosaic of habitats (Guthrie 1982, Edwards and Armbruster 1989, Yurtsev 2001, Elias and Crocker 2008). Fossil insect remains suggests that in addition to tundra, there existed at various times forest, flood plain, desert, and grassland (Matthews 1982, Young 1982).

Furthermore, the BLB environment was temporally dynamic, and the flooding of the Bering Strait during interglacials periodically reset the BLB environment. It is probable that some forest and shrub species crossed via “steppingstones” of suitable habitat or during periods of favorable conditions, making community-level patterns difficult to detect. Nevertheless, taxonomic revisions and more complete distribution data may reveal these patterns and improve our understanding of Pleistocene dispersal.

3.6 References

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3.7 Figures

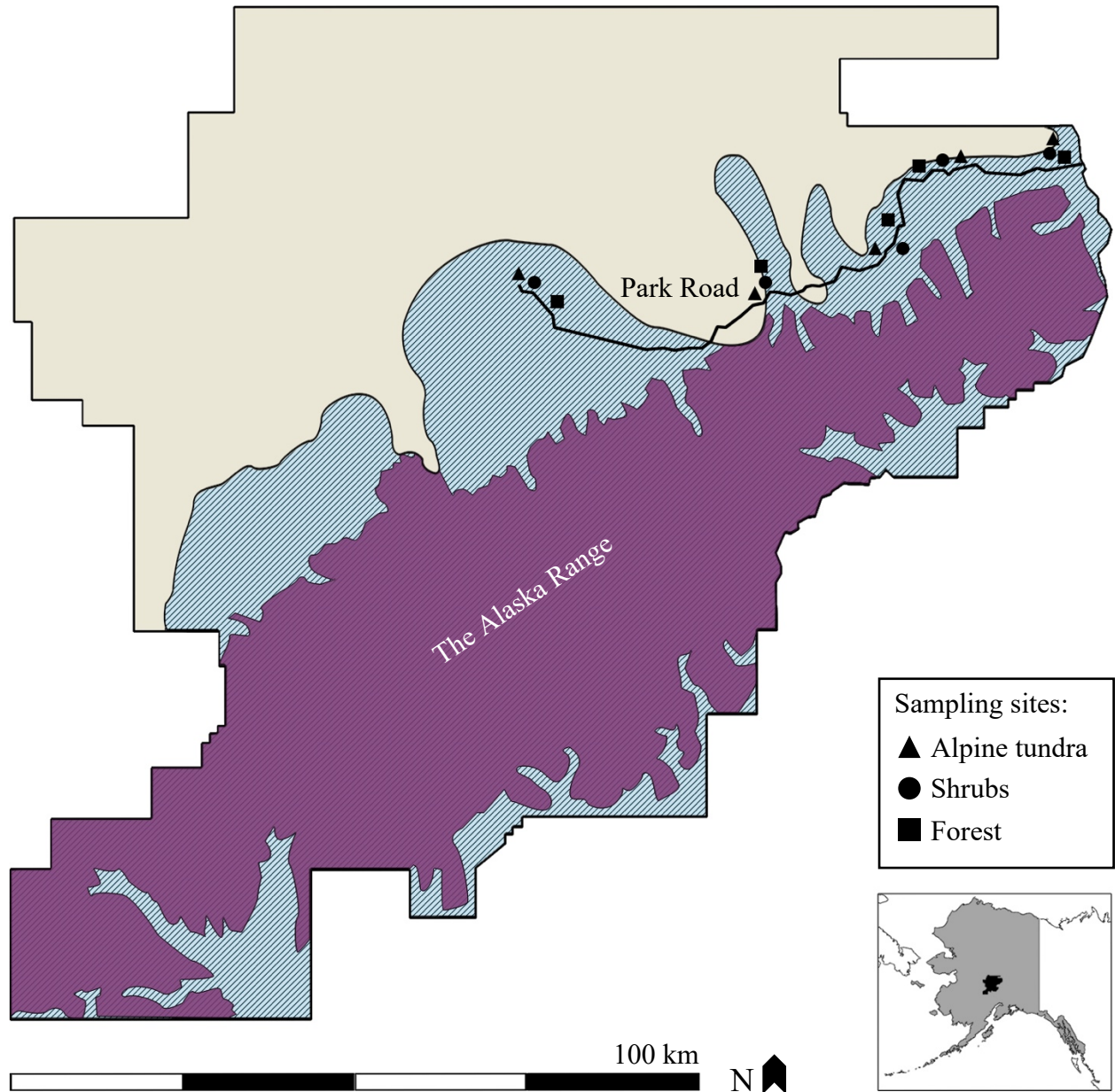


Figure 3.1: Maximum extent of glacialiation in Denali National Park and Preserve, Alaska. The blue hatching indicates glaciated areas. Purple hatching indicates the modern boundary of the Alaska Range, which was glaciated throughout most of the Pleistocene. We sampled arthropods from 15 sites along the Park Road north of the Alaska Range. Sites represented three different habitats. Figure adapted from Kaufman et al. (2011).

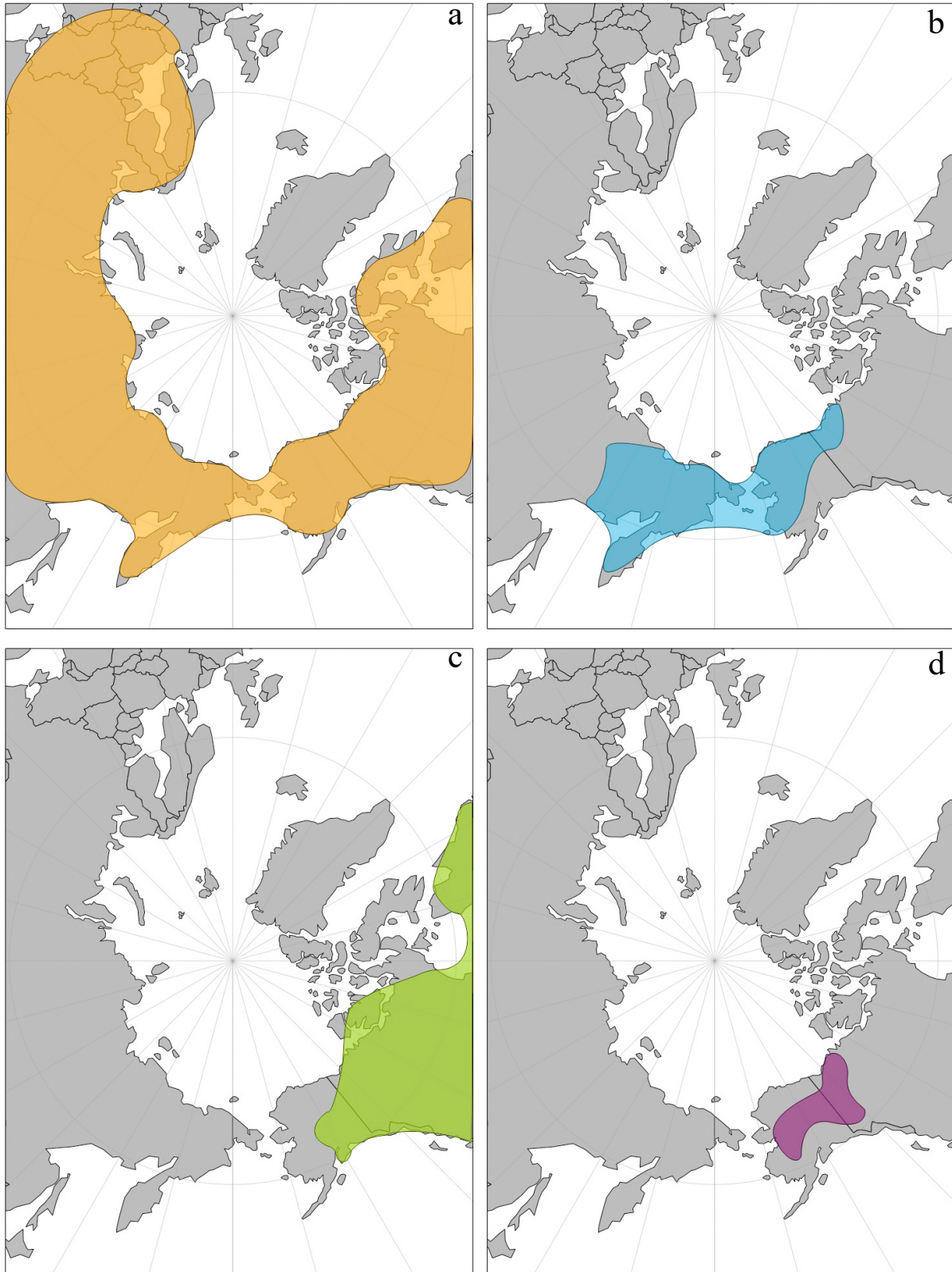


Figure 3.2: Examples of geographical distributions: a) Holarctic, b) Amphi-Beringian, c) North American, d) Alaska–Yukon endemic.

3.8 Tables

Table 3.1: Summary of beetle geographic distributions for 155 species collected in Denali National Park and Preserve, Alaska.

Alaska–Yukon endemics (16)				
<i>Antherophagus suturalis</i>	<i>Colon liebecki</i>	<i>Dorytomus alaskanus</i>	<i>Neohypdonus restrictulus</i>	<i>Proteinus parvulus</i>
<i>Atomaria kamtschatica</i>	<i>Dendroctonus punctatus</i>	<i>Dorytomus frostii</i>	<i>Olophrum latum</i>	<i>Tachinus instabilis</i>
<i>Atomaria tenebrosa</i>	<i>Denticollis varians</i>	<i>Dorytomus lecontei</i>	<i>Proteinus limbatus</i>	<i>Pterostichus bryanti</i>
<i>Bellatheta microptera</i>				
North American (80)				
<i>Agathidium angulares</i>	<i>Byturus unicolor</i>	<i>Dorytomus leucophyllus</i>	<i>Neothetalia canadiana</i>	<i>Quedius molochinoides</i>
<i>Agathidium athabascanum</i>	<i>Caenocara scymnoides</i>	<i>Dorytomus mannerheimi</i>	<i>Neothetalia pallitarsis</i>	<i>Quedius simulator</i>
<i>Agoliinus piceatus</i>	<i>Calathus ingratus</i>	<i>Eanus decoratus</i>	<i>Notiophilus borealis</i>	<i>Scaphium castanipes</i>
<i>Aleochara castaneipennis</i>	<i>Carabus chamissonis</i>	<i>Hypnoidus bicolor</i>	<i>Notiophilus semistriatus</i>	<i>Sericus incongruus</i>
<i>Anthaxia expansa</i>	<i>Catops luridipennis</i>	<i>Ischnosoma fimbriatum</i>	<i>Orthocis punctatus</i>	<i>Silusa californica</i>
<i>Ascoliocerus sanborni</i>	<i>Ceratomegilla ulkei</i>	<i>Lepidophorus lineaticollis</i>	<i>Oxypoda frigida</i>	<i>Stenus austini</i>
<i>Atheta capsularis</i>	<i>Chaetocnema protensa</i>	<i>Liogluta granulosa</i>	<i>Oxypoda sylvia</i>	<i>Stenus noctivagus</i>
<i>Atheta prudhoensis</i>	<i>Coccinella transversoguttata</i>	<i>Lordithon fungicola</i>	<i>Pseudanostirus ochreipennis</i>	<i>Sylvanelater mendax</i>
<i>Atheta stercoris</i>	<i>Colon discretum</i>	<i>Lypoglossa angularis</i>	<i>Pterostichus barryorum</i>	<i>Tachinus frigidus</i>
<i>Atheta terranova</i>	<i>Cryptophagus bidentatus</i>	<i>Megarthus angulicollis</i>	<i>Pterostichus hudsonicus</i>	<i>Tachinus quebecensis</i>
<i>Bembidion concolor</i>	<i>Cryptophagus difficilis</i>	<i>Micropeplus laticollis</i>	<i>Pterostichus riparius</i>	<i>Tachyporus canadensis</i>
<i>Boreophila nomensis</i>	<i>Curimopsis moosilauke</i>	<i>Mniusa yukonensis</i>	<i>Quedionuchus plagiatus</i>	<i>Tachyporus nimbicola</i>
<i>Boreostiba parvipennis</i>	<i>Cymindis unicolor</i>	<i>Mordellaria borealis</i>	<i>Quedius brunnipennis</i>	<i>Tachyporus rulomus</i>
<i>Bryophacis smetanai</i>	<i>Cytilus alternatus</i>	<i>Mycetoporus americanus</i>	<i>Quedius criddlei</i>	<i>Tetratoma concolor</i>
<i>Byrrhus cyclophorus</i>	<i>Dicheirotichus mannerheimii</i>	<i>Mycetoporus rugosus</i>	<i>Quedius frigidus</i>	<i>Thanatophilus sagax</i>
<i>Byrrhus geminatus</i>	<i>Dorytomus laticollis</i>	<i>Nebria frigida</i>	<i>Quedius labradorensis</i>	<i>Tychius tectus</i>
Amphi-Beringian (7)				
<i>Atomaria elongatula</i>	<i>Diacheila polita</i>	<i>Nicrophorus vespilloides</i>	<i>Olisthaerus megacephalus</i>	<i>Planolinoides borealis</i>
<i>Carabus truncaticollis</i>	<i>Leiodes punctulata</i>			

Table 3.1: Continued.

Holarctic (47)				
<i>Acidota crenata</i>	<i>Caenoscelis ferruginea</i>	<i>Dyschirius melancholicus</i>	<i>Mycetoporus nigrans</i>	<i>Quedius fellmani</i>
<i>Acidota quadrata</i>	<i>Cartodere constricta</i>	<i>Eucnecosum brachypterum</i>	<i>Olophrum boreale</i>	<i>Quedius fulvicollis</i>
<i>Adalia bipunctata</i>	<i>Catops alpinus</i>	<i>Eucnecosum brunnescens</i>	<i>Olophrum consimile</i>	<i>Sericoda quadripunctata</i>
<i>Amara alpina</i>	<i>Catops luteipes</i>	<i>Gonioctena nivosa</i>	<i>Olophrum rotundicolle</i>	<i>Stereocerus haematopus</i>
<i>Amara brunnea</i>	<i>Coccinella trifasciata</i>	<i>Harpalus laevipes</i>	<i>Pachyta lamed</i>	<i>Tachinus basalis</i>
<i>Amara hyperborea</i>	<i>Corticarina arctophila</i>	<i>Harpalus nigratarsis</i>	<i>Phloeostiba lapponica</i>	<i>Tachinus elongatus</i>
<i>Atheta munsteri</i>	<i>Cryptophagus corticinus</i>	<i>Hippodamia arctica</i>	<i>Pterostichus adstrictus</i>	<i>Tachyporus nitidulus</i>
<i>Bembidion grapii</i>	<i>Cryptophagus lapponicus</i>	<i>Hypera diversipunctata</i>	<i>Pterostichus brevicornis</i>	
<i>Bolitobius cingulatus</i>	<i>Cryptophagus tuberculosus</i>	<i>Ischnosoma splendidum</i>	<i>Pterostichus pinguedineus</i>	
<i>Bromius obscurus</i>	<i>Dryocoetes autographus</i>	<i>Miscodera arctica</i>	<i>Pterostichus ventricosus</i>	
Data deficient (5)				
<i>Agathidium repentinum</i>	<i>Agonum quinquepunctatum</i>	<i>Corticaria ferruginea</i>	<i>Leiodes rhaetica</i>	<i>Loborhynchapion cyanitinctum</i>

Table 3.2: Summary of spider geographic distributions for 180 species collected in Denali National Park and Preserve, Alaska.

Alaska–Yukon endemics (8)				
<i>Bathypantes umiatus</i>	<i>Oreoneta arctica</i>	<i>Procerocymbium sibiricum</i>	<i>Spiracme triangulosus</i>	<i>Tibioplus diversus</i>
<i>Horcotes strandi</i>	<i>Oreoneta fortyukon</i>	<i>Scotinotylus protervus</i>		
North American (100)				
<i>Acanthoneta aggressa</i>	<i>Ceratinella acerea</i>	<i>Hackmania saphes</i>	<i>Pardosa mackenziana</i>	<i>Sisis rotundus</i>
<i>Agelenopsis utahana</i>	<i>Chalcoscirtus alpicola</i>	<i>Hahnia glacialis</i>	<i>Pardosa moesta</i>	<i>Sittisax ranieri</i>
<i>Agnyphantes arboreus</i>	<i>Chalcoscirtus glacialis</i>	<i>Hilaira vexatrix</i>	<i>Pardosa podhorskii</i>	<i>Tapinocyba bicarinata</i>
<i>Agroeca ornata</i>	<i>Clubiona bryantae</i>	<i>Hybauchenidium gibbosum</i>	<i>Pardosa xerampelina</i>	<i>Tapinocyba cameroni</i>
<i>Agyneta allosubtilis</i>	<i>Clubiona canadensis</i>	<i>Hypsosinga groenlandica</i>	<i>Phlathothranta parva</i>	<i>Tapinocyba prima</i>
<i>Agyneta jacksoni</i>	<i>Clubiona praematura</i>	<i>Incestophantes duplicatus</i>	<i>Pirata bryantae</i>	<i>Thanatus arcticus</i>
<i>Agyneta protrudens</i>	<i>Dendryphantes nigromaculatus</i>	<i>Incestophantes washingtoni</i>	<i>Pityohyphantes subarcticus</i>	<i>Titanoeca nigrella</i>
<i>Agyneta simplex</i>	<i>Dictyna alaskae</i>	<i>Leptyphantes alpinus</i>	<i>Pocadicnemis occidentalis</i>	<i>Titanoeca nivalis</i>
<i>Alopecosa pictilis</i>	<i>Dictyna minuta</i>	<i>Mecynargus tungusicus</i>	<i>Pociloneta calcaratus</i>	<i>Tunagyna debilis</i>
<i>Arctobius agelenoides</i>	<i>Diplocentria perplexa</i>	<i>Micaria constricta</i>	<i>Pociloneta theridiformis</i>	<i>Walckenaeria auranticeps</i>
<i>Arctosa insignita</i>	<i>Dismodicus decemoculatus</i>	<i>Micrargus longitarsus</i>	<i>Robertus arcticus</i>	<i>Walckenaeria castanea</i>
<i>Arctosa littoralis</i>	<i>Drassodes mirus</i>	<i>Microlinyphia mandibulata</i>	<i>Robertus fuscus</i>	<i>Walckenaeria communis</i>
<i>Bathypantes brevipes</i>	<i>Enoplognatha intrepida</i>	<i>Oreoneta brunnea</i>	<i>Sciastes truncatus</i>	<i>Walckenaeria directa</i>
<i>Bathypantes eumenis</i>	<i>Enoplognatha marmorata</i>	<i>Oreonetides beringianus</i>	<i>Scotinotylus alpinus</i>	<i>Xysticus britcheri</i>
<i>Bathypantes pallidus</i>	<i>Eris militaris</i>	<i>Pardosa albomaculata</i>	<i>Scotinotylus majesticus</i>	<i>Xysticus canadensis</i>
<i>Ceraticelus alticeps</i>	<i>Evarcha proshynskii</i>	<i>Pardosa algens</i>	<i>Semljicola obtusus</i>	<i>Xysticus durus</i>
<i>Ceraticelus crassiceps</i>	<i>Gnaphosa borea</i>	<i>Pardosa concinna</i>	<i>Sisicottus montanus</i>	<i>Xysticus gosiutus</i>
<i>Ceraticelus fissiceps</i>	<i>Gnaphosa brumalis</i>	<i>Pardosa dorsuncata</i>	<i>Sisicottus nesides</i>	<i>Xysticus keyserlingi</i>
<i>Ceraticelus laticeps</i>	<i>Gnaphosa orites</i>	<i>Pardosa furcifera</i>	<i>Sisicottus orites</i>	<i>Zelotes sula</i>
<i>Ceraticelus silus</i>	<i>Gonatium crassipalpus</i>	<i>Pardosa fuscula</i>	<i>Sisicottus panopeus</i>	<i>Zornella armata</i>
Amphi-Beringian (12)				
<i>Agyneta conigera</i>	<i>Agyneta rurestris</i>	<i>Islandiana cristata</i>		<i>Psammitis deichmanni</i>
<i>Agyneta decora</i>	<i>Arctella lapponica</i>	<i>Islandiana falsifica</i>		<i>Scotinotylus sacer</i>
<i>Agyneta maritima</i>	<i>Hybauchenidium aquilonare</i>	<i>Micrargus apertus</i>		<i>Walckenaeria fraudatrix</i>

Table 3.2: Continued.

Holarctic (57)				
<i>Agyneta olivacea</i>	<i>Diplocephalus barbiger</i>	<i>Hypselistes jacksoni</i>	<i>Oreonetides vaginatus</i>	<i>Semljicola lapponicus</i>
<i>Alopecosa aculeata</i>	<i>Diplocephalus subrostratus</i>	<i>Improphantes complicatus</i>	<i>Ozyptila arctica</i>	<i>Sisicus apertus</i>
<i>Arctosa alpigena</i>	<i>Dismodicus bifrons</i>	<i>Ivielum sibiricum</i>	<i>Ozyptila sincera</i>	<i>Styloctetor compar</i>
<i>Baryphyma trifrons</i>	<i>Enoplognatha caricis</i>	<i>Lathys alberta</i>	<i>Pardosa hyperborea</i>	<i>Thanatus formicinus</i>
<i>Canalidion montanum</i>	<i>Estrandia grandaeva</i>	<i>Macrargus multesimus</i>	<i>Pardosa lapponica</i>	<i>Tibellus maritimus</i>
<i>Centromerus sylvaticus</i>	<i>Gnaphosa microps</i>	<i>Maso sundevalli</i>	<i>Pardosa modica</i>	<i>Tiso aestivus</i>
<i>Clubiona kulczynskii</i>	<i>Gnaphosa muscorum</i>	<i>Metopobactrus prominulus</i>	<i>Pardosa palustris</i>	<i>Walckenaeria atrotibialis</i>
<i>Cnephalocotes obscurus</i>	<i>Hackmania prominula</i>	<i>Micaria aenea</i>	<i>Pardosa tesquorum</i>	<i>Walckenaeria clavicornis</i>
<i>Collinsia holmgreni</i>	<i>Hahnia ononidum</i>	<i>Micaria alpina</i>	<i>Pardosa uintana</i>	<i>Walckenaeria karpinskii</i>
<i>Dictyna major</i>	<i>Haplodrassus hiemalis</i>	<i>Micaria tripunctata</i>	<i>Philodromus rufus</i>	<i>Xysticus emertoni</i>
<i>Diplocentria bidentata</i>	<i>Haplodrassus signifer</i>	<i>Microneta viaria</i>	<i>Poecilometes variegata</i>	<i>Xysticus luctuosus</i>
<i>Diplocentria rectangulata</i>	<i>Hilaira herniosa</i>			
Data deficient (2)				
<i>Hilaira gibbosa</i>	<i>Hilaira sibirica</i>			

Table 3.3: Chi-squared test for independence results, $\chi^2 = 8.612$, $p = 0.4668$. Distributions are Amphi-Beringian (AB), Alaska–Yukon endemics (AK), Holarctic (HOL), and North American (NAM). Expected values are given in parenthesis.

Distribution	Forest	Shrub	Tundra	Generalist	Total
AB	2 (1.9)	1 (2.5)	3 (2.8)	9 (7.8)	15
AK	1 (2.7)	3 (3.5)	7 (3.9)	10 (10.9)	21
HOL	10 (11.2)	16 (14.6)	11 (16.2)	50 (45)	87
NAM	20 (17.2)	23 (22.4)	27 (25)	64 (69.3)	134
Total	33	43	48	133	257

Chapter 4: General Conclusion

Elevational shifts in vegetation cover in response to anthropogenic climate change are causing a worldwide reduction in alpine tundra (Wang et al. 2012). The effects are especially pronounced in Denali National Park and Preserve (DNPP), Alaska, which is warming faster than the global average (Serreze et al. 2000, Meyer et al. 2014). The expansion of woody vegetation is likely to alter alpine arthropod communities. Ground-dwelling beetles and spiders were most diverse in the alpine tundra, and alpine tundra communities included a high proportion of unique species. Among these were Beringian endemics that have survived there since the end of the Pleistocene. Alpine arthropods perform critical ecosystem services such as pollination and decomposition. They are also an important food source for DNPP's vertebrates including nesting shorebirds (Gill et al. 2015), songbirds (e.g. Antor 1995), and brown bears (*Ursus arctos*) (Chapman et al. 1955). The loss of arthropod species could therefore have cascading effects throughout the ecosystem. Considering that the alpine tundra also supports DNPP's greatest diversity of vascular plants (Roland and Schmidt 2015), a substantial portion of DNPP's biodiversity is at risk from habitat loss. Long-term monitoring is needed to evaluate how alpine communities change and the ecological consequences thereof.

This study represented the largest effort to catalog DNPP's terrestrial arthropod fauna. However, my study area represented only a fraction of DNPP's 24,000 km², much of which has never been sampled. Of particular interest is the land south of the Alaska Range. This area has a warmer and wetter climate and likely contains species absent from the northern region. Likewise, my collection methods only targeted arthropods living on the ground or in the leaf litter. Additional methods are needed to sample arboreal, subterranean, and subcortical beetles and

spiders. This study therefore represents only a small step towards a complete inventory of DNPP's arthropod fauna.

4.1 Future Directions

This study was the beginning of a long-term arthropod monitoring project in DNPP, with the intention of resampling my study plots approximately every ten years. Several changes can be made to the sampling protocol to improve future efforts. First, I suggest that pitfall samples not be pooled. I pooled pitfall trap contents from each sample because pooling reduced the cost of supplies and simplified sample processing. However, it greatly reduced my statistical power. For example, I was unable to detect a significant difference in Chao1 estimated species richness even though the means differed by over 25%. Keeping the pitfall contents separate would allow for the calculation of a mean and variance for each sample. It would also eliminate the need to weigh the linear regressions by the number of surviving pitfall traps because destroyed traps could simply be removed from the data set.

Second, I suggest that temperature loggers should always be deployed contemporaneously with pitfall traps. Pitfall traps are biased towards more active species, and individual activity increases with temperature (Saska et al. 2013). Abundance estimates can be corrected for temperature bias using exponential models if the air temperature at the time of collection is known. I was unable to do this because I did not deploy temperature loggers in 2016 and 2017.

Third, our understanding of the relationship between arthropod communities and vegetation can be improved by conducting taxonomic vegetation surveys rather than growth-form surveys. Plant species richness has been shown to be strongly correlated with arthropod

species richness (Haddad 2009, Ebeling 2018). Furthermore, the relative proportions of specific plant species can alter arthropod community composition (Bangert et al. 2013). Plant species richness is known to vary among habitats in DNPP (Roland and Schmidt 2015). I observed differing proportions of willow, alder, and birch among my shrub plots. Taxonomic vegetation surveys would allow us to explicitly test hypotheses regarding the relationship between plant and arthropod species richness, and also compare community composition among shrub plots.

Finally, I sampled sites between 595 – 1252 m, but alpine tundra extends to approximately 2,000 m. While hiking near this elevation, I have observed that the plant community appears different from that of my alpine tundra study plots, with fewer dwarf and prostrate shrubs and more herbs, graminoids, and lichens. I suspect these elevations may also contain an arthropod community that differs from that of lower elevation tundra.

These modifications will not interfere with inter-annual comparisons because they do not alter the core sampling procedure; they merely add complexity allowing for additional analyses and more robust inferences.

4.2 References

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Appendix

This checklist includes all extant arthropods known from Denali National Park and Preserve (DNPP), Alaska, based on the results of this project and records from a literature search. The boundaries of DNPP have been expanded several times since its establishment in 1917. This list includes all records from within the modern park boundaries, regardless of the area's designation at the time of collection. Higher taxa are arranged phylogenetically, and species/genera are arranged alphabetically within each family. Subfamilies were included for the most speciose families. Synonyms are not included. More detailed records for these species, including specific localities, collection dates, identification determiner, and source publications, can be found in the Arctos database at <https://arctos.database.museum/saved/DenaliNP>.

Prior to the start of this project, only 354 species or genera were known from DNPP. After this project, the number has been increased to 814. Many specimens from this project have yet to be identified so this number is undoubtedly an underestimate of DNPP's true biodiversity.

Table A1: Denali National Park and Preserve, Alaska, arthropod checklist.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Arachnida	Acari			
	Araneae			
		Agelenidae	<i>Agelenopsis utahana</i>	(Chamberlin & Ivie, 1933)
		Amaurobiidae	<i>Arctobius agelenoides</i>	(Emerton, 1919)
		Araneidae	<i>Araneus nordmanni</i> <i>Araneus saevus</i> <i>Araniella proxima</i> <i>Hypsosinga groenlandica</i>	(Thorell, 1870) (Koch, 1872) (Kulczyński, 1885) Simon, 1889
		Clubionidae	<i>Clubiona bryantae</i> <i>Clubiona canadensis</i> <i>Clubiona kulczynskii</i> <i>Clubiona praematura</i>	Gertsch, 1941 Emerton, 1890 Lessert, 1905 Emerton, 1909
		Dictynidae	<i>Arctella lapponica</i> <i>Dictyna alaskae</i> <i>Dictyna major</i> <i>Dictyna minuta</i> <i>Emblyna annulipes</i> <i>Hackmania prominula</i> <i>Hackmania saphes</i> <i>Lathys alberta</i>	Holm, 1945 Chamberlin & Ivie, 1947 Menge, 1869 Emerton, 1888 (Blackwall, 1846) (Tullgren, 1948) (Chamberlin, 1948) Gertsch, 1946
		Gnaphosidae	<i>Drassodes mirus</i> <i>Gnaphosa borea</i> <i>Gnaphosa brumalis</i> <i>Gnaphosa microps</i> <i>Gnaphosa muscorum</i> <i>Gnaphosa orites</i> <i>Haplodrassus hiemalis</i> <i>Haplodrassus signifer</i> <i>Micaria aenea</i> <i>Micaria alpina</i> <i>Micaria constricta</i> <i>Micaria tripunctata</i> <i>Zelotes sula</i>	Platnick & Shadab, 1976 Kulczyński, 1908 Thorell, 1875 Holm, 1939 (Koch, 1866) Chamberlin, 1922 (Emerton, 1909) (Koch, 1839) Thörell, 1871 Koch, 1872 Emerton, 1894 Holm, 1978 Lowrie & Gertsch, 1955
		Hahniidae	<i>Hahnia glacialis</i> <i>Hahnia ononidum</i> <i>Neoantistea magna</i>	Sørensen, 1898 Simon, 1875 (Keyserling, 1887)
		Linyphiidae (Erigoninae) (Linyphiinae)	<i>Acanthoneta aggressa</i> <i>Agniphantes arboreus</i> <i>Agyneta allosubtilis</i> <i>Agyneta conigera</i> <i>Agyneta decora</i> <i>Agyneta jacksoni</i> <i>Agyneta maritima</i> <i>Agyneta mollis</i> <i>Agyneta olivacea</i>	(Chamberlin & Ivie, 1943) (Emerton, 1915) Loksa, 1965 (Pickard-Cambridge, 1863) (Pickard-Cambridge, 1871) (Brandegaard, 1937) (Emerton, 1919) (Pickard-Cambridge, 1871) (Emerton, 1882)

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Arachnida	Araneae	Linyphiidae (Linyphiinae)	<i>Agyneta protrudens</i>	(Chamberlin & Ivie, 1933)
			<i>Agyneta rurestris</i>	(Koch, 1836)
			<i>Baryphyma trifrons</i>	(Pickard-Cambridge, 1863)
			<i>Bathyphantes brevipes</i>	(Emerton, 1917)
			<i>Bathyphantes eumenis</i>	(Koch, 1879)
			<i>Bathyphantes pallidus</i>	(Banks, 1892)
			<i>Bathyphantes umiatus</i>	Ivie, 1969
			<i>Centromerus sylvaticus</i>	(Blackwall, 1841)
			<i>Ceraticelus alticeps</i>	(Fox, 1891)
			<i>Ceraticelus crassiceps</i>	Chamberlin & Ivie, 1939
			<i>Ceraticelus fissiceps</i>	(Pickard-Cambridge, 1874)
			<i>Ceraticelus laticeps</i>	(Emerton, 1894)
			<i>Ceraticelus silus</i>	Dondale, 1958
			<i>Ceratinella acerea</i>	Chamberlin & Ivie, 1933
			<i>Ceratinella brunnea</i>	Emerton, 1882
			<i>Cnephalocotes obscurus</i>	(Blackwall, 1834)
			<i>Collinsia holmgreni</i>	(Thorell, 1871)
			<i>Diplocentria bidentata</i>	(Emerton, 1882)
			<i>Diplocentria perplexa</i>	(Chamberlin & Ivie, 1939)
			<i>Diplocentria rectangulata</i>	(Emerton, 1915)
			<i>Diplocephalus barbiger</i>	(Roewer, 1955)
			<i>Diplocephalus subrostratus</i>	(Pickard-Cambridge, 1873)
			<i>Dismodicus bifrons</i>	(Blackwall, 1841)
			<i>Dismodicus decemoculatus</i>	(Emerton, 1882)
			<i>Entelecara sombra</i>	(Chamberlin & Ivie, 1947)
			<i>Erigone arctica</i>	Chamberlin & Ivie, 1947
			<i>Erigone atra</i>	Blackwall, 1833
			<i>Estrandia grandaeva</i>	(Keyserling, 1886)
			<i>Eulaira arctoa</i>	Holm, 1960
			<i>Gnathonarium taczanowskii</i>	(Pickard-Cambridge, 1873)
			<i>Gonatium crassipalpus</i>	Bryant, 1933
			<i>Halorates holmgrenii</i>	(Thorell, 1871)
			<i>Hilaira gibbosa</i>	Tanasevitch, 1982
			<i>Hilaira herniosa</i>	(Thorell, 1875)
			<i>Hilaira sibirica</i>	Eskov, 1987
			<i>Hilaira vexatrix</i>	(Pickard-Cambridge, 1877)
			<i>Horcotes strandi</i>	(Sytshevskaja, 1935)
			<i>Hybauchenidium aquilonare</i>	(Koch, 1879)
			<i>Hybauchenidium gibbosum</i>	(Sørensen, 1898)
			<i>Hypselistes florens</i>	(Pickard-Cambridge, 1875)
			<i>Hypselistes jacksoni</i>	(Pickard-Cambridge, 1903)
			<i>Improphantes complicatus</i>	(Emerton, 1882)
			<i>Incestophantes duplicatus</i>	(Emerton, 1913)
			<i>Incestophantes washingtoni</i>	(Zorsch, 1937)
			<i>Islandiana cristata</i>	Eskov, 1987
			<i>Islandiana falsifica</i>	(Keyserling, 1886)
			<i>Islandiana princeps</i>	Braendegaard, 1932
			<i>Ivielum sibiricum</i>	Eskov, 1988
			<i>Lepthyphantes alpinus</i>	(Emerton, 1882)
			<i>Macrargus multesimus</i>	(Pickard-Cambridge, 1875)
			<i>Maso sundevalli</i>	(Westring, 1851)
			<i>Mecynargus tungusicus</i>	(Eskov, 1981)
			<i>Metopobactrus prominulus</i>	(Pickard-Cambridge, 1873)

Table A1: Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS/SPECIES	AUTHOR(S)
Arachnida	Araneae	Linyphiidae (Linyphiinae)	<i>Micrargus apertus</i>	(Pickard-Cambridge, 1871)
			<i>Micrargus longitarsus</i>	(Emerton, 1882)
			<i>Microlinyphia mandibulata</i>	(Emerton, 1882)
			<i>Microneta viaria</i>	(Blackwall, 1841)
			<i>Oedothorax</i> sp.	Bertkau, 1883
			<i>Oreoneta arctica</i>	(Holm, 1960)
			<i>Oreoneta brunnea</i>	(Emerton, 1882)
			<i>Oreoneta fortyukon</i>	Saaristo & Marusik, 2003
			<i>Oreoneta leviceps</i>	(Koch, 1879)
			<i>Oreonetides beringianus</i>	Eskov, 1991
			<i>Oreonetides vaginatus</i>	(Thorell, 1872)
			<i>Phlathothranta parva</i>	(Kulczyński, 1926)
			<i>Pityohyphantes subarcticus</i>	Chamberlin & Ivie, 1943
			<i>Pocadicnemis occidentalis</i>	Millidge, 1976
			<i>Poeciloneta bihamata</i>	(Emerton, 1882)
			<i>Poeciloneta calcaratus</i>	(Emerton, 1909)
			<i>Poeciloneta theridiformis</i>	(Emerton, 1911)
			<i>Poeciloneta variegata</i>	(Blackwall, 1841)
			<i>Procerocymbium sibiricum</i>	Eskov, 1989
			<i>Sciastes truncatus</i>	(Emerton, 1882)
			<i>Scotinotylus alpinus</i>	(Banks, 1896)
			<i>Scotinotylus majesticus</i>	(Chamberlin & Ivie, 1947)
			<i>Scotinotylus protervus</i>	(Koch, 1879)
			<i>Scotinotylus sacer</i>	(Crosby, 1929)
			<i>Sisicottus nesides</i>	(Chamberlin, 1921)
			<i>Sisicottus orites</i>	(Chamberlin, 1919)
			<i>Sisicottus panopeus</i>	Miller, 1999
			<i>Sisicus apertus</i>	(Holm, 1939)
			<i>Sisis rotundus</i>	(Emerton, 1925)
			<i>Styloctetor compar</i>	(Westring, 1861)
			<i>Styloctetor lehtineni</i>	Marusik & Tanasevitch, 1998
			<i>Tapinocyba bicarinata</i>	(Emerton, 1913)
			<i>Tapinocyba cameroni</i>	Dupérré & Paquin, 2007
			<i>Tapinocyba prima</i>	Dupérré & Paquin, 2005
			<i>Tibioplus diversus</i>	(Koch, 1879)
			<i>Tiso aestivus</i>	(Koch, 1872)
			<i>Tunagyna debilis</i>	(Banks, 1892)
			<i>Walckenaeria atrotibialis</i>	(Pickard-Cambridge, 1878)
			<i>Walckenaeria auranticeps</i>	(Emerton, 1882)
			<i>Walckenaeria castanea</i>	(Emerton, 1882)
			<i>Walckenaeria clavicornis</i>	(Emerton, 1882)
			<i>Walckenaeria communis</i>	(Emerton, 1882)
			<i>Walckenaeria directa</i>	(Pickard-Cambridge, 1874)
			<i>Walckenaeria fraudatrix</i>	Millidge, 1983
			<i>Walckenaeria karpinskii</i>	(Pickard-Cambridge, 1873)
			<i>Zornella armata</i>	(Banks, 1906)
		Liocranidae		
			<i>Agroeca ornata</i>	Banks, 1892
		Lycosidae		
			<i>Alopecosa aculeata</i>	(Clerck, 1757)
			<i>Alopecosa pictilis</i>	(Emerton, 1885)
			<i>Arctosa alpigena</i>	(Doleschall, 1852)

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Arachnida	Araneae	Lycosidae	<i>Arctosa insignita</i> <i>Arctosa littoralis</i> <i>Pardosa albomaculata</i> <i>Pardosa algens</i> <i>Pardosa beringiana</i> <i>Pardosa concinna</i> <i>Pardosa dorsuncata</i> <i>Pardosa furcifera</i> <i>Pardosa fuscula</i> <i>Pardosa groenlandica</i> <i>Pardosa hyperborea</i> <i>Pardosa lapponica</i> <i>Pardosa mackenziana</i> <i>Pardosa modica</i> <i>Pardosa moesta</i> <i>Pardosa palustris</i> <i>Pardosa podhorskii</i> <i>Pardosa tesquorum</i> <i>Pardosa uintana</i> <i>Pardosa xerampelina</i> <i>Pirata bryantae</i>	(Thorell, 1872) (Hentz, 1844) Emerton, 1885 (Kulczyński, 1908) Dondale & Redner, 1987 (Thorell, 1877) Lowrie & Dondale, 1981 (Thorell, 1875) (Thorell, 1875) (Thorell, 1872) (Thorell, 1872) (Thorell, 1872) (Keyserling, 1877) (Blackwall, 1846) Banks, 1892 (Linnaeus, 1758) (Kulczyński, 1907) (Odenwall, 1901) Gertsch, 1933 (Keyserling, 1877) Kurata, 1944
		Philodromidae	<i>Philodromus rufus</i> <i>Thanatus arcticus</i> <i>Thanatus formicinus</i> <i>Tibellus maritimus</i>	Walckenaer, 1826 Thorell, 1872 (Clerck, 1757) (Menge, 1875)
		Salticidae	<i>Chalcoscirtus alpicola</i> <i>Chalcoscirtus carbonarius</i> <i>Chalcoscirtus glacialis</i> <i>Dendryphantes nigromaculatus</i> <i>Eris militaris</i> <i>Evarcha proshynskii</i> <i>Sittisax ranieri</i> <i>Synageles sp.</i>	(Koch, 1876) Emerton, 1917 Caporiacco, 1935 (Keyserling, 1885) (Hentz, 1845) Marusik & Logunov, 1998 (Peckham & Peckham, 1909) Simon, 1876
		Tetragnathidae	<i>Tetragnatha laboriosa</i>	Hentz, 1850
		Theridiidae	<i>Canalidion montanum</i> <i>Enoplognatha caricis</i> <i>Enoplognatha intrepida</i> <i>Enoplognatha marmorata</i> <i>Robertus arcticus</i> <i>Robertus fuscus</i> <i>Steatoda albomaculata</i>	(Emerton, 1882) (Fickert, 1876) (Sørensen, 1898) (Hentz, 1850) (Chamberlin & Ivie, 1947) (Emerton, 1894) (De Geer, 1778)
		Thomisidae	<i>Ozyptila arctica</i> <i>Ozyptila sincera</i> <i>Psammitis deichmanni</i> <i>Spiracme triangulosus</i> <i>Xysticus britcheri</i> <i>Xysticus canadensis</i> <i>Xysticus deichmanni</i> <i>Xysticus durus</i>	Kulczyński, 1908 Kulczyński, 1926 (Sørensen, 1898) (Emerton, 1894) Gertsch, 1934 Gertsch, 1934 Sørensen, 1898 (Sørensen, 1898)

Table A1: Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS/SPECIES	AUTHOR(S)	
Arachnida	Araneae	Thomisidae	<i>Xysticus emertoni</i>	Keyserling, 1880	
			<i>Xysticus gosiutus</i>	Gertsch, 1933	
			<i>Xysticus keyserlingi</i>	Bryant, 1930	
			<i>Xysticus luctuosus</i>	(Blackwall, 1836)	
			<i>Xysticus triangulosus</i>	Emerton, 1894	
		Titanoecidae	<i>Titanoeca nigrella</i>	(Chamberlin, 1919)	
			<i>Titanoeca nivalis</i>	Simon, 1874	
		Opiliones	Phalangiiidae		
		Pseudoscorpiones	Cheliferidae	<i>Liopilio yukon</i>	Cokendolpher, 1981
<i>Chelifer cancroides</i>	(Linnaeus, 1758)				
	Chernetidae	<i>Wyochernes asiaticus</i>	(Redikorzev 1922)		
Chilopoda	Geophilomorpha				
	Lithobiomorpha				
Insecta	Protura Collembola	Isotomidae Neanuridae Sminthuridae			

Table A1: Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS/SPECIES	AUTHOR(S)
Insecta	Orthoptera		<i>Melanoplus sanguinipes</i>	(Fabricius, 1798)
		Tetrigidae	<i>Tetrix sp.</i>	Latreille, 1802
		Libellulidae	<i>Leucorrhinia sp.</i>	Brittinger, 1850
	Plecoptera	Capniidae	<i>Capnia confusa</i>	Claassen, 1936
			<i>Capnia petila</i>	Jewett, 1954
			<i>Mesocapnia variabilis</i>	(Klapálek, 1920)
		Chloroperlidae	<i>Alloperla delicata</i>	Frison, 1935
			<i>Alloperla serrata</i>	Needham & Claassen, 1925
			<i>Haploperla sp.</i>	Navás, 1934
			<i>Neaviperla forcipata</i>	(Neave, 1929)
			<i>Paraperla sp.</i>	Banks, 1906
			<i>Plumiperla diversa</i>	(Frison, 1935)
			<i>Suwallia starki</i>	Alexander & Stewart, 1999
			<i>Utaperla sopladora</i>	Ricker, 1952
			<i>Plumiperla sp.</i>	Surdick, 1985
			<i>Suwallia sp.</i>	Ricker, 1943
		Leuctridae	<i>Paraleuctra occidentalis</i>	(Banks, 1907)
		Nemouridae	<i>Nemoura arctica</i>	Esben-Petersen, 1910
			<i>Ostrocerca sp.</i>	Ricker, 1952
			<i>Podmosta weberi</i>	(Ricker, 1952)
			<i>Prostoia besametsa</i>	(Ricker, 1952)
			<i>Zapada cinctipes</i>	(Banks, 1897)
			<i>Zapada columbiana</i>	(Claassen, 1923)
			<i>Zapada haysi</i>	(Ricker, 1952)
	<i>Zapada oregonensis</i>		(Claassen, 1923)	
	Perlodidae	<i>Arcynopteryx compacta</i>	(McLachlan, 1872)	
		<i>Cascadoperla sp.</i>	Szczytko & Stewart, 1979	
		<i>Isoperla decolorata</i>	(F. Walker, 1852)	
		<i>Isoperla petersoni</i>	Needham & Christenson, 1927	
		<i>Isoperla sobria</i>	(Hagen, 1874)	
		<i>Skwala sp.</i>	Ricker, 1943	
	Taeniopterygidae	<i>Doddsia occidentalis</i>	(Banks, 1900)	
		<i>Taenionema sp.</i>	Banks, 1905	
	Psocodea	Siphonaptera	<i>Megabothris calcarifer</i>	(Wagner, 1913)
	<i>Peromyscopsylla ostsibirica</i>		(Scalon, 1936)	
	Thysanoptera		<i>Doddsia occidentalis</i>	(Banks, 1900)
			<i>Taenionema sp.</i>	Banks, 1905
	Hemiptera	Acanthosomatidae		
		Aleyrodidae		
		Anthocoridae	<i>Anthocoris aquilivenis</i>	Lewis & Horton 2012

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Insecta	Hemiptera	Aphididae		
		Cercopidae		
		Cicadellidae		
			<i>Colladonus torneelus</i>	Zetterstedt, 1828
		Delphacidae		
		Geocoridae		
			<i>Geocoris howardi</i>	Montandon, 1908
		Gerridae		
			<i>Limnoporus sp.</i>	Stål, 1868
		Lygaeidae		
			<i>Nysius sp.</i>	Dallas, 1852
		Miridae		
		Nabidae		
		Pentatomidae		
		Psyllidae		
			<i>Cacopsylla toolikensis</i>	(Hodkinson, 1978)
		Reduviidae		
		Saldidae		
		Scutelleridae		
		Tingidae		
	Coleoptera		<i>Acalypta sp.</i>	Westwood, 1840
		Trioizidae		
			<i>Bactericera atkasookensis</i>	(Hodkinson, 1978)
			<i>Trioza sp.</i>	Foerster, 1848
		Carabidae (Nebriinae)		
			<i>Nebria frigida</i>	R. E. Sahlberg, 1844
			<i>Nebria nivalis</i>	(Paykull, 1790)
			<i>Notiophilus borealis</i>	Harris, 1869
			<i>Notiophilus semistriatus</i>	Say, 1823
		(Carabinae)		
			<i>Carabus chamissonis</i>	Fischer von Waldheim, 1820
			<i>Carabus truncaticollis</i>	Eschscholtz, 1833
		(Elaphrinae)		
			<i>Diacheila polita</i>	(Faldermann, 1835)
		(Trechinae)		
			<i>Asaphidion alaskanum</i>	Wickham, 1919
			<i>Asaphidion alaskanum</i>	Wickham, 1919
			<i>Bembidion compressum</i>	Lindroth, 1963
			<i>Bembidion concolor</i>	(Kirby, 1837)
			<i>Bembidion grapii</i>	Gyllenhal, 1827
			<i>Bembidion gratiosum</i>	Casey, 1918
			<i>Bembidion mckinleyi</i>	Fall, 1926
			<i>Bembidion planatum</i>	(LeConte, 1847)
			<i>Bembidion sordidum</i>	(Kirby, 1837)
		(Scaritinae)		
			<i>Dyschirius melancholicus</i>	Putzeys, 1867
		(Broscinae)		
			<i>Miscodera arctica</i>	(Paykull, 1798)
			<i>Asaphidion alaskanum</i>	Wickham, 1919
			<i>Bembidion compressum</i>	Lindroth, 1963
			<i>Bembidion concolor</i>	(Kirby, 1837)
			<i>Bembidion grapii</i>	Gyllenhal, 1827
			<i>Bembidion gratiosum</i>	Casey, 1918

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Insecta	Coleoptera	Carabidae (Broscinae)	<i>Bembidion mckinleyi</i> <i>Bembidion planatum</i> <i>Bembidion sordidum</i>	Fall, 1926 (LeConte, 1847) (Kirby, 1837)
		(Harpalinae)	<i>Agonum quinquepunctatum</i> <i>Amara alpina</i> <i>Amara brunnea</i> <i>Amara colvillensis</i> <i>Amara erratica</i> <i>Amara glacialis</i> <i>Amara hyperborea</i> <i>Amara quenseli</i> <i>Calathus ingratus</i> <i>Cymindis unicolor</i> <i>Dicheirotichus mannerheimii</i> <i>Harpalus laevipes</i> <i>Harpalus nigratarsis</i> <i>Pterostichus adstrictus</i> <i>Pterostichus brevicornis</i> <i>Pterostichus bryanti</i> <i>Pterostichus hudsonicus</i> <i>Pterostichus pinguedineus</i> <i>Pterostichus riparius</i> <i>Pterostichus ventricosus</i> <i>Sericoda quadripunctata</i> <i>Stereocerus haematopus</i>	Motschulsky, 1844 (Paykull, 1790) (Gyllenhal, 1810) Lindroth, 1968 (Duftschmid, 1812) (Mannerheim, 1853) Dejean, 1831 (Schönherr, 1806) Dejean, 1828 Kirby, 1837 (R.F. Sahlberg, 1844) C.R. Sahlberg, 1827 C.R. Sahlberg, 1827 Eschscholtz, 1823 (Kirby, 1837) (Van Dyke, 1951) LeConte, 1863 (Eschscholtz, 1823) (Dejean, 1828) (Eschscholtz, 1823) (DeGeer, 1774) (Dejean, 1831)
		Haliplidae	<i>Halipus cribrarius</i>	LeConte, 1850
		Dytiscidae	<i>Agabus sp.</i> <i>Hydroporus sp.</i>	Leach, 1817 Clairville, 1806
		Hydrophilidae	<i>Cercyon sp.</i> <i>Hydrobius fuscipes</i>	Leach, 1817 (Linnaeus, 1758)
		Ptiliidae	<i>Acrotichis sp.</i>	Motschulsky, 1848
		Leiodidae	<i>Agathidium angulare</i> <i>Agathidium athabaskanum</i> <i>Agathidium repentinum</i> <i>Catops alpinus</i> <i>Catops luridipennis</i> <i>Catops luteipes</i> <i>Colon discretum</i> <i>Colon liebecki</i> <i>Leiodes punctulata</i> <i>Leiodes rhaetica</i>	Mannerheim, 1852 Fall, 1934 Horn, 1880 Gyllenhal, 1827 Mannerheim, 1853 Thomson & C. G., 1884 Hatch, 1933 Wickham, 1902 (Gyllenhal, 1810) (Erichson, 1845)
		Silphidae	<i>Nicrophorus vespilloides</i> <i>Thanatophilus lapponicus</i> <i>Thanatophilus sagax</i>	Herbst, 1783 (Herbst, 1793) (Mannerheim, 1853)
		Staphylinidae (Omaliinae)		

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Insecta	Coleoptera	Staphylinidae (Omaliinae)	<i>Acidota crenata</i> <i>Acidota quadrata</i> <i>Dropephylla</i> sp. <i>Eucnecosum brachypterum</i> <i>Eucnecosum brunnescens</i> <i>Olophrum boreale</i> <i>Olophrum consimile</i> <i>Olophrum latum</i> <i>Olophrum rotundicollis</i> <i>Omalius</i> sp. <i>Phlaeopterus elongatus</i> <i>Phloeostiba lapponica</i> <i>Porrhodites fenestralis</i>	(Fabricius, 1792) (Zetterstedt, 1838) Mulsant & Rey, 1880 (Gravenhorst, 1802) (J.R. Sahlberg, 1871) (Paykull, 1792) (Gyllenhal, 1810) Mäklin, 1853 (C.R. Sahlberg, 1830) Gravenhorst, 1802 Mullen & Campbell, 2018 (Zetterstedt, 1838) (Zetterstedt, 1828)
		(Proteininae)	<i>Megarthus angulicollis</i> <i>Proteinus parvulus</i>	Mäklin, 1852 LeConte, 1863
		(Micropeplinae)	<i>Micropeplus laticollis</i>	Mäklin, 1853
		(Tachyporinae)	<i>Bolitobius cingulatus</i> <i>Bryophacis smetanai</i> <i>Ischnosoma fimbriatum</i> <i>Lordithon fungicola</i> <i>Mycetoporus americanus</i> <i>Mycetoporus nigrans</i> <i>Mycetoporus rugosus</i> <i>Tachinus basalis</i> <i>Tachinus elongatus</i> <i>Tachinus frigidus</i> <i>Tachinus instabilis</i> <i>Tachinus quebecensis</i> <i>Tachyporus canadensis</i> <i>Tachyporus nitidulus</i>	Mannerheim, 1830 Campbell, 1993 Campbell, 1991 Campbell, 1982 Erichson, 1839 Mäklin, 1853 Hatch, 1957 Erichson, 1839 Gyllenhal, 1810 Erichson, 1839 Mäklin, 1853 Robert, 1946 Campbell, 1979 (Fabricius, 1781)
		(Aleocharinae)	<i>Aleochara castaneipennis</i> <i>Aleochara verna</i> <i>Atheta altaica</i> <i>Atheta capsularis</i> <i>Atheta munsteri</i> <i>Atheta prudhoensis</i> <i>Atheta stercoris</i> <i>Atheta strigosula</i> <i>Atheta terranova</i> <i>Bellatheta microptera</i> <i>Boreophilia nomensis</i> <i>Boreostiba parvipennis</i> <i>Cypha</i> sp. <i>Dinaraea</i> sp. <i>Liogluta granulosa</i> <i>Lypoglossa angularis</i> <i>Mniusa yukonensis</i> <i>Neothetalia canadiana</i> <i>Neothetalia pallitarsis</i>	Mannerheim, 1843 Say, 1833 Bernhauer, 1901 Klimaszewski, 2005 Bernhauer, 1902 (Lohse, 1990) Fenyés, 1920 Casey, 1910 Klimaszewski & Langor, 2011 (Lohse, Klimaszewski & Smetana, 1990) (Casey, 1910) (Bernhauer, 1907) Leach, 1819 Thomson, 1858 Lohse, 1990 (Mäklin, 1853) (Klimaszewski & Godin, 2012) Klimaszewski, 2004 (Kirby, 1837)

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Insecta	Coleoptera	Staphylinidae (Aleocharinae)	<i>Olisthaerus megacephalus</i> <i>Oxypoda demissa</i> <i>Oxypoda frigida</i> <i>Oxypoda sylvia</i> <i>Silusa californica</i>	(Zetterstedt, 1828) Casey, 1911 Bernhauer, 1907 Casey, 1906 Bernhauer, 1905
		(Scaphidiinae)	<i>Scaphium castanipes</i>	Kirby, 1837
		(Oxyporinae)	<i>Oxyporus occipitalis</i>	Fauvel, 1864
		(Oxytelinae)	<i>Oxytelus sp.</i> <i>Syntomium sp.</i> <i>Thinobius procerus</i>	Gravenhorst, 1802 Curtis, 1828 Eppelsheim, 1893
		(Scydmaeninae)	<i>Stenichnus sp.</i> <i>Veraphis sp.</i>	Thomson, 1859 Casey, 1897
		(Steninae)	<i>Stenus austini</i> <i>Stenus noctivagus</i> <i>Stenus umbratilis</i>	Casey, 1884 Casey, 1884 (Casey, 1884)
		(Euaesthetinae)	<i>Euaesthetus sp.</i>	Gravenhorst, 1806
		(Staphylininae)	<i>Quedionuchus plagiatu</i> <i>Quedius brunnipennis</i> <i>Quedius criddlei</i> <i>Quedius fellmani</i> <i>Quedius frigidus</i> <i>Quedius fulvicollis</i> <i>Quedius labradorensis</i> <i>Quedius molochinoides</i> <i>Quedius simulator</i>	Mannerheim, 1843 Mannerheim, 1843 (Casey, 1915) (Zetterstedt, 1838) Smetana, 1971 (Stephens, 1833) Smetana, 1965 Smetana, 1965 Smetana, 1971
		Scarabaeidae	<i>Aegialia lacustris</i> <i>Agoliinus piceatus</i> <i>Planolinoides borealis</i>	LeConte, 1850 (Robinson, 1946) (Gyllenhal, 1827)
		Eucinetidae	<i>Nycteus sp.</i>	Latreille, 1829
		Buprestidae	<i>Anthaxia expansa</i> <i>Melanophila acuminata</i>	LeConte, 1857 (DeGeer, 1774)
		Byrrhidae	<i>Arctobyrrhus subcanus</i> <i>Byrrhus cyclophorus</i> <i>Byrrhus fasciatus</i> <i>Byrrhus geminatus</i> <i>Byrrhus kirbyi</i> <i>Curimopsis sp.</i> <i>Cytilus alternatus</i>	(LeConte, 1878) Kirby, 1837 Forster, 1771 LeConte, 1854 LeConte, 1854 Ganglbauer, 1902 (Say, 1825)
		Byturidae	<i>Byturus unicolor</i>	Say, 1823
		Elateridae	<i>Ascoliocerus sanborni</i>	(Horn, 1871)

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Insecta	Coleoptera	Elateridae	<i>Berninelsonius hyperboreus</i> <i>Denticollis varians</i> <i>Eanus decoratus</i> <i>Fleutiauxellus extricatus</i> <i>Hypnoidus bicolor</i> <i>Neohypdonus restrictulus</i> <i>Pseudanostirus ochreipennis</i> <i>Sericus incongruus</i> <i>Sylvanelater mendax</i>	(Gyllenhal, 1827) (Germar, 1846) (Mannerheim, 1853) (Fall, 1926) (Eschscholtz, 1829) (Mannerheim, 1853) (LeConte, 1863) (LeConte, 1853) (LeConte, 1853)
		Lycidae	<i>Dictyoptera aurora</i>	(Herbst, 1784)
		Lampyridae	<i>Ellychnia sp.</i>	Dejean, 1833
		Cantharidae	<i>Dichelotarsus sp.</i>	Motschulsky, 1860
		Dermestidae	<i>Pseudohadrotoma perversa</i>	(Fall, 1926)
		Ptinidae	<i>Caenocara sp.</i>	Thomson, 1859
		Nitidulidae	<i>Cryptarcha sp.</i> <i>Epuraea sp.</i>	Shuckard, 1839 Erichson, 1843
		Cucujidae	<i>Pediacus fuscus</i>	Erichson, 1845
		Cryptophagidae	<i>Antherophagus suturalis</i> <i>Atomaria tenebrosa</i> <i>Caenoscelis ferruginea</i> <i>Cryptophagus bidentatus</i> <i>Cryptophagus confertus</i> <i>Cryptophagus corticinus</i> <i>Cryptophagus difficilis</i> <i>Cryptophagus lapponicus</i> <i>Cryptophagus tuberculosus</i>	Mäklin, 1853 (Casey, 1900) (Sahlberg, 1820) Mäklin, 1853 Casey, 1900 C.G. Thomson, 1863 Casey, 1900 Gyllenhal, 1827 Mäklin, 1852
		Coccinellidae	<i>Adalia bipunctata</i> <i>Ceratomegilla ulkei</i> <i>Coccinella transversoguttata</i> <i>Coccinella trifasciata</i> <i>Hippodamia arctica</i>	(Linnaeus, 1758) Crotch, 1873 Faldermann, 1835 Linnaeus, 1758 (Schneider, 1792)
		Latridiidae	<i>Cartodere constricta</i> <i>Corticaria ferruginea</i> <i>Corticarina arctophila</i> <i>Latridius sp.</i> <i>Stephostethus liratus</i>	(Gyllenhal, 1827) (Linnaeus, 1758) Reitter, 1881 Herbst, 1793 (LeConte, 1863)
		Tetratomidae	<i>Tetratoma concolor</i>	LeConte, 1879
		Mordellidae	<i>Mordellaria borealis</i> <i>Mordellistena sp.</i>	(LeConte, 1862) Costa, 1854

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Insecta	Coleoptera	Ciidae		
			<i>Orthocis punctatus</i>	(Mellié, 1848)
		Tenebrionidae		
			<i>Upis ceramboides</i>	(Linnaeus, 1758)
		Pythidae		
			<i>Pytho americanus</i>	Kirby, 1837
		Cerambycidae		
			<i>Acmaeops proteus</i>	(Kirby, 1837)
			<i>Gnathacmaeops pratensis</i>	(Laicharting, 1784)
			<i>Judolia montivagans</i>	(Couper, 1864)
			<i>Monochamus scutellatus</i>	(Say, 1824)
			<i>Pachyta lamed</i>	(Linnaeus, 1758)
			<i>Phymatodes dimidiatus</i>	(Kirby, 1837)
		Orsodacnidae		
			<i>Orsodacne atra</i>	(Ahrens, 1810)
		Chrysomelidae		
			<i>Altica sp.</i>	Geoffroy, 1762
			<i>Bromius obscurus</i>	(Linnaeus, 1758)
			<i>Chaetocnema protensa</i>	LeConte, 1878
			<i>Chrysolina sp.</i>	Motschulsky, 1860
			<i>Galerucella nymphaeae</i>	(Linnaeus, 1758)
			<i>Gonioctena nivosa</i>	(Suffrian 1851)
		Brentidae		
			<i>Loborhynchapion cyanitinctum</i>	(Fall, 1927)
			<i>Perapion sp.</i>	Wagner, 1907
		Curculionidae		
			<i>Ceutorhynchus sp.</i>	Germar, 1824
			<i>Dendroctonus punctatus</i>	LeConte, 1868
			<i>Dorytomus alaskanus</i>	Faust, 1882
			<i>Dorytomus frostii</i>	Blatchley, 1916
			<i>Dorytomus laticollis</i>	LeConte, 1876
			<i>Dorytomus lecontei</i>	O'Brien, 1970
			<i>Dorytomus leucophyllus</i>	(Motschulsky, 1845)
			<i>Dorytomus mannerheimi</i>	(Gemming, 1871)
			<i>Dryocoetes affaber</i>	LeConte, 1876
			<i>Dryocoetes autographus</i>	(Ratzeburg, 1837)
			<i>Hypera diversipunctata</i>	(Schränk, 1798)
			<i>Ips tridens</i>	Wood, 1982
			<i>Isochnus sp.</i>	Thomson, 1859
			<i>Lepidophorus lineaticollis</i>	Kirby, 1837
			<i>Lepyrus gemellus</i>	Kirby, 1837
			<i>Magdalis sp.</i>	Germar, 1817
			<i>Polygraphus rufipennis</i>	Wood & Bright, 1992
			<i>Tychius tectus</i>	LeConte, 1876
	Neuroptera			
		Hemerobiidae		
			<i>Wesmaelius sp.</i>	Krüger, 1922
	Hymenoptera			
		Tenthredinidae		
			<i>Pristiphora erichsonii</i>	(Hartig)
		Cimbicidae		
			<i>Cimbex americana</i>	Leach, 1817
		Braconidae		
		Ichneumonidae		
		Pteromalidae		

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Insecta	Hymenoptera	Platygastridae		
		Pompilidae		
		Proctotrupidae		
		Megaspilidae		
		Pteromalidae		
		Scelionidae		
		Mymaridae		
		Mymarommatidae		
		Ceraphronidae		
		Charipidae		
		Diapriidae		
		Dryinidae		
		Encyrtidae		
		Eurytomidae		
		Chrysididae		
		Apidae		
			<i>Bombus bohemicus</i>	Seidl, 1837
			<i>Bombus cryptarum</i>	(Fabricius, 1775)
			<i>Bombus flavidus</i>	Eversmann, 1852
			<i>Bombus flavifrons</i>	Cresson, 1863
			<i>Bombus frigidus</i>	Smith, 1854
			<i>Bombus insularis</i>	(Smith, 1861)
			<i>Bombus jonellus</i>	(Kirby, 1802)
			<i>Bombus kirbiellus</i>	Curtis, 1835
			<i>Bombus kluanensis</i>	Williams et al., 2019
			<i>Bombus lapponicus</i>	(Fabricius, 1793)
			<i>Bombus melanopygus</i>	Nylander, 1848
			<i>Bombus mixtus</i>	Cresson, 1878
			<i>Bombus natvigi</i>	Richards, 1931
			<i>Bombus neoboreus</i>	Sladen, 1919
			<i>Bombus occidentalis</i>	Greene, 1858
			<i>Bombus polaris</i>	Curtis, 1835
			<i>Bombus sylvicola</i>	Kirby, 1837
			<i>Nomada sp.</i>	Scopoli, 1770
		Andrenidae		
			<i>Andrena nigrihirta</i>	(Ashmead, 1890)
			<i>Andrena rufosignata</i>	Cockerell, 1902
			<i>Panurginus ineptus</i>	Cockerell, 1922
		Megachilidae		
			<i>Osmia sp.</i>	Panzer, 1806
		Colletidae		
			<i>Colletes impunctatus</i>	Nylander, 1852
			<i>Hylaeus annulatus</i>	(Linnaeus, 1758)
		Halictidae		
			<i>Lasioglossum boreale</i>	Ebmer & Sakagami, 1977
		Vespidae		
			<i>Ancistrocerus sp.</i>	Semper, 1898
			<i>Dolichovespula albida</i>	(Sladen, 1918)
			<i>Dolichovespula arenaria</i>	(Fabricius, 1775)
			<i>Dolichovespula maculata</i>	(Linnaeus, 1763)
			<i>Dolichovespula norvegicoides</i>	(Sladen, 1918)
			<i>Vespula acadica</i>	(Sladen, 1918)
			<i>Vespula alascensis</i>	Packard, 1870
		Formicidae		
			<i>Camponotus herculeanus</i>	(Linnaeus, 1758)

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Insecta	Hymenoptera	Formicidae	<i>Formica aserva</i>	Forel, 1901
			<i>Formica neorufibarbis</i>	Emery, 1893
			<i>Formica subaenescens</i>	Emery, 1893
			<i>Leptothorax acervorum</i>	(Fabricius, 1793)
			<i>Leptothorax canadensis</i>	
			<i>Myrmica alaskensis</i>	Wheeler, 1917
			<i>Myrmica quebecensis</i>	Francoeur, 1981
			<i>Myrmica incompleta</i>	Provancher, 1881
	Trichoptera	Apataniidae	<i>Allomyia sp.</i>	Banks, 1916
			<i>Apatania sp.</i>	Kolenati, 1847
		Brachycentridae	<i>Brachycentrus americanus</i>	(Banks, 1899)
		Glossosomatidae	<i>Glossosoma sp.</i>	Curtis, 1834
		Limnephilidae	<i>Ecclisomyia sp.</i>	Banks, 1907
			<i>Hydatophylax sp.</i>	Wallengren, 1891
			<i>Limnephilus sp.</i>	Leach, 1815
		Rhyacophilidae	<i>Rhyacophila sp.</i>	Pictet, 1834
	Lepidoptera	Pieridae	<i>Colias canadensis</i>	Ferris, 1982
			<i>Colias gigantea</i>	Strecker, 1900
			<i>Colias hecla</i>	Lefebvre, 1836
			<i>Colias nastes</i>	Boisduval, 1832
			<i>Colias palaeno</i>	(Linnaeus, 1761)
			<i>Colias philodice</i>	Godart, 1819
			<i>Pieris marginalis</i>	Scudder, 1861
			<i>Pontia occidentalis</i>	(Reakirt, 1866)
		Nymphalidae	<i>Boloria alaskensis</i>	(Holland, 1900)
			<i>Boloria chariclea</i>	(Schneider, 1794)
			<i>Boloria eunomia</i>	(Esper, 1799)
			<i>Boloria freija</i>	(Becklin, 1791)
			<i>Boloria improba</i>	(Butler, 1877)
			<i>Boloria polaris</i>	(Boisduval, 1828)
			<i>Coenonympha tullia</i>	(Muller, 1764)
			<i>Erebia disa</i>	(Thunberg, 1791)
			<i>Erebia fasciata</i>	Butler, 1868
			<i>Erebia lafontainei</i>	Troubridge & Philip, 1983
			<i>Erebia mackinleyensis</i>	Gunder, 1932
			<i>Erebia mancinus</i>	Doubleday, 1849
			<i>Erebia occulta</i>	Roos & Kimmich, 1983
			<i>Erebia pawloskii</i>	Ménétriés, 1859
			<i>Erebia rossii</i>	(Curtis, 1834)
			<i>Erebia youngi</i>	Holland, 1900
			<i>Limenitis arthemis</i>	Drury, 1773
			<i>Oeneis bore</i>	(Schneider, 1792)
			<i>Oeneis jutta</i>	(Hubner, 1806)
			<i>Oeneis melissa</i>	(Fabricius, 1775)
			<i>Oeneis polixenes</i>	(Fabricius, 1775)
			<i>Phyciodes pulchella</i>	Boisduval, 1852

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Insecta	Lepidoptera	Nymphalidae	<i>Colias hecla</i> <i>Colias nastes</i> <i>Colias palaeno</i> <i>Colias philodice</i> <i>Pieris marginalis</i> <i>Pontia occidentalis</i>	Lefebvre, 1836 Boisduval, 1832 (Linnaeus, 1761) Godart, 1819 Scudder, 1861 (Reakirt, 1866)
		Papilionidae	<i>Papilio canadensis</i> <i>Papilio machaon</i> <i>Parnassius corybas</i> <i>Parnassius eversmanni</i>	Rothschild & Jordan, 1906 Linnaeus, 1758 Fischer de Waldheim, 1823 Ménétriés, 1855
		Lycaenidae	<i>Agriades glandon</i> <i>Agriades optilete</i> <i>Cupido amyntula</i> <i>Glaucopsyche lygdamus</i> <i>Icaricia saepiolus</i> <i>Lycaena dorcas</i> <i>Lycaena phlaeas</i> <i>Plebejus idas</i>	(Prunner, 1798) (Knoch, 1781) (Boisduval, 1852) (Doubleday, 1842) Boisduval, 1852 Kirby, 1837 (Linnaeus, 1761) (Linnaeus, 1761)
		Hesperiidae	<i>Carterocephalus palaemon</i> <i>Hesperia comma</i>	(Pallas, 1771) (Linnaeus, 1758)
		Gracillariidae		
		Psychidae		
		Oecophoridae		
		Momphidae	<i>Polix coloradella</i>	Walsingham, 1888
			<i>Mompha sp.</i>	Hübner, 1825
		Gelechiidae	<i>Chionodes viduella</i>	(Fabricius, 1794)
		Tortricidae	<i>Apotomis tertiana</i> <i>Eana argentana</i> <i>Eana osseana</i> <i>Epinotia solandriana</i> <i>Epinotia trigonella</i>	McDunnough, 1922 (Clerck, 1759) (Scopoli, 1763) (Linnaeus, 1758) (Linnaeus, 1758)
		Sesiidae		
		Crambidae		
		Geometridae	<i>Aspitates forbesi</i> <i>Aspitates orciferaria</i> <i>Aspitates taylori</i> <i>Colostygia circumvallaria</i> <i>Dysstroma pseudimmanata</i> <i>Ecliptopera silaceata</i> <i>Entephria polata</i> <i>Epelis truncataria</i> <i>Epirrhoe alternata</i> <i>Epirrhoe sperryi</i> <i>Eulithis destinata</i> <i>Eulithis populata</i> <i>Eupithecia nimbicolor</i> <i>Macaria boreata</i>	(Munroe, 1963) (Walker, 1862) (Butler, 1893) (Taylor, 1906) Heydemann, 1929 (Denis & Schiffermuller, 1775) (Duponchel, 1830) Walker, 1862 (Muller, 1764) Herbulot, 1951 Möschler, 1860 (Linnaeus, 1758) Hulst, 1896 Curtis, 1826

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Insecta	Lepidoptera	Geometridae	<i>Holarctias sentinaria</i>	Hübner & Geyer, 1837
			<i>Lobophora nivigerata</i>	Walker, 1862
			<i>Macaria brunneata</i>	(Thunberg, 1784)
			<i>Rheumaptera hastata</i>	(Linnaeus, 1758)
			<i>Scopula cajanderi</i>	(Herz, 1904)
			<i>Scopula frigidaria</i>	(Moschler, 1860)
			<i>Scopula sentinaria</i>	(Geyer, 1837)
			<i>Selenia alciphearia</i>	Walker, 1860
			<i>Xanthorhoe algidata</i>	(Möschler, 1874)
			<i>Xanthorhoe ferrugata</i>	(Clerck, 1759)
			<i>Xanthorhoe labradorensis</i>	Packard, 1867
			<i>Xanthorhoe pontiaria</i>	Taylor, 1906
		Erebidae	<i>Arctia lapponica</i>	(Thunberg, 1791)
			<i>Arctia opulenta</i>	(Edwards, 1881)
			<i>Arctia parthenos</i>	Harris, 1850
			<i>Arctia subnebulosa</i>	Dyar, 1899
			<i>Caenurgina crassiuscula</i>	Haworth, 1809
		Noctuidae	<i>Drasteria hudsonica</i>	(Grote & Robinson, 1865)
			<i>Anarta nigrolunata</i>	Packard, 1867
			<i>Andropolia contacta</i>	Walker, 1856
			<i>Apamea zeta</i>	(Treitschke, 1825)
			<i>Coranarta luteola</i>	(Grote & Robinson, 1865)
			<i>Eurois occulta</i>	(Linnaeus, 1758)
			<i>Lasionycta quadrilunata</i>	Grote, 1874
			<i>Parabarrovia keelei</i>	Gibson, 1920
			<i>Polia richardsoni</i>	(Curtis, 1835)
			<i>Sympistis heliophila</i>	(Paykull, 1793)
			<i>Sympistis zetterstedtii</i>	Staudinger, 1857
			<i>Syngrapha diasema</i>	(Boisduval, 1829)
			<i>Syngrapha interrogationis</i>	(Linnaeus, 1758)
			<i>Xestia alaskae</i>	(Grote, 1876)
			<i>Xestia lupa</i>	Lafontaine & Mikkola
			<i>Xestia okakensis</i>	(Packard, 1867)
	<i>Xestia speciosa</i>	(Hubner, 1813)		
	Diptera	Tipulidae	<i>Dicranota sp.</i>	Zetterstedt, 1838
			<i>Arctoconopa aldrichi</i>	(Alexander, 1924)
			<i>Cheilotrichia toklat</i>	(Alexander, 1955)
			<i>Gonomyodes tacoma</i>	(Alexander, 1955)
			<i>Hoplolabis asiatica</i>	(Alexander, 1918)
			<i>Hoplolabis estella</i>	(Alexander, 1955)
			<i>Limonia sp.</i>	Meigen, 1800
			<i>Molophilus sp.</i>	Curtis, 1833
			<i>Ormosia sp.</i>	Rondani, 1856
<i>Pedicia sp.</i>			Latreille, 1809	
<i>Rhabdomastix sp.</i>			Skuse, 1890	
<i>Symplecta denali</i>			(Alexander, 1955)	
<i>Symplecta mckinleyana</i>			(Alexander, 1955)	
<i>Symplecta sheldoni</i>			(Alexander, 1955)	
<i>Tipula denali</i>			Alexander, 1969	
<i>Tipula mckinleyana</i>			Alexander, 1969	

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Insecta	Diptera	Chironomidae	<i>Brillia</i> sp.	Kieffer, 1913
			<i>Bryophaenocladius</i> sp.	Thienemann, 1934
			<i>Chaetocladius</i> sp.	Kieffer, 1911
			<i>Corynoneura</i> sp.	Winnertz, 1846
			<i>Cricotopus</i> sp.	Wulp, 1874
			<i>Diamesa</i> sp.	Walts, 1837
			<i>Diplocladius</i> sp.	Kieffer, 1908
			<i>Eukiefferiella brehmi</i>	Gouin, 1943
			<i>Eukiefferiella claripennis</i>	(Lundbeck, 1898)
			<i>Eukiefferiella</i> sp.	Thienemann, 1926
			<i>Heterotrissocladius</i> sp.	Spärck, 1923
			<i>Hydrobaenus</i> sp.	Fries, 1830
			<i>Krenosmittia</i> sp.	Thienemann & Kruger, 1939
			<i>Limnophyes</i> sp.	Eaton, 1875
			<i>Mesorthocladius</i> sp.	Sæther, 2005
			<i>Micropsectra</i> sp.	Kieffer, 1908
			<i>Neozavrelia</i> sp.	Goetghebuer, 1941
			<i>Orthocladius rivulorum</i>	Kieffer, 1909
			<i>Orthocladius</i> sp.	Wulp, 1874
			<i>Pagastia</i> sp.	Oliver, 1959
			<i>Paralimnophyes</i> sp.	Brundin, 1956
			<i>Paratanytarsus</i> sp.	Thienemann & Bause, 1913
			<i>Parorthocladius</i> sp.	Thienemann, 1935
			<i>Psectrocladius limbatellus</i>	(Holmgren, 1869)
			<i>Psectrocladius</i> sp.	Kieffer, 1906
			<i>Pseudodiamesa</i> sp.	Goetghebuer, 1939
			<i>Pseudokiefferiella</i> sp.	Zavrel, 1941
			<i>Pseudosmittia</i> sp.	Goetghebuer, 1932
			<i>Rheocricotopus</i> sp.	Thienemann & Harnisch, 1932
			<i>Symposiocladius</i> sp.	Cranston, 1982
			<i>Syndiamesa</i> sp.	Kieffer, 1918
			<i>Synorthocladius</i> sp.	Thienemann, 1935
			<i>Thienemanniella</i> sp.	Kieffer, 1911
			<i>Tokunagaia</i> sp.	Sæther, 1973
			<i>Trichotanypus</i> sp.	Kieffer, 1906
			<i>Trichotanypus</i> sp.	Kieffer, 1906
			<i>Tvetenia</i> sp.	Kieffer, 1922
		Culicidae		
		Dixidae	<i>Dixella</i> sp.	Dyar & Shannon, 1924
		Simuliidae	<i>Gymnopais</i> sp.	Stone, 1949
			<i>Helodon</i> sp.	Enderlein, 1921
			<i>Metacnephia</i> sp.	Corsskey, 1969
			<i>Prosimulium</i> sp.	Roubaud, 1906
			<i>Simulium vittatum</i>	(Zetterstedt, 1838)
		Bibionidae	<i>Bibio</i> sp.	Geoffroy, 1762
		Cecidomyiidae		
		Mycetophilidae		
		Empididae	<i>Clinocera</i> sp.	Meigen, 1803
			<i>Empis</i> sp.	Linnaeus, 1758
			<i>Oreogeton</i> sp.	Schiner, 1860

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Insecta	Diptera	Empididae	<i>Rhamphomyia sp.</i>	Meigen, 1822
		Phoridae		
		Syrphidae (Eristalinae)	<i>Cheilosia bigelowi</i>	(Curran, 1926)
			<i>Cheilosia columbiae</i>	(Curran, 1922)
			<i>Cheilosia laevis</i>	(Bigot, 1884)
			<i>Cheilosia latrans</i>	(Walker, 1849)
			<i>Cheilosia rita</i>	(Curran, 1922)
			<i>Cheilosia yukonensis</i>	(Shannon, 1922)
			<i>Eristalis cryptarum</i>	(Fabricius, 1794)
			<i>Eristalis flavipes</i>	Walker, 1849
			<i>Eristalis hirta</i>	Loew, 1866
			<i>Eristalis interrupta</i>	(Poda, 1761)
			<i>Eristalis obscura</i>	Loew, 1866
			<i>Eristalis rupium</i>	Fabricius, 1805
			<i>Helophilus hybridus</i>	Loew, 1846
			<i>Helophilus neoaffinis</i>	Fluke, 1949
			<i>Hiatomyia sp.</i>	Shannon, 1922
			<i>Sericomyia nigra</i>	Portschinsky, 1873
			<i>Sphegina sp.</i>	Meigen, 1822
			<i>Volucella bombylans</i>	(Linnaeus, 1758)
			<i>Volucella facialis</i>	Williston, 1882
			<i>Xylota subfasciata</i>	Loew, 1866
		(Syrphinae)	<i>Baccha elongata</i>	(Fabricius, 1775)
			<i>Chrysotoxum ventricosum</i>	Loew, 1864
			<i>Dasysyrphus amalopis</i>	(Osten Sacken, 1875)
			<i>Dasysyrphus venustus</i>	(Meigen, 1822)
			<i>Epistrophe grossulariae</i>	(Meigen, 1822)
			<i>Eriozona latus</i>	(Osten Sacken, 1875)
			<i>Eupeodes americanus</i>	(Wiedemann, 1830)
			<i>Eupeodes curtus</i>	(Hine, 1922)
			<i>Eupeodes flukei</i>	(Jones, 1917)
			<i>Eupeodes luniger</i>	(Meigen, 1822)
			<i>Eupeodes perplexus</i>	(Osburn, 1910)
			<i>Melangyna arctica</i>	(Zetterstedt, 1838)
			<i>Melanostoma mellinum</i>	(Linnaeus, 1758)
			<i>Meligramma triangulifera</i>	(Zetterstedt, 1843)
			<i>Meliscaeva cinctella</i>	(Zetterstedt, 1843)
			<i>Neocnemodon rita</i>	(Curran)
			<i>Parasyrphus genualis</i>	(Williston, 1887)
			<i>Parasyrphus tarsatus</i>	(Zetterstedt, 1838)
			<i>Pipiza macrofemoralis</i>	Curran, 1921
			<i>Platycheirus aeratus</i>	(Coquillett, 1900)
			<i>Platycheirus amplus</i>	(Curran, 1927)
			<i>Platycheirus angustatus</i>	(Zetterstedt, 1843)
			<i>Platycheirus ciliatus</i>	Bigot, 1884
			<i>Platycheirus coerulescens</i>	(Williston, 1887)
			<i>Platycheirus flabella</i>	Hull, 1944
			<i>Platycheirus holarcticus</i>	Vockeroth, 1990
			<i>Platycheirus hyperboreus</i>	(Staeger, 1845)
			<i>Platycheirus naso</i>	(Walker, 1849)
			<i>Platycheirus nigrofemoratus</i>	(Kanervo, 1934)

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Insecta	Diptera	Syrphidae (Syrphinae)	<i>Platycheirus obscurus</i> <i>Platycheirus parmatus</i> <i>Platycheirus peltatoides</i> <i>Platycheirus podagratus</i> <i>Platycheirus setitarsis</i> <i>Platycheirus striatus</i> <i>Sphaerophoria abbreviata</i> <i>Sphaerophoria philanthus</i> <i>Syrphus attenuatus</i> <i>Syrphus ribesii</i> <i>Syrphus torvus</i>	(Say, 1824) Rondani, 1857 Curran, 1923 (Zetterstedt, 1838) Vockeroth, 1990 Vockeroth, 1990 Zetterstedt, 1849 (Meigen, 1822) Hine, 1922 (Linnaeus, 1758) Osten Sacken, 1875
		Anthomyiidae	<i>Anthomyia</i> sp. <i>Botanophila</i> sp. <i>Chirosia</i> sp. <i>Eutrichota</i> sp. <i>Pegomya</i> sp.	Meigen, 1803 Liroy, 1864 Rondani, 1856 Kowarz, 1893 Robineau-Desvoidy, 1830
		Calliphoridae	<i>Calliphora alaskensis</i> <i>Calliphora loewi</i> <i>Calliphora montana</i> <i>Calliphora stelviana</i> <i>Cynomya cadaverina</i>	(Shannon, 1923) Enderlein, 1903 (Shannon, 1926) (Brauer & Bergenstamm, 1891) Robineau-Desvoidy, 1830
		Fanniidae	<i>Fannia</i> sp.	Robineau-Desvoidy, 1830
		Muscidae	<i>Helina luteisquama</i> <i>Lophosceles</i> sp. <i>Mesembrina</i> sp. <i>Muscina</i> sp. <i>Opsolasia orichalcea</i> <i>Phaonia</i> sp. <i>Spilogona fulvibasis</i> <i>Thricops septentrionalis</i>	(Zetterstedt, 1845) Ringdahl, 1922 Meigen, 1826 Robineau-Desvoidy, 1830 (Zetterstedt, 1849) Reichardt, 1941 Huckett, 1965 (Stein, 1898)
		Sarcophagidae	<i>Brachicoma</i> sp. <i>Ravinia</i> sp. <i>Sarcophaga furcata</i>	Rondani, 1856 Robineau-Desvoidy, 1863 Huckett, 1965
		Scathophagidae	<i>Parallelomma vittatum</i> <i>Scathophaga</i> sp.	(Meigen, 1826) Meigen, 1803
		Tachinidae	<i>Istocheta claripennis</i> <i>Linnaemya</i> sp. <i>Macquartia</i> sp.	Rondani, 1859 Robineau-Desvoidy, 1830 Robineau-Desvoidy, 1830
		Dryomyzidae	<i>Paradryomyza setosa</i>	(Bigot, 1886)
		Sciomyzidae	<i>Pherbellia</i> sp. <i>Tetanocera</i> sp.	Robineau-Desvoidy, 1830 Latreille, 1804
		Heleomyzidae	<i>Borboropsis fulviceps</i> <i>Neoleria inscripta</i>	(Strobl, 1898) (Meigen, 1830)

Table A1: Continued.

<u>CLASS</u>	<u>ORDER</u>	<u>FAMILY</u> <u>(Subfamily)</u>	<u>GENUS/SPECIES</u>	<u>AUTHOR(S)</u>
Insecta	Diptera			
		Heleomyzidae	<i>Neoleria prominens</i> <i>Oecotheca fenestralis</i> <i>Suillia convergens</i>	(Becker, 1897) (Fallen, 1820) (Walker, 1849)
		Asilidae	<i>Laphria sp.</i>	Meigen, 1803
		Chaoboridae	<i>Chaoborus sp.</i>	Lichtenstein, 1800
		Chloropidae	<i>Chlorops sp.</i> <i>Oscinella sp.</i> <i>Tricimba sp.</i>	Meigen, 1803 Becker, 1910 Lioy, 1864
		Drosophilidae		
		Oestridae	<i>Hypoderma tarandi</i>	(Linnaeus 1758)
		Piophilidae	<i>Neopiophila setaluna</i>	McAlpine, 1977
		Pipunculidae	<i>Cephalosphaera sp.</i>	Enderlein, 1936
		Rhagionidae	<i>Ptiolina sp.</i>	Zetterstedt, 1842
		Sciaridae		
		Stratiomyidae	<i>Beris sp.</i> <i>Sargus decorus</i> <i>Stratiomys sp.</i>	Zetterstedt, 1842 Say, 1824 Ouchi, 1940
		Tabanidae	<i>Hybomitra sp.</i>	Enderlein, 1922
		Therevidae		
		Ephydriidae	<i>Parydra sp.</i>	Stenhammer, 1844
		Sphaeroceridae	<i>Crumomyia sp.</i>	Macquart, 1835