PATTERNS OF DIVERSITY IN HIGH ELEVATION GRASSLAND DIPTERA

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PREFACE

This thesis is composed of three chapters, one of which is an original manuscript that will be submitted for publication in a refereed journal.

Chapter 1

This chapter is a general introduction and literature review.

Chapter 2

This chapter is a manuscript in preparation for publication in a refereed journal. MacLeod, A.M. and Wheeler, T.A. Patterns of diversity in high elevation grassland Diptera.

Chapter 3

This chapter is a general conclusion.

CONTRIBUTION OF AUTHORS

A. MacLeod designed the research and was responsible for the field sampling, specimen preparation, identification of Diptera, data analysis, and writing the manuscript. T.A. Wheeler supervised the research, helped in field sampling, edited the manuscript, provided facilities and financial support for the equipment, the field season, the specimen preparation and conference travel.

ABSTRACT

Species diversity patterns of high elevation grassland Diptera (Brachycera) were assessed to determine the community structure, species turnover, and species abundance patterns along a latitudinal gradient. Fieldwork took place in May 2008 in the Appalachian Mountains of North Carolina and June-July 2010 in the Rocky Mountains at sites in Colorado, Wyoming, and Alberta. Two spatial scales were used: sample area and site. There was a slight latitudinal turnover of species, with latitude, longitude, and elevation being the most strongly associated with species composition. All sites were significantly different except the two sites in Alberta. Close proximity and site similarity may be responsible for this. There were similarities between all sample areas except Colorado. These results are attributed to the Wyoming basin, possibly a considerable barrier to dispersal. Patterns were driven mostly by rare species. High beta-diversity was found between sites, even in patterns of common species. Species abundance patterns in both the Rockies and the Appalachians revealed that although ecologically diverse and broad generalist families were more reliably dominated by a few species, trophic guild may not always accurately predict dominance/evenness patterns.

RESUMÉ

La structure des communautés, le renouvellement et les patrons d'abondance des espèces de Diptera (Brachycera) ont été évalués le long de gradients latitudinaux dans les montagnes appalachiennes (Caroline du Nord) et les montagnes rocheuses (Colorado, Wyoming, Alberta). Deux échelles spatiales ont été utilisées dans chacune des montagnes: l'aire d'échantillonnage et le site. Il y avait un renouvellement des espèces, avec la latitude, la longitude et l'élévation étant les facteurs les plus fortement associés à la composition en espèces. Les communautés de chacun des sites étaient significativement différentes, excepté les deux sites de l'Alberta. La proximité et la similarité des sites étaient probablement responsables de cette différence. Les sites du Colorado étaient significativement différents des autres sites des Rocheuses, probablement à cause du bassin du Wyoming de faible altitude créant une barrière pour la dispersion des espèces retrouvées en haute altitude. Les patrons étaient en grande partie dirigés par les espèces rares. Une haute diversité-béta était retrouvée entre les sites, même chez les espèces communes. Les patrons d'abondance des espèces dans les Rocheuses et les Appalaches ont révélé que bien que les familles diverse écologiquement et les familles généralistes étaient dominées par quelques espèces, les groupes trophiques ne prédisent pas toujours avec précision les patrons de dominance/uniformité.

CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW

General introduction

Alpine habitat, as determined by elevation, is a zone of treeless vegetation, often called the "land above the trees" (National Park Service, 2012). It is, by definition, that area in the mountains above the limit of upright tree growth, characterized by soil and weather extremes (Douglas and Bliss 1977). Treeline marks the lower limit of this zone, but it may be fragmented over several hundred meters in elevation (Körner 2003). Summer temperature and length of the growing season are the most important determinants of treeline (Tomback and Kendall 2002) although duration and depth of snowpack also have an effect (Bliss 1971). Using this definition, 3% of the terrestrial surface of Earth is covered by alpine ecosystems and 75% of the world's alpine areas are found in the Holarctic mountains between 30° and 70°N (Nagy and Grabherr 2009). Since alpine regions are created by elevation, not latitude, they can be found in many different places around the world. Closer to the Equator, alpine habitat is found at higher elevations compared with latitudes nearer the poles (Tomback and Kendall 2002; Nagy and Grabherr 2009), ranging from 4000m above sea level in the tropics and subtopics to several hundred meters above sea level in the subarctic (Körner 2003).

Elevation, latitude, and continentality all affect the regional climate (Sømme 1989; Meyer and Thaler 1995). Factors that affect the local climate are primarily exposure to wind and sun (Nagy and Grabherr 2009). Wind will have an impact on evapotranspiration as well as winter snow cover (Bliss 1971), due to high winter winds blowing ice crystals across the vegetation, abrading their cuticles, and causing water stress at the onset of the growing season (Tomback and Kendall 2002). Alpine zones have a large diurnal temperature fluctuation, exposing organisms to cold nights and mornings and hot afternoons (Nagy and Grabherr 2009). This is especially true for tropical alpine areas (Wharton 2002). Seasonal changes are small in the tropics, but at high altitudes rapid temperature changes between sun and shade are due in part to the reduction of haze and dust particles (Sømme 1989). Alpine areas are subject to an array of severe conditions including strong winds, high ultraviolet radiation, low temperatures, a short growing period, and low atmospheric and soil moisture levels (Bliss 1971; Wharton, 2002). All of these, as well as high albedo and low soil temperature (influenced by the substrate), permafrost, and depth and time of snowmelt help shape community patterns (Bliss 1971; Billings 1988) and may strongly influence plant and insect phenology (Inouye 2008; Høye and Forchhammer 2008; Forrest and Thomson 2011). Unfortunately, alpine areas are extremely sensitive to disturbance (Fields et al. 2007), which has been considerable (Tomback and Kendall 2002).

Alpine ecosystems have been assessed as vulnerable and at risk of irreversible damage (Fields et al., 2007). With temperature warming in high mountain areas, upward migration is required for certain species to persist (Fields et al. 2007), and species restricted to the tops of mountains are at high risk of extinction (Wilson et al. 2007). This is due in part to reduced genetic diversity along with increased probability of stochastic extinction (Gottfried et al. 1999). Organisms that do persist in the alpine are forced to deal with this extreme environment, and must cope with less biologically useable energy compared with other biomes (Bliss 1971).

Plants restricted to the alpine are not able to move to different microhabitats for shelter and consequently are forced to adapt to the harsh conditions with an array of strategies (Wharton 2002). They have done this so well that some plants will flower under 10cm of snow cover (Bliss 1971). Some have hairs that trap a layer of air for insulation. In addition to providing insulation, downy or woolly coverings also protect against harmful UV radiation and desiccation. Many alpine plants are small and stay close to the ground, anchored with extensive root systems, to avoid the wind (Wharton 2002). High elevation grasslands are characterized by various forbs, grasses, sedges, shrubs (mostly *Salix*, *Betula*, and Ericaceae in North America), lichens and mosses (Bliss 1971). Forests that border these areas are usually coniferous; in North America they are comprised mostly of *Picea*, *Abies*, and *Pinus* (Bliss 1971).

Alpine and arctic floras probably diversified in the late Miocene and early Pliocene in the central Asian highlands and Rocky Mountains and spread during the Pleistocene (Bliss 1971). Within the Rocky Mountain chain, mid latitudes tend to have plants and animals found at higher altitudes. Swan (1967) attributes this to protection of interior ranges by surrounding ranges. This reduces snowfall and brings a longer growing season. Although depth and time of snowpack will influence community patterns, the longer the growing season, the less important are influences of snowpack (Körner 2003).

Alpine insects

Insects make up a large proportion of arthropods in alpine areas (Edwards 1987). Alpine insects are frequently small and dark, allowing them to survive in thinly oxygenated air and to absorb heat faster, respectively (Wharton 2002). Small size also allows insects to exploit habitats and food resources at micro-scales and allows many to use different components of the same resource (Showalter 2006).
Some alpine insects rely heavily on wind-transported material for sustenance, mostly arthropod fallout (Edwards 1987). Being small also results in sensitivity to changes in temperature and humidity (Kumar et al. 2009). As a consequence of surviving low temperatures, alpine insects often have protracted life cycles (Wharton 2002). Insects here are often brachypterous or apterous, which helps prevent adults being blown into unsuitable habitat (Schowalter 2006). Examples include aphids (Hemiptera), carabid beetles (Coleoptera), grasshoppers (Orthoptera), lacewings (Neuroptera), scorpionflies (Mecoptera), and some flies (Diptera) (Hodkinson 2005). This adaptation can lead to isolation of populations and rapid speciation (Schowalter 2006). However, there are also species with larger wings associated with an increase in elevation in order to cope with flying in thinner air, as is the case with a *Drosophila* species (Diptera) in Chile (Budnik et al. 1988). Along elevational gradients there may also be increased melanization in

many species including spittlebugs and leafhoppers (Hemiptera), ladybird beetles, (Coleoptera) grasshoppers, and butterflies (Lepidoptera) (Hodkinson 2005).

Much of the research on alpine insect diversity focuses on aquatic species, the effects of climate change, and/or genetic work. The Rocky Mountain Apollo butterfly, *Parnassius smintheus*, for example, has received considerable attention in the context of the effects of climate change (DeChaine and Martin 2004, 2006; Illerbrun and Roland 2011a; Matter et al. 2011) and is a commonly studied alpine species (e.g. Matter et al. 2003, 2004; Keyghobadi et al. 2005; Ross et al. 2005; Matter and Roland 2010; Illerbrun and Roland 2011b). The aquatic alpine species studied are frequently Diptera or the EPTs – Ephemeroptera, Plecoptera, and Trichoptera (e.g. Hieber et al. 2003; Finn et al. 2006; Finn and Poff 2005, 2008, 2011).

Alpine soils are also rich with other taxa, such as Coleoptera and Diptera larvae (Meyer and Thaler 1995) as well as spiders, Acari and Collembola (Wharton 2002; Jing et al. 2005; Bowden and Buddle 2010). Along an alpine elevational gradient, Diptera larvae, Protura, and Homoptera are frequently the most abundant taxa (Jing et al. 2005). Hemiptera, Thysanoptera, and Protura tend to occur only at the lower alpine elevations (Jing et al. 2005). There is a shift in dominant mite taxa with elevation, from Prostigmata to Oribatida (Jing et al. 2005).

Above ground, spiders and Acari are extremely abundant as well (Wharton 2002), but alpine taxonomic diversity also consists of many Hymenoptera, Lepidoptera, Coleoptera, and Diptera, the latter of which make up a large portion of both the soil and above-ground fauna, although their distribution may be patchy (Kaufmann et al. 2002).

Within the Hymenoptera, although bee diversity decreases with elevation (Warren et al. 1988; Arnold et al. 2009), bumblebee (*Bombus*) diversity remains relatively high in alpine habitat (Pyke et al. 2011). Bumblebees are important pollinators of some alpine plants, especially at higher elevations. At treeline, flowers of *Polemonium viscosum* (Sky Pilot) are visited by flies, solitary bees, and bumblebees, with over half of seed set a result of the smaller insects (Galen 1995). Higher in the alpine over 95% of seed set is attributed to *Bombus* species (Galen 1995). The flowers accommodate their more frequent bumblebee visitors with more broadly flared flowers (Galen et al. 1987; Galen 1996).

High elevation phenologies differ from those at lower elevation. Both flower phenology and peak bee and wasp diversity occur later in the alpine than at lower elevations (Forrest and Thomson 2011; Pyke et al. 2011). Some have proposed that climate change may lead to a phenological decoupling of plants and insects (Høye and Forchhammer 2008), but for generalist solitary bees at least, even for some of the earliest emerging *Osmia* species, these phenological shifts may not have a strong impact, perhaps due to the fact that both may respond to the same environmental cues, in this case temperature (Forrest and Thomson 2011).

As a group, Lepidoptera are less important pollinators in the alpine than bumblebees. Bergman et al. (1996) found that 69% of observed bumblebees were visiting flowers compared to only one percent of butterflies. Bumblebees tend to have shorter inter-plant distances, and also visit more heads per plant and more plants per foraging trip (Schmitt 1980). Conversely, butterflies have bigger neighborhoods to pollinate. Like the bumblebees, butterflies may be very important for pollination of specific plant species (Porter et al. 1992). However, butterflies may be more important than bees at the order level at high elevations (Arroyo et al. 1982). Butterflies have several advantages over bees in the alpine habitat. They are less energy-demanding pollinators, do not need to care for their young, and can complete their lifecycles more rapidly than bees, thus exposing themselves to less environmental hazards (Arroyo et al. 1982).

In general, butterflies are found to increase in diversity with elevation (Arroyo et al. 1982; Arnold et al. 2009). The Rocky Mountain Apollo (*Parnassius smintheus)*, is common in alpine meadows, and will likely be affected by variability of snow cover and habitat loss brought about by the changing climate (Matter et al. 2011). Warming temperatures result in increased connectivity between alpine meadows (DeChaine and Martin 2006). Natural climate cycles have promoted habitat expansion and mixing of alpine populations (DeChaine and Martin 2006) and have played a role in determining current ranges (Britten and Brussard 1992), but if such warming persists, reduced connectivity of habitats may result in increased genetic differentiation among populations and lower level of gene flow (Keyghobadi et al. 2005). This may increase risk of local extinction, but decrease risk of regional extinction in such a mercurial environment (Roland and Matter 2007). Encroaching treeline may also impact the species since *Parnassius smintheus* larvae prefer to feed on host plants some distance away from this border (Illerbrun and Roland 2011a).

Another common alpine butterfly, the Labrador Sulphur (*Colias nastes*) displays higher rates of melanism at high elevations. These dark individuals are better adapted to the cold alpine environment, being more active, and traveling farther than lighter individuals (Roland 2006). Increased melanism also results in faster emigration and more frequent and longer feeding behaviours (Roland 1982). At high elevations, paler individuals are preyed on more heavily than dark individuals.

Although beetles are not as prevalent in alpine systems (Arnold et al. 2009), they also exhibit a gradient. Similar to bees, higher elevations show decreases in beetle diversity (Arnold et al. 2009). Perhaps because there is low alpine beetle diversity, there has been relatively little research on the group. Carabidae has been a frequent focus. Some ground beetles, such as *Pterostichus surgens*, are found only in the alpine meadows of the Rocky Mountains (Short and Elias 1987). Others, such as *Amara alpina*, are found more broadly in alpine environments (Reiss et al. 1999). Alpine carabids are well adapted to their environment and may be capable of responding to any increase in prey that would be caused by an increase in temperature (Nash 2011). Other alpine beetle families that have been studied include Hydrophilidae, Staphylinidae, and Dytiscidae (Short and Elias 1987; Franzén and Molander 2011).

Clearly, insects are responsible for the majority of pollination in alpine areas. This may drive the flower color seen in this area. Bliss (1971) reported white flowers as unattractive, purple and blue-black flowers as attractive, and yellow, with or without ultraviolet coloration, as the most visited by insects. Lázaro et al. (2008) show this may be due to bee preference, with honey and bumble bees preferentially selecting purple or pink flowers, whereas solitary bees, as well as flies, beetles, and ants choosing yellow flowers. With an increase in elevation, composition of the pollinating fauna shifts. Beetles and butterflies become less important than bees and flies (Körner 2003; Arnold et al. 2009). At the highest elevations, dominance shifts from Hymenoptera, more specialized pollinators, to generalist Diptera pollinators (Bliss 1971; Makrodimos et al. 2008; Arnold et al. 2009). Of the pollinating fauna below 2000m, Hymenoptera account for 44–59% and Diptera for 8–31%, whereas above 2000m, Diptera account for 33–63% and Hymenoptera for 13–41% (Warren et al. 1988). At low elevations, flies tend to visit white flowers, whereas at higher elevations, they visit both white and yellow flowers, perhaps due to lower bee abundance (Lázaro et al. 2008).

Alpine Diptera

Diptera fill many ecological roles and occupy a range of trophic groups including predaceous, phytophagous, parasitic, and saprophagous (Marshall 2006). Ecological diversity can be high even within a single family (Triplehorn et al. 2005). Small body size allows Diptera to exploit many components of the same resource (Schowalter 2006) and additionally allows them to reach high population densities (Stork and Blackburn 1993). The diversity, abundance, and ecological importance of Diptera in alpine zones underline the need for more baseline research on diversity patterns in alpine flies.

Although the nematocerous Diptera dominate in both biomass and abundance in alpine habitat (Kaufmann et al. 2002), higher flies (Brachycera) may be easier study taxa due to their more robust nature when collecting and better overall taxonomic resolution. Muscidae, Phoridae, and Empidoidea are some of the most prevalent Brachycera in alpine habitats (Kaufmann et al. 2002) as are Syrphidae (Makrodimos et al. 2008; Ssymank et al. 2008), Anthomyiidae (Abbott 2002; Konno 2006), and Tachinidae (Primack 1983). Muscoid flies (Muscidae, Anthomyiidae, Scathophagidae) as a group are quite common in alpine areas (Shaw and Taylor 1986; Kearns 1992). Less important for pollination, but similarly high in abundance, are Chloropidae and Agromyzidae (Boucher and Wheeler 2001), both of which are diverse in open habitats dominated by grasses and forbs. Diptera are the dominant insects in alpine habitat in terms of abundance (Levesque and Burger 1982).

Adult Syrphidae are extremely important as pollinators, with most of the roughly 6,000 species worldwide having pollination roles; syrphid larvae also act as biological control agents (Ssymank et al. 2008). They are some of the most common insects in alpine habitat (Levesque and Burger 1982; Kudo 1993; Larson et al. 2001; Konno 2006). In New Zealand, this has a strong affect on the montane floral color scheme, with over 70% of flowers white or near-white (Campbell et al. 2010).

Calyptrate flies are also very common (Shaw and Taylor 1986). Different families within the group may be dominant depending on the area studied. In general, Anthomyiidae, Muscidae, and Tachinidae are all abundant in the alpine (Levesque and Burger 1982; Primack 1983; Shaw and Taylor 1986; Kearns 1992; Konno 2006; Campbell et al. 2010). Calliphoridae may also be important as they are some of the first to emerge after winter (Campbell et al. 2010), although they are not as abundant (Primack 1983).

Empididae (*sensu lato*) are another family often associated with high elevation, although their abundance is not consistent. In some cases, they are some of the most common flies (Kudo 1993; Larson et al. 2001; Konno 2006), whereas other studies report them as rare (Levesque and Burger 1982; Primack 1983; Shaw and Taylor 1986). Their abundance may be more related to latitude than elevation. Empidids, as well as muscids, are the most widespread flower-vising families in the arctic. Although arctic and alpine areas are similar, they should not be too readily compared. The main difference is in temperature; arctic temperatures are constantly low, compared to the diel fluctuation in the alpine. Alpine areas should have more species, shorter development, stronger soil bacterial activity, and faster turnover of organic substance than arctic areas with equivalent medium summer temperature (Remmert and Wunderling 1969).

Many other Diptera families may be frequently encountered in the alpine, but usually in lower abundance. These include Dolichopodidae, Stratiomyiidae, Tabanidae, Asilidae, and Bibionidae (Primack 1983). Abundance and diversity of acalyptrate Diptera in the alpine has not been well documented (see Larson et al. 2001 for review of literature). Chloropidae and Agromyzidae are two acalyptrate families that are particularly diverse in alpine habitats (T.A. Wheeler, unpublished data). Previous studies have shown that Agromyzidae are widespread and diverse in high elevation grasslands (Boucher and Wheeler 2001), although most other records of alpine agromyzids are in specimen lists within taxonomic papers. Similarly, alpine chloropid diversity is not well documented except in scattered taxonomic papers.

Diptera are crucial for pollination services, especially at high elevations (Kearns 2001). With at least 71 families containing anthophilous species they are pollinators of over 100 cultivated plants, and many more uncultivated (Larson et al 2001). They are the major pollinators in montane, alpine, and arctic areas and are among the dominant insects in these habitats (Kearns 1992). Not only do flies get food (pollen and nectar) from flowers, they also receive shelter, mates, protection from predators, floral heat, and oviposition sites (Larson et al. 2001; Kearns 2002). Despite the significance of flies, concerns about pollinator declines in North America have not extended to dipteran pollinators (Kearns 2001; Ssymank et al. 2008).

Yellow and white flowers are widespread in alpine habitats because these colors are most attractive to Diptera pollinators (Pickering and Stock 2004; Lázaro et al. 2008; Makrodimos et al. 2008). Although the prevalence of white flowers shows a slight increase with elevation in many areas (e.g. McQuillan 2002; Arnold et al. 2009), this is not necessarily statistically significant (Arnold et al. 2009). However, this increase may suggest an appeal to less specialized pollinators (McQuillan 2002). It may also reveal the importance of Diptera in this habitat, considering the unattractiveness of this color to other insects (Bliss 1971; Lázaro et al. 2008).

Patterns and components of diversity

One of the early objectives of ecologists was to explain the spatial patterns of species distributions (Wallace 1876) and documenting these patterns has remained an integral part of ecology. Partly because of the vast number of species on Earth and partly because of the complexity of ecological systems, this task is far from completed (Rosenzweig 1995). Baseline studies are still required on many taxa and habitats before their diversity patterns can be described and analysed in a meaningful way. Such analyses are necessary to gain potential predictive power for testing ecological hypotheses (Holloway and Stork 1991), to document change over time (Schaffer et al. 1998), and to build a framework for future ecological, systematic, or other work.

Whittaker (1972) divided diversity into three components: alpha- (α), beta- (β), and gamma- (γ) diversity. The alpha-diversity is representative of the average local species richness, beta-diversity is richness among sites, or turnover between sites, and gamma-diversity is the total species richness for the extent of the area sampled.

Originally, Whittaker (1972) defined gamma-diversity as the product of alpha- and beta-diversities. Later, Lande (1996) used additive partitioning ($\gamma = \alpha + \beta$) using Whittaker's terms (but see Cody 1975), although the idea itself was not entirely new. Additive partitioning allows for easier, direct comparison of the different components of diversity since they all have the same units (Fournier and Loreau 2001; Veech et al. 2002). A multiplicative method tends to overestimate gamma-diversity when samples or communities share species (Lande 1996). Differences between observed and expected partitions may be due to ecological processes that lead to a non-random dispersion of individuals such as intraspecific aggregation, habitat selection, and limited dispersal capacity (Veech et al. 2002).

Many other researchers have since embraced additive partitioning. Loreau (2000) encouraged the study of the relationships between alpha- and beta-diversities at multiple scales, and the processes that determine these relationships. Likewise, Veech et al. (2002) explained the importance of additive partitioning for testing ecological theory concerned with the determinants of species diversity at multiple spatial scales. Gering and Crist (2002) helped start this investigation and found that dominance switches over a range of spatial scales. Alpha-diversity becomes more important than beta-diversity at broader scales and vice versa. Additive partitioning has been used to evaluate spatial patterns of insect species diversity and develop conservation strategies (Gering et al. 2003), to test effects of habitat fragmentation on beetles (Fournier and Loreau 2001), and to identify diversity patterns in various arthropod taxa (Gering and Christ 2000; Summerville et al. 2003; Novotny et al. 2007; Lindo and Winchester 2008; Ribeiro et al. 2008; Levesque-Beaudin and Wheeler 2011), plants (Wagner et al. 2000), and birds (Kattan et al. 2006). Crist and Veech (2006) claimed that recognition of the linkages among additive diversity partitions may help improve approaches to analyzing and comparing species diversity and will lead to a better understanding of how species diversity is influenced by spatial and temporal scales of sampling. Although additive partitioning is gaining in popularity, there are criticisms. Jost

(2007) claimed that beta-diversity in this system is dependent on alpha-diversity. This causes spurious results when beta-diversity values of areas with different levels of alpha-diversity are compared.

The role of scale

Species diversity patterns must be considered in the context of scale because scale has a profound impact on apparent patterns (Levin 1992). At the finest[1] scale - the grain or focus - factors affecting patterns include many local biological interactions (Wiens 1989). These can be temporal (seasonal changes, the flowering time of a host plant, when a stream starts flowing, etc.) or spatial (spacing between host plants, structure of the substrate, etc.). Webs of indirect effects may also be created at fine scales. Local factors influencing these biological interactions are primarily exposure to wind and sun, which will affect evapotranspiration, and winter snow cover (Bliss 1971), local seasonality, geomorphology, the geological history of the area, as well as the biota present (Schowalter 2006; Nagy and Grabherr 2009).

At the broadest scale - the extent - physical processes are usually the dominating influence on patterns found. These include continental boundaries, the presence of mountains or lakes, and general weather patterns (Wiens 1989). Weather patterns are not uniform across the globe. Regional climate is affected by variation with latitude, general weather circulation patterns, and distance from the ocean (Nagy and Grabherr 2009).

Although there has been a trend of increased research interest in the effects of scales and spatial hierarchies over the past decade or so (Rahbek 2005), the effects of scale are not often adequately addressed (Whittaker et al. 2001). Patterns and heterogeneity of different variables have been shown to change

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[1] The terms fine and broad will be used in place of small and large to avoid confusion with geography terms where sizes are in ratios and an ecologist's small scale (1: 100,000) is actually a geographer or cartographer's large scale (1: 20).

when viewed at different spatial scales (Whittaker et al. 2001). For example, Great Barrier Reef fish composition is unpredictable at the local scale, but at a broader scale, composition becomes more predictable due to niche diversification and habitat selection (Wiens 1989). Scale of species ranges should also be considered. Species with small and medium ranges show more complex patterns than species with large or mixed range sizes (Colwell et al. 2009).

Changing the extent or grain of a study may also affect the patterns and processes (Rahbek 2005). Grain is a very important factor to consider (Palmer and White 1994). Coarser grain size causes mean, median, and modal range size to make up a bigger proportion of the extent and can therefore result in overgeneralizations of patterns of range size distributions. Furthermore, rare species are less likely to be recorded as grain size increases, especially if they are scattered (Wiens 1989). Pattern bias and distortions tend to increase with grain size (Rahbek 2005).

There are many consequences of disregarding the effects of scale. The lack of consensus of broad-scale patterns may be attributed to the way we standardize our basic descriptions of patterns before even comparing and explaining them (Rahbek 2005). There is also potential for research to show fundamentally different species richness patterns than actually exist (Rahbek 2005). For example, at the local scale in the northeastern U.S., presence of *Empidonax minimus* (the Least Flycatcher) negatively influences the distribution of the American Redstart, but at the regional scale the species are positively associated (Wiens 1989). Mixed observations may result from studying incomplete gradients, failure to deal with uneven sampling, or disregarding species' range sizes and/or extent of the study.

Certain broad-scale patterns remain more contentious than others. Latitudinal and elevational gradients are two well-known examples that are impacted by the scale at which they are observed.

Elevational diversity patterns

Intuitively, “alpine” evokes a sense of elevation. In alpine environments, elevation often determines diversity (Meyer and Thaler 1995). Elevational gradients have been extensively studied, depending on the taxon. Proportionally more studies of elevational gradients have been carried out for plant and vertebrate taxa than for invertebrates (Rahbek 1995, 1997; Kessler 2001; Grytnes 2003; McCain 2004, 2005, 2007, 2009; Grytnes and Beaman 2006; Grytnes et al. 2008; VanDerWal et al. 2008; Pickering and Butler 2009; Rowe and Lidgard 2009; Sang 2009). Plants are particularly useful study taxa for several reasons: they do not move, they are relatively easy to identify, and there is ample background information available. Vertebrates are also relatively easy to study due to their large size and ease of identification.

Many of the invertebrate studies have focused on Lepidoptera (Holloway 1987; Fleishman et al. 1998; Pyrcz and Wojtusiak 2002; Axmacher et al. 2004; Brehm et al. 2007; Beck and Chey 2008; Chen et al. 2009). Other taxa that have been studied less frequently include wasps (Kumar et al. 2009), ants (Sanders et al. 2003), flies (Wilson et al. 2007), true bugs (Whittaker and Tribe 1996), and spiders (Bowden and Buddle 2010). Other studies have examined invertebrates in general (Wolda 1987; McCoy 1990; Olson 1994).

The elevational gradient is often assumed to mirror the latitudinal gradient (Stevens 1992) although a literature review (Rahbek 1995) concluded that elevational gradient patterns often do not mirror latitudinal gradients. However, elevational gradients may provide an easier system in which to study the patterns and drivers of spatial variation in diversity (Sanders and Rahbek 2011). There are multiple reasons for this: a single mountain is easier to observe and perform manipulative studies on, has less variation in history and climate, has a smaller extent, and each is essentially a replicate (Sanders and Rahbek 2011).

Two major diversity patterns are found along elevational gradients (Rahbek 2005). The first is that of a linear, or, monotonic decline in species richness as one moves up a slope. The second, which is becoming more commonly documented, is a mid-elevational peak in species richness. Both types of studies can be faulted for not addressing the effects of scale (Whittaker et al. 2001), which may have profound impacts (Rahbek 2005). However, justification can be provided for both arguments.

It has been proposed that a monotonic decline in species richness with elevation may be due, at least in part, to the decrease in habitat area at higher elevations (Rosenzweig 1995). With less area available, fewer species are able to coexist. In addition, reduced resource diversity, partially due to climatic conditions that continue to worsen upslope (Rosenzweig 1995), creates an increasingly unfavorable environment for species that must adapt and specialize in order to survive here. This is especially hard with reduced productivity (Rosenzweig 1995). Another hypothesis is Rapoport's rule (Stevens 1992), which states that climates at higher elevations are more variable, so species at higher elevations can tolerate more variability and therefore have larger elevational ranges (Sanders 2002). Conversely low elevation species have lower tolerance and smaller ranges, inflating richness and leading to a monotonic decline (Sanders 2002). This pattern has been found in many taxa, such as butterflies, trees, amphibians, bats, and ants (Stevens 1992; Fleishman et al. 1998; Gaston 2000; Majer et al. 2001).

It is also quite common for elevational gradients to exhibit a mid-elevation peak in species richness. There are several proposed causes for this pattern. One is the presence of a mid-domain effect (MDE) (Rahbek 1995; Lees et al. 1999; Colwell and Lees 2000; Jetz and Rahbek 2001; Kolef and Gaston 2001; McCain 2003). This is generated when there is increasing overlap of species ranges toward the center of the domain because the extent of the elevational ranges of species are bounded by the highest and lowest elevation possible in the region (Colwell and Hurtt 1994).

It has also been reported that human disturbance at low elevations pushes species upslope, simply moving a once low elevation peak to mid-elevation (McCoy 1990). Another way of explaining this phenomenon is by way of the Goldilocks hypothesis. Essentially, the “ends are bad” and the “middle is good”. The ends are bad due to high predation on the bottom, resource restriction on the top, and climatic severity on either end (McCoy 1990), such as disturbance, floods, droughts, and intense heat at low elevations and cold temperatures, low humidity, strong winds, and large diurnal temperature fluctuations at high elevations (Wharton 2002). Mid-elevations have the largest resource base, the highest photosynthate levels, and fewer climatic extremes (McCoy 1990), making it easier to survive.

Some of the more commonly stated underlying causes for a mid-domain effect include climate and productivity (Grytnes 2003, Rowe 2009), source-sink dynamics (Kessler et al. 2011), disturbance (Bunn et al. 2011), area (Rosenzweig 1995; Romdal et al. 2005), and geometric constraints (Sanders 2002; Rowe et al. 2009). As discussed earlier, scale is a key component in any study. Elevational gradient patterns are no exception and may change depending on the scale studied (e.g. Pickering and Butler 2009). The conclusion to draw from this is that no single mechanism is responsible for all elevational diversity gradients (Sanders and Rahbek 2011).

Several studies demonstrate the range of responses found in invertebrate taxa. It can be difficult to find consistent patterns. Even the geometrid moths, which have been well studied (Axmacher et al. 2004; Brehm and Fiedler 2004; Brehm et al. 2007; Beck and Chey 2008; Axmacher et al. 2011) show multiple patterns. Many lepidopteran families and groups of families display mid elevation peaks in richness (Holloway 1987; Gutiérrez 1997; Fleishman et al 1998; Pyrcz and Wojtusiak 2002; Brehm et al. 2007; Beck and Chey 2008; Munoz and Amarillo-Suarez 2010; Rosser et al. 2012). Others decrease with elevation (Axmacher et al

2004; Munoz and Amarillo-Suarez 2010; Axmacher et al. 2011), while still more exhibit the opposite (Wettstein and Schmid 2001).

Less researched taxa also have variable patterns. Within the Hymenoptera, ant richness has been found to increase (Sanders et al. 2003), peak at mid elevations (Sanders 2002), and decrease with elevation (Majer et al. 2001). Vespid wasps also decrease with elevation (Kumar et al. 2009). Elevational gradients in other taxa have not been investigated thoroughly enough to show clear patterns. Orthoptera and Coleoptera richness may decrease with elevation (Wettstein and Schmid 2001; Touaylia et al. 2011) while Diptera diversity may tend to peak at mid elevations (Wilson et al. 2007; Hackenberger et al. 2009). Hodkinson (2005) also provides an excellent overview of elevational variation in species richness in assorted insect communities, reinforcing the conclusion that there exists a variety of responses of richness to elevation. More research needs to be undertaken before we gain a strong predictive ability.

Latitudinal diversity patterns

The two main patterns found in elevational gradients have been found along latitudinal gradients as well. It has become largely accepted that there are more species in the tropics, steadily decreasing towards the poles. Wallace (1878) was the first to propose this and it is one of the oldest and most thoroughly studied patterns in ecology (Arita 2005). Numerous reports in the literature support this (e.g., Dobzhanksy 1950; Kusnezov 1957; Wolda 1987; Majer et al. 2001; Lyons and Willig 2002; Progar and Schowalter 2002; Hillebrand 2004; Andrew and Hughs 2005).

Although there is no single best explanation for a latitudinal monotonal decline in richness, more than 30 ecological and evolutionary hypotheses have been proposed for it (Arita 2005). There are, however, some explanations for higher diversity at the tropics. The tropical biome is arguably the largest biome (Rosenzweig 1995). With more area, theoretically more species are able to coexist.

The environment is also more stable at the tropics, having less severe conditions for species to adapt to and therefore allowing them to persist (Rohde 1992). Historically, glaciations prevented many species from inhabiting the northern regions for as long a continuous period as the tropics. It is possible that the northern regions simply have not reached saturation yet and niches are still being filled (Rohde 1992). Surface area and energy availability, speciation and extinction rates, environmental complexity and stability, patterns of competition and predation are all factors that could help explain high diversity in the tropics (Koleff and Gaston 2001). The tropics have more energy, more mutation, and shorter generation times, and therefore may support more rapid speciation (Rohde 1992; Rosenzweig 1995; Koleff and Gaston 2001).

Rapoport's Rule (Stevens 1989) may also provide an explanation. In a latitudinal context, this rule states that species ranges are largest in the more climatically intolerable areas such as near the poles and at high elevations. Smaller range sizes in the tropics allow for more species to coexist, which leads to higher species richness, and a monotonic decline (Stevens 1989). However, many claim that this effect is a local phenomenon only (Rohde 1996).

Similarly, there are explanations supporting a mid-latitude peak in richness. Weather is not uniform across the globe. Regions above the equator receive a range of different weather types due to weather circulation patterns, effects of the sun, and distance from the ocean (Nagy and Grabherr 2009). The wide range of habitat types may also be partially responsible for a mid-latitude peak (Rosenzweig 1995). Increased habitat heterogeneity above the equator provides many niches for species. In conclusion, a steady decrease in richness from the equator towards the poles should no longer be considered an ecological dogma. Many other patterns have been found; some studies have found multiple patterns depending on the scale observed (Progar and Schowalter 2005; Keil et al. 2008).

Objectives

Alpine research has been relatively thorough for certain taxonomic groups such as butterflies (e.g. Swengel 1990; Kocher and Williams 2000; Matter et al. 2011) and plants (e.g. Kikvidze 2005; Johnson et al. 2007), but much less so for other groups, such as Diptera, despite the fact that flies are crucial players in these environments, providing up to 63% of the pollination services here (Warren et al. 1988). This project addresses two components of the diversity of higher Diptera in alpine meadows: 1) community structure and species turnover of higher Diptera in alpine habitat along a latitudinal gradient, and 2) the effect of ecological diversity on species abundance patterns within families in alpine meadows. The first component has been addressed in other types of habitat, such as forest (e.g. Dajoz 2000; Summerville et al 2003; Levesque-Beaudin and Wheeler 2011), but has not been studied exclusively in alpine areas, where it is highly relevant in light of climate change and conservation implications (Kearns 2001). The first objective uses data collected from the alpine meadows in the front range of the Rocky Mountains, while the second objective uses additional data from treeless high-elevation meadows in the southern Appalachian Mountains to determine if similar patterns are found in alpine meadows with different geological and biotic histories.

Predictions

With regard to the first research objective, it was predicted that beta-diversity would be higher between sites than between sample areas within the same site due to isolation and low dispersal of the study taxa. This has been found in other studies (e.g. Hui 2008). A latitudinal turnover in species assemblages was also predicted to result in a mid-domain effect.

For the second objective, ecologically uniform Diptera families that are specialized to a particular resource were expected to show higher evenness whereas families comprised of generalists, or showing broad trophic diversity should tend to be dominated by one or a few species.

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CONNECTING TEXT

Despite the importance and vulnerability of alpine habitats, there has been relatively little study of arthropod communities in these habitats in North America. This is especially true of the Diptera, one of the most diverse and ecologically important groups of arthropods in the alpine zone. Most studies to date of alpine Diptera have focused on aquatic flies, or on selected, usually single, families of terrestrial higher flies. The diverse acalyptrate Diptera have been especially ignored, despite their abundance and diversity in alpine habitats. In Chapter 2, I contribute to the baseline data on the species diversity and ecological community structure of selected families of acalyptrate Diptera in high elevation habitats in two North American mountain ranges – the Rockies, and the southern Appalachians. Such baseline inventories and descriptions of ecological structure are necessary first steps in framing more focused ecological questions in future studies.

CHAPTER 2: PATTERNS OF DIVERSITY IN HIGH-ELEVATION GRASSLAND DIPTERA

INTRODUCTION

Although alpine areas are often regarded as cold and desolate, they are in reality teeming with life. Diversity of plants and arthropods is especially high, and flies (Diptera) are one of the most abundant and diverse groups of arthropods in these systems(Kearns 1992). There is, however, relatively little research on species richness and abundance patterns of alpine Diptera. Most research on this order in high elevation habitats deals with aquatic species, and studies usually address climate change impacts (e.g. Lamontagne et al. 1994; Ahumada et al. 2004; Larocque et al. 2006; Shields et al. 2007; Eisen et al. 2008; Finn and Poff 2008; Hamerlik and Bitusik 2009; Forrest and Thomson 2011; Matter et al. 2011). Diptera comprise an incredibly abundant and diverse group (Brown 2001) that performs several crucial roles in alpine habitats (Kearns 2001). A greater understanding of species diversity patterns of alpine Diptera is necessary in order to create a more complete picture of the alpine ecosystem and to predict the effects of changes in these systems (Erschbamer et al. 2011; Li et al. 2011; Malanson et al. 2011).

Species assemblages are almost always comprised of a few very common species and many rare species (Tokeshi 1993, 1999). To test this, species abundance distributions (SADs) can be used to examine patterns (Magurran 1988, 2004) and reveal the relative contribution of rare and common species, even at different spatial scales (Tokeshi 1999), which is particularly useful as scale may change patterns (Wiens 1989; Levin 1992). The scale-dependency of diversity patterns highlights the usefulness of a spatial hierarchical approach to analyzing patterns (Noda 2004).

Community patterns and processes are easier to understand in a spatial context when using a spatial hierarchical approach (Noda 2004). However, patterns of diversity are only properly interpreted within the broad context of regional and historical influences (Ricklefs 2004). For this reason, ecologists should collect data that match the scale of the processes they are studying (Ricklefs 2004). For broad scale patterns, this means collecting local estimates of species diversity in nested sets up to the regional scale (Ricklefs 2004). Nevertheless, changes in sampling design (grain and extent) will advance community ecology by revealing how this affects detected patterns (Noda 2004). Documented diversity patterns to date are mixed, partly due to an avoidance of addressing spatial and/or temporal scale (Whittaker et al. 2001). Patterns along altitudinal and latitudinal gradients are some of the most controversial.

Most species abundance data is on a few favored groups, such as trees, mammals, birds, butterflies, and ants. It is often assumed that variation in diversity of these groups closely resembles that of unrepresented groups (Colwell and Coddington 1994). However, relying on just a few groups does not optimally preserve others (Colwell and Coddington 1994). Similarly, there is no one mechanism that will adequately explain all examples of a given pattern (Gaston 2000). Observed patterns vary with spatial scale (Levin 1992; Wiens 1989; Rahbek 2005). Processes that operate at regional scales influence patterns observed at local ones, and the relative balance of causal mechanisms means there will invariably be variations in and exceptions to any given pattern (Gaston 2000).

It is therefore necessary to study an array of taxa at varying scales, especially ecologically dominant groups, in order to glean as much information as possible about species diversity and abundance patterns in a given ecosystem. This research addressed such patterns in high-elevation grassland Diptera. I examined the community structure, species turnover, and species abundance patterns of selected families of higher Diptera in alpine habitat along a latitudinal gradient. Four alpine sites were sampled in the Rocky Mountains; one each in Colorado and Wyoming, and two in Alberta. Six sites were sampled in the southern Appalachian Mountains, all in North Carolina.

MATERIALS AND METHODS

Study sites and sampling design

The primary fieldwork for this study was carried out along the eastern edge of the Rocky Mountains in the summer of 2010. The Rocky Mountains, raised around 70-40 million years ago (USGS 2004), form the backbone of the North American continent (Billings 1988). This range extends from New Mexico up to the northernmost part of British Columbia and has vast expanses of forest as well as alpine areas (Cannings 2007). The Wyoming Basin, a low-lying, arid plain of short grass prairie, cuts the southern Rockies into two distinct ranges. Many species do not cross this barrier (Cannings 2007).

Four study sites in the Rockies (Figure 1) were located in Colorado, Wyoming, and Alberta, which had two. Each site had multiple sample areas in alpine meadow habitat. Sample areas were in one of three ecozones – below treeline, at treeline, or above treeline.

Sampling was undertaken using an unbalanced nested design with two scales. More standardized replication was desired, but unfortunate weather allowed for uneven sampling only. The finest scale was the sample area. Some sample areas were sampled more than once, while others were only visited once. Sample areas were habitat patches of alpine meadow, some within a forest landscape mosaic. The highest scale was at the site level.

Site 1 in Colorado had three sampling areas: Spring Creek Pass (3332m; 37.9416, −107.1606), Little Molas Lake (3487m; 37.7379, −107.6949), and Molas Pass (3280m; 37.7511, −107.7125). These areas were the driest areas at which we collected, with ground cover ranging from 60% to 85%. Some of the most dominant plants in these areas included mostly Poaceae species with many *Taraxacum* and *Fragaria*. Sparse *Ribes*, some *Mertensia*, *Thlispe*, *Ranunculus*, *Castellejas*, and *Artemesia* were also present.

Site 2 in Wyoming also had three sample areas: Bald Mountain (2860m; 44.7886. −107.8126), an area in the Bighorn National Forest near Dayton (2245m; 44.7995, −107.3675), and Tongue Creek (2450m; 44.8062, −107.5399). Here ground cover was very high, ranging from 90% to 100%. Dominant plants in these areas included, again, mostly Poaceae species, as well as *Lupinus* and *Geranium*. Others present included *Myosotis*, *Potentilla, Polygonom*, *Clematis*, *Pulsatilla*, *Dodecatheon*, *Taraxacum.*

Site 3 in Waterton Lakes, Alberta had six sample areas: Redrock Parkway (1390m; 49.0996, −113.9061), Ruby Ridge (1676m and 1800m; 49.00683, −114.0082 and 49.0706, −114.0081 respectively), Rowe Creek (1722m; 49.0609, −114.0188), and Coppermine Creek (1509m and 1634m; 49.1066, −113.9600 and 49.1104, −113.9579 respectively). Ground cover at these areas was high for the most part, between 80% and 100%, but a couple areas had poor cover at around 55%. Dominant plants in these areas included Poaceae, *Lupinus*, *Mertensia*, *Antennaria*, *Cerastium*, and *Juniperus*.

Site 4, also in Alberta, contained four sampling areas: Powderface Trail (1759m; 50.9198, −114.9213), Powderface Ridge (2097m and 2146m; 50.8187, −114.8394 and 50.8194, −114.8368 respectively), and Jumping Pound Mountain (2222m; 50.9506, −114.9088). Ground cover ranged from 65% to 90%. Dominant plants in these areas included Poaceae, *Potentilla*, *Myosotis*, *Arctostaphylos*, *Hedysarum*, *Dryas*, and *Juniperus*

Data from the Appalachian Mountains, collected in 2008, was used to compare species abundance distributions of a few key families from different types of high elevation habitat. The sampling sites were all in North Carolina (Figure 2), an area unaffected by the most recent glaciations (Frick-Ruppert 2010). The Appalachian Mountains have a different history from the Rockies. These mountains are much older, raised approximately 450-270 million years ago (Clark 2008), and have thus been worn down comparatively more by wind, ice, and rain (Frick-Ruppert 2010). Instead of sharp jagged peaks like the Rockies, rolling hills are more typical of the Appalachians. The high peaks of this range, once a towering 8,000m, now stand at 2,000m (Frick-Ruppert 2010).

Six sites were sampled. Three southern sites were in Pisgah National Forest, Haywood County. Sam Knob (SAM) was a relatively level high-elevation meadow that had previously been used as a hayfield and pasture. It was dominated by mixed grasses and forbs, with very few shrubs. Black Balsam Knob (BBK) was a north-facing slope with relatively natural vegetation dominated by grasses, a variety of forbs, and scattered shrubs (*Rhododendron*, *Azalea* and other Ericaceae). Little Pisgah Mountain (PIS) was a north-facing slope with similar understory vegetation to BBK, but scattered tree cover dominated by small oaks, giving it a more savanna-like appearance.

Three northern sites were located in the Roan Mountains on the Tennessee/North Carolina border in Mitchell and Avery Counties. Round Bald (ROND) and Jane Bald (JANE) were both east-facing open slopes dominated by natural assemblages of mixed grasses and sedges, ferns, several forbs, and scattered ericaceous shrubs. Grassy Ridge Bald (GRAS) was similar in elevation and aspect, but maintained as an open area by regular mowing; plant diversity was lower, with dominant grasses and sedges and a forb community dominated by *Erythronium* lilies, and scattered other genera, most shrubs were mown down.

Diptera sampling and preparation

Sampling in the Rockies was conducted from 22 June to 16 July, 2010 to collect during the peak of adult Diptera activity (Totland 1994). Sweep netting was carried out by two people at each sample area for one hour each with all samples stored in vials of 95% ethanol.

Diptera were removed from sample residues and dried using Hexamethyldisilazane (HMDS) and mounted on points. All acalyptrate Diptera and several Schizophora families were identified to morphospecies or to named species using published taxonomic keys and expert confirmation. All specimens are deposited in the Lyman Entomological Museum (McGill University, Ste-Anne-de-Bellevue, QC).

Environmental variables

Environmental variables measured include slope angle, latitude and longitude using Global Positioning System (GPS) coordinates, elevation, percent ground cover, ecozone, and some of the dominant plants. Slope angle, ground cover, and ecozone were rough estimates only. GPS coordinates and elevation was recorded in the middle of the sample areas to compensate for very steep slopes. Other site characteristics (e.g. surrounding trees, presence of water bodies, etc.) were noted as extra information.

Data analyses

For each sample area in the Rocky Mountains, multiple collection efforts were pooled. Rarefaction curves were generated to assess sampling effort. Individual-based rarefaction was used instead of sample-based rarefaction. The uneven sampling effort at the sites made sample-based rarefaction less applicable (Buddle et al. 2005). Individual-based rarefaction reduces the sample data to a common abundance level in order to directly compare species richness of different communities (Magurran 2004). This was performed with EcoSim 7.71 using 10,000 randomizations (Gotelli and Entsminger 2007) to compare species richness of the sites. Abundance was standardized at 645 individuals. Total estimated species richness was estimated for the Rocky Mountain sites using the non-parametric abundance-based coverage estimator (ACE). This is based on abundances of species with 1-10 individuals, where the number of species with more than 10 individuals is added to complete the estimate (Magurran 2004). ACE results were generated with EstimateS 8.2 using 10,000 randomizations (Colwell 2006).

Rank abundance curves were generated in Excel 2011 for selected families from both the Rocky and Appalachian Mountain sites in order to display dominance / evenness patterns for various trophic groups. Within each family, the abundance of each species is represented as a percentage of the total diversity of all species within that family. Families were chosen based on ecological role so as to compare the patterns of different functional groups.

Additive partitioning was used for the Rocky Mountain data to compare the different components of diversity at both the local and regional scale, using the program PARTITION version 2.0 (Veech and Crist 2007). This program conducts randomization tests to determine whether the observed diversity partitions are statistically different from those expected by chance (Veech and Crist 2007). The null hypothesis was the absence of any difference between observed alpha- and beta-diversities and a random distribution. The random distribution was generated with 10,000 randomizations (individual-based with weighted data) (Veech and Crist 2007). Results were statistically significant with a P value of 0.05 or less. This is determined by assessing the probability of obtaining a test statistic at least as extreme as the one that was actually observed. Partitioning was done for the whole acalyptrate community, as well as for rare versus common species. Species were categorized as rare and common based on Gering et al. (2003), where rare species represented <0.05% of the total number of individuals and common species represented >0.5% of the total.

Co-occurrence analysis was used for the Rocky Mountain data to determine co-occurrence patterns at the regional and site levels, using the C-score index (Stone and Roberts 1990) with fixed rows and fixed columns. This combination was used due to its surprisingly good statistical properties and its ability to limit the risk of Type I and II error (Gotelli 2000). The C-score index itself does a good job of detecting significant patterns in non-random datasets that have a good deal of random noise in the co-occurrence patterns (Gotelli 2000). A null distribution was obtained with 5,000 iterations of the matrix, to see if the observed C-score index differed significantly from the null hypothesis that the number of checkerboard pairs is random, thus that co-occurrence does not occur. All co-occurrence analysis was done in EcoSim 7.71 (Gotelli and Entsminger 2007).

Community composition of the Rocky Mountain data (differentiation or similarity of species assemblages in sites) was analyzed based on log-transformed (log (x + 1)) relative abundance of species excluding singletons and doubletons. Using non-metric multidimensional scaling (NMDS) (Clark 1993), an initial 6-dimensional analysis was performed, stepping down in dimensionality until the number of ordination axes was sufficient to achieve low stress values. The final ordination was a 3-dimensional ordination using Sorensen (Bray-Curtis) distances, 100 runs with real data, and 200 Monte Carlo simulations. Joint plot analysis tested whether environmental variables influenced the species assemblage. Multi-response permutation procedures (MRPP) (Mielke and Berry 2007) verified if the sites were significantly different using pairwise comparison based on Bray-Curtis distances. Because MRPP cannot be applied at the finer scale, sample areas were compared using the Bray-Curtis similarity index in EstimateS 8.2. NMDS and MRPP were performed with PC-ORD 4 (McCune and Grace 2002).

RESULTS

Species diversity – Appalachian sites

In the Appalachians, a total of 8,548 specimens belonging to three target acalyptrate families were collected and sorted to species or morphospecies, representing a gamma-diversity of 51 species (Appendix 1). These families were chosen to represent an array of functional groups that are the same or equivalent to those in the Rockies in order to compare rank abundance patterns in different types of alpine habitats. Of these three families, the Chloropidae were by far the most abundant with 5,834 specimens (68%), followed by Sphaeroceridae (n =

2117, 25%) and Agromyzidae (n = 597, 7%). There were 10 singletons and 6 doubletons (Table 1).

Species diversity – Rocky Mountain sites

In the Rockies, a total of 3,940 specimens belonging to 18 acalyptrate families were collected and sorted to species or morphospecies, representing a gamma-diversity of 166 species (Appendix 2). The most abundant families were the Ephydridae (n = 1534, 39% of total abundance) and the Chloropidae (n = 1145, 29%). Species richness was also skewed with the Agromyzidae (61 species), Chloropidae (33 species) and Tephritidae (21 species) making up 69% of the total species richness. There were 66 singletons and 29 doubletons (Table 2).

ACE values estimated that 66% of the expected species richness for all sites was collected. Individual site values were extremely variable, ranging from 38% to 79% (Table 2). Waterton Lakes, AB (site 3), had the most individuals and species collected, but Wyoming had the highest rarefied species richness estimate (Table 2). The rarefaction curves for the individual sites did not reach an asymptote (Figure 3), corresponding with the results of ACE. The most notable rarefaction curve is that of Wyoming (site 2), which predicts the highest species richness of all sites. Conversely, rarefied richness estimates put sites 1 and 4 very similar as the least diverse.

Scale and diversity patterns – Rocky Mountain sites

Partitioned data (Figure 4) showed lower alpha-diversity than expected in all groups ($P = 1$), while beta-diversity at all scales was higher than expected ($P = 0$), except $beta_1$ for rare species and all acalyptrates, which was lower than expected ($P > 0.99$) (Table 4). For the entire community, $beta_2$-diversity was responsible for the most diversity at 60% (Figure 4).

$Beta_2$-diversity accounted for most of the richness (71%) in rare species, while alpha-diversity accounted for most richness (42%) in the common species. Rare species ($n \leq 2$) were a major component of the community, accounting for only 3% of the total abundance, but 58% of total richness. Common species ($n \geq 20$) on the other hand accounted for 88% of total abundance, but only 10% of total richness.

Co-occurrence patterns (Table 5) were random at the regional level and all sites except site 3. The observed C-score index (0.7487) at the regional level was not significantly higher than expected with p(observed > expected) = 0.41. At the site level, the C-score index for sites 1, 2, and 4 (0.5420, 0.4216, 0.4835 respectively) were not significantly different either with p(observed < expected) equaling 0.52, 0.31, and 0.34 respectively. Site 3 (C-score index of 1.0743) was significantly higher than expected with p(observed < expected) = 0.05. This means co-occurrence was less than expected, representing a competitively structured community.

NMDS ordination (Figure 5) was used to show species assemblages among all sample areas. A three-dimensional solution yielded a stress value of 8.502. These first three axes combined were able to explain 87.1% of the variance in species composition ($p = 0.005$). All sites were significantly different ($p > 0.05$) based on MRPP except sites 3 and 4. The chance-corrected within-group agreements (A) were all under 0.03, which is considered normal for community ecology data (McCune and Grace 2002). MRPP also showed significant differences between extreme slope angles when categorized from 1 (0-14°) to 4 (45-60°) ($p = 0.02$), but not between any other slope pairwise comparisons. Joint plot analysis showed latitude (cumulative $R^2 = 0.818$), longitude (cumulative $R^2 = 0.731$), and elevation (cumulative R2 = 0.606) explained much of the variance in species diversity. The Bray-Curtis similarity measure found several similarities (similarity index above 0.6) between sample areas in Wyoming and Alberta, but never in Colorado (Table 3).

Trohic comparisons

Families used to assess species abundance distributions were chosen based on ecological habits so as to compare the abundance patterns of different trophic groups. Families selected in the Rocky Mountains (Table 6; Figure 6) were Agromyzidae, Tephritidae, Chloropidae, and Ephydridae. At the regional level, the agromyzids displayed the highest evenness, with the dominant species (*Ophiomyia nasuta*) comprising 15% of all agromyzid specimens. Ephydridae had the highest dominance, with one species (*Philygria debilis*) making up 91% of all ephydrids. Chloropids were intermediate with the dominant species, *Incertella incerta,* making up 46% of the specimens within this family. Tephritids were in between the agromyzids and chloropids, with the most dominant species, *Euarestoides acutangulus*, representing 30% of all tephritids.

These patterns were broken down and analyzed at the site level (Table 6; Figure 6), but only considered when $n \geq 50$. Results show similar patterns with the agromyzids having a long gentle curve and the ephydrids having a short, steep curve, with one dominant species. The chloropids and tephritids fall somewhere in between, but have more varied patterns.

Families selected in the Appalachian Mountains (Table 7; Figure 7) were Agromyzidae, Chloropidae, and Sphaeroceridae. Here, the sphaerocerids have comparable trophic habits and abundance levels to the ephydrids that were selected in the Rockies. At all sites pooled the most dominant species were *Cerodontha dorsalis* (Agromyzidae) at 76%, *Rhopalopterum carbonarum* (Chloropidae) at 39%, and *Leptocera erythrocera* (Sphaeroceridae) at 87%.

When analyzed at the site level (Table 7; Figure 7), again, patterns were only considered when $n \geq 50$. Although one sphaerocerid species was dominant at each site, there were no more than three sphaerocerid species present at any given site. The chloropids maintained their variable patterns, while the agromyzids consistently had steep curves with one species (*Cerodontha dorsalis*) dominating at each site.

Discussion

Although raw species richness and the number of specimens collected were highest at site 3 (Waterton Lakes, AB), rarefaction estimated species richness was higher at site 2 (Bighorn Mountains, WY). Standardizing the data with rarefaction (Gotelli and Colwell 2001; Magurran 2004) overcomes the biases of diversity indices, which may provide contradictory results (Buddle et al. 2005). Rarefaction also reveals the effectiveness of sampling effort. Rarefaction curves for each site did not level off. This may be explained by the large number of rare species, which is generally encountered when sampling at broader scales (Gering et al. 2003; Gabriel et al. 2006, Hui 2008). Due to the increasing number of rare species at increasing scales, rarefaction curves that level off are difficult to obtain, even with extensive sampling.

The increase in species diversity predicted at site 2 in Wyoming may be a result of the sampling effort at this location. This was the only site at which each sample area was sampled twice. ACE still predicted the highest number of species to be present at site 3. ACE predicted the second highest total richness at site 1, a somewhat surprising result since this site had the lowest rarefied species richness estimate. Sampling at this site was confounded by weather problems. A late snowpack followed by an extreme summer drought resulted in this site, and much of the surrounding areas, being extremely dry, leading to delayed flowering (Inouye et al. 2000) and low levels of insect activity (but see Forrest and Thomson 2011). We suspect this is why little was collected, but much was expected, as rarefaction curves for each site did not level off. Conversely, high observed diversity and abundance at site 3 may be related to the sample areas' proximity to many small water bodies in the Waterton Lakes area. Sites 2 and 3 also had the highest ground cover of all sites.

Although the available data was insufficient to allow rigorous analyses of latitudinal and elevational patterns per se, NMDS ordination did show a slight latitudinal turnover of species richness, with latitude, longitude, and elevation as the major variables contributing to species composition. Latitude varied much more than longitude in our samples, and absolute elevation varied more than the transition between forest and alpine zone because of the effect of latitude on treeline (Tomback and Kendall 2002). Alpine sites in Colorado for example were above 3000m, whereas in Alberta the same vegetation transitions were approximately 1000m lower. These results are similar to many other studies that have shown high species turnover with both elevation and latitude (e.g. Rahbek 2005; Hillebrand 2004). The two Alberta sites were not significantly different based on MRPP. The distance between these sites was less than the other sites, and they were most similar in elevation and plant composition.

The Bray-Curtis similarity measures revealed similarities between many sites in Wyoming and Alberta but none involving Colorado. This may be a result of the Wyoming Basin, a large, flat expanse of low elevation short grass prairie that cuts the Rockies into two distinct ranges (Cannings 2007; Rowland and Leu 2011). Climate is arid, with an average annual precipitation of 15-25 cm and vegetation communities are dominated by rolling sagebrush uplands in this 134,000 km^2 area (Rowland and Leu 2011). This is a significant barrier to insect dispersal (Dechaine and Martin 2004), especially small-sized acalyptrate flies, which are often poor fliers. Assemblages of butterflies and plants on either side of the Wyoming Basin have been shown, using population genetics, to be quite different, moreso than amongst populations on either side of the basin (Nice and Shapiro 2001; Dechaine and Martin 2004, 2005a, 2005b). Differences in beetle populations have been found as well (Reiss et al. 1999; Noonan 2001). It appears that this pattern may also hold for acalyptrate Diptera, but a genetic analysis is needed to confirm this.

Dipteran species diversity and composition was non-random at each scale and changed between scales. The scale most responsible for diversity was not the same between rare and common species, with rare species driving the patterns of the whole community. The acalyptrate community varied highly at broad scales, supported by additive partitioning, NMDS, MRPP, and the Bray-Curtis similarity index. This is probably due to the very broad scale of this study. The latitudinal coverage likely resulted in turnover even at the highest scale because of isolation and low dispersal (Hui 2008).

Only common species were driven by finer scales. Common species may have higher dispersal abilities, which will homogenize communities by decreasing beta-diversity (Loreau 2000, Gering and Crist 2002, Cadotte 2006). High dispersal also increases alpha-diversity through rescue effects (Willig et al. 2003) that refill the outskirts of ranges with individuals from the center. Rare species patterns, and thus the acalyptrate patterns in general, were mostly structured by beta$_2$, diversity among sites. Rare species tend to have patchy distributions and specific habitat requirements (Tokeshi 1999), a possible explanation for the significantly lower than expected alpha-diversity. Rare species tend to aggregate together, and thus are less likely to be collected (Tokeshi 1999, Veech et al. 2003, Schowalter 2006), decreasing alpha- and increasing beta-diversity. Insect surveys have similar findings with broad scale patterns structuring the community (Colwell and Coddington 1994, Dajoz 2000, Novotny and Basset 2000, Magurran 2004, Schowalter 2006, Wilson et al. 2007).

Co-occurrence patterns were random at the regional level and at all sites except Waterton Lakes, AB. At this site, co-occurrence was less than expected and represented a competitively structured community (Gotelli and Entsminger 2007). Again, sampling effort may be a factor. Many sample areas were visited at this site, with only some of them revisited. Throughout the sample areas at this site, the habitat was more heterogeneous than other sites, perhaps providing more niches and allowing more species to coexist. Windthrow disturbance at this site may also have reduced co-occurrence. Waterton Lakes was the windiest of all sites. Acalyptrate flies are strongly impacted by windthrow due to their small size, especially in open alpine habitats (Totland 1994).

Families chosen (Agromyzidae, Tephritidae, Chloropidae, Sphaeroceridae, and Ephydridae) to compare rank abundance patterns were all widespread, speciose, and abundant, allowing for easy systematic sampling. Studying large, widespread families provides different ecological contexts for assessing the factors influencing diversity. Covering a wide range of ecological roles makes them good representatives of any patterns that may be found.

Many Agromyzids are mainly host-specific, relying on a single plant species or genus to complete their life cycle (Grimaldi and Engel 2005; Marshall 2006). The larvae of most species are leaf miners and are frequently easily recognizable by their mines (Triplehorn et al*.* 2005). The species that are not leaf miners develop in roots, stems, tree cambium, or seed heads (Marshall 2006). This is, at present, the largest family of acalyptrate flies in North America, consisting of over 700 described species (Triplehorn et al*.* 2005).

Tephritidae are also a mainly phytophagous family, although there are saprophages and saproxylophages (Aluja and Norrbom 2000). This family, with roughly 300 North American species (Triplehorn et al. 2005) contains leaf-miners, seed feeders, gall formers, and root and stem borers (Foote et al. 1993; Triplehorn et al. 2005).

Chloropids are another diverse families of Diptera, with around 290 recorded North American species (Triplehorn et al. 2005) and a corresponding number of habitats (Marshall 2006). These small flies have an extremely broad range of ecological roles, as both specialist and generalist predators, parasites, saprophages, and phytophages (Triplehorn et al*.* 2005; Marshall 2006). Several larvae are stem borers in grasses and sedges (Triplehorn et al*.* 2005; Marshall 2006). Some species are known as “eye gnats”, feeding on mucous membranes and animal secretions

(Triplehorn et al. 2005; Marshall 2006). Chloropids are especially common in meadows and grasslands (Triplehorn et al. 2005).

Sphaerocerids and ephydrids, on the other hand, are primarily generalist scavengers. The sphaerocerids, sometimes called the "most inconspicuously successful of all flies", are extremely common (Marshall 2006) and are often found on manure or decaying matter (Triplehorn et al. 2005). A few species are specialists, surviving only in millipede dung or the green glands of crabs (Marshall 2006). This group of small, black or brown flies contains 250 North American species (Triplehorn et al. 2005). Ephydridae contains over 450 North American species (Zach 1998; Triplehorn et al. 2005) and are usually found in moist places. Larvae are usually aquatic but may survive in brackish, saline, or alkaline water (Cole 1969; Triplehorn et al. 2005). One species even breeds in crude petroleum.

Species abundance distributions in the Rocky Mountains (Figure 6) showed highest evenness in the Agromyzidae, probably because host specificity in these phytophagous species reduces interspecific competition. The other phytophagous group, Tephritidae, displayed similar, but steeper, patterns, perhaps because the collected species may be less specialized, or suitable host plants favoured the dominant species. In contrast, Ephydridae were dominated by a single species, *Philygria debilis*, which may have reduced numbers of other generalist saprophagous species within the family. This species is one of the most common and widespread Nearctic ephydrids (Cole 1969; Edmiston and Mathis 2005). However, immature stages are unknown, and information is limited to habitat descriptions (Edmiston and Mathis 2005). The Chloropidae were intermediate, probably due to the mix of specialist phytophagous or predaceous species, which likely do not compete, and generalist saprophagous species.

These patterns were broken down and analyzed at the site level (Figure 6) when each family had n ≥ 50. Sites reveal the same basic patterns, with Agromyzidae having a relatively even curve with a long tail and the ephydrids having a steep curve with a one very dominant species and a short, abrupt tail. The chloropids, which have a mix of ecological habits, tend to fall somewhere in between, depending on the subset of species present at a given site and their trophic association. The tephritids were also somewhat variable, possibly because the collected species are not as host specific as the agromyzids or because suitable host plants were more abundant.

Patterns in the Appalachian Mountains (Figure 7) varied slightly. Chloropids displayed the same variable patterns here as in the Rockies. Where the ephydrids had one dominant species in the Rockies, two species of sphaerocerids tended to dominate in the Appalachians, with *Leptocera erythrocera* usually more prevalent than *Lotophila atra* except at site JANE, where *Lotophila atra* was dominant. The most dramatic change was with the Agromyzidae. One species (*Cerodontha dorsalis*) was highly dominant over other agromyzid species at all sites pooled and each site individually (where n ≥ 50). The host plants for this species are several species of Poaceae, where the larvae feed mainly in the leaf sheath and where pupation takes place (Cole 1969; Spencer 1969). Only at site SAM was *Ophiomyia nasuta* at similar abundance levels to *C. dorsalis*. Grasses were dominant and diverse at all the Appalachian sites, but the cultivation history of the SAM site may have been a factor here because of a change in the diversity and density of vegetation.

Agromyzid patterns might have changed between eastern and western mountain chains based on the presence of host plants. *C. dorsalis* has been recorded from 16 genera of Poaceae (Boucher 2002), none of which were dominant plants at sites from the Rocky Mountains, whereas the Appalachian sites were more heavily dominated by mixed grasses. Patterns of generalist scavengers were similar between the two mountain ranges. Whereas one species within the target families dominated in the western sites, two species tended to dominate the eastern sites (although the number of families considered was admittedly low). At all sites except in Waterton Lakes, no more than three species each of ephydrids and sphaerocerids were collected. This may be partly related to the short duration of the sampling or the reliance on sweeping, but it may also reflect heavy competition within the families. Chloropid patterns were variable at all sites. The abundance patterns of this family may not be predictable, even in seemingly similar habitat type, due to the range of ecological roles they perform.

These results suggest that species abundance patterns within taxa of similar body size and species richness, even in the same type of habitat, may not be predictable and may be heavily influenced by the ecological diversity within the taxon. Families exhibited different patterns between the Rockies and Appalachian, although patterns of generalist scavengers might be more predictable than other trophic guilds. This result was unexpected and the generality of this pattern has not been explored in other studies. This may be a fruitful area of research for future studies of the impact of ecological diversity of taxa on their species-abundance curves.

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Table 1. Number of individuals (N), raw species richness (S_{obs}), and number of singletons and doubletons of Chloropidae, Sphaeroceridae, and Agromyzidae for flies (Acalyptratae) at six high elevation sites in the Appalachian Mountains. (SAM: Sam Knob; BBK: Black Balsam Knob; PIS: Little Pisgah Mountain.; ROND: Round Bald; JANE: Jane Bald; GRAS: Grassy Ridge Bald).

Site	N	S_{obs}	Singletons	Doubletons
SAM	1016	23	2	2
BBK	812	19	1	0
PIS	1034	24	4	3
ROND	1927	31	8	7
JANE	1204	28	10	3
GRAS	2555	17	4	2
All	**8548**	**51**	**10**	**6**

Table 2. Number of individuals (N), raw species richness (S_{obs}), rarefied species richness (S_{rar} ± SD, standardized at 645 individuals), mean ACE value, and number of singletons and doubletons for flies (Acalyptratae) at four alpine sites in the Rocky Mountains. (1: Molas Pass, CO; 2: Bighorn Mountains, WY; 3: Waterton Lakes, AB; 4: Kananaskis, AB).

Site	N	S_{obs}	S_{rar} ± SD	ACE	Singletons	Doubletons
1	648	46	45.85 ± 0.37	120.57	29	7
2	787	73	68.09 ± 1.96	91.85	23	20
3	1514	78	51.53 ± 3.60	126.29	37	10
4	991	55	44.63 ± 2.61	88.38	26	9
All	**3940**	**164**		**249.18**	**65**	**29**

Table 3. Bray-Curtis similarity measures above 0.6 for Rocky Mountain sample area pairwise comparisons.

Sample areas	Bray-Curtis similarity measure
2.1 and 3.4	0.750
2.1 and 4.1	0.850
2.3 and 3.1	0.686
2.3 and 4.3	0.767
3.1 and 4.3	0.765
3.4 and 4.1	0.755
3.6 and 4.3	0.714
4.1 and 4.3	0.602

Table 4. Additive partitioning results of alpha- and beta-diversity components across scales for the entire community as well as for common and rare species. The average richness value obtained within each spatial scale and the total richness (gamma-diversity) is shown.

Component	Community	Common species	Rare species
Gamma (γ)	164	18	94
Beta$_2$ (β_2)	99.05*	4.34*	67.89*
Beta$_1$ (β_1)	36.63**	6.29*	14.82**
Alpha (α)	29.32**	7.37**	11.29**

* Significantly higher than expected, $P < 0.0001$; ** significantly lower than expected, $P > 0.99$. Significance value is based on the expected values generated with 10,000 randomizations with PARTITION software.

Table 5. Rocky Mountain co-occurrence data at regional and site levels.

	All Sites	**1**	**2**	**3**	**4**
p(obs. > exp.)	0.41	--	--	**0.05360**	--
p(obs. < exp.)	--	0.51600	0.31360	**--**	0.34340
C-score	0.74871	0.54203	0.42161	**1.07426**	0.48350

Table 6. Rocky Mountain species abundance distribution data for the most dominant species for all sites pooled and for sites individually. Percentages represent that species' proportion to the total diversity within the family. (2: Bighorn Mountains, WY; 3: Waterton Lakes, AB; 4: Kananaskis, AB).

	All Sites	**1**	**2**	**3**	**4**
Agromyzidae	Onas	*Onas	Lele	Psp8	*Onas
	15%	71%	24%	28%	18%
Chloropidae	Iinc	Tpul	*Tpul	Iinc	Ofri
	46%	47%	26%	81%	81%
Ephydridae	Pdeb	*Hfur/Lsib	Pdeb	Pdeb	Pdeb
	91%	50%	99%	85%	92%
Tephritidae	Eacu	Eacu	Ppyg	*Psab	*Ppyg
	31%	70%	34%	41%	56%

Species abbreviations: Eacu *(Euarestoides acutangulus),* Hfur *(Hyadina furva),* Iinc *(Incertella incerta),* Lsib *(Lamproscatella sibilins),* Lele *(Liriomyza elevata),* Onas *(Ophiomyia nasuta),* Ofri *(Oscinella frit* group*),* Ppyg *(Paroxyna pygmaea),* Psab *(Paroxyna sabroskyi),* Pdeb *(Philygria debilis),* Psp8 *(Phytomyza sp.8),* Tpul *(Thaumatomia pulla).* *Less than 50 individuals in the family.

Table 7. Appalachian Mountain species abundance distribution data for the most dominant species for all sites pooled and for sites individually. Percentages represent that species' proportion to the total diversity within the family. (SAM: Haywood Co, Pisgah NF, Sam Knob; BBK: Haywood Co, Pisgah NF, Black Balsam Knob; PIS: Haywood Co, Pisgah NF, Little Pisgah Mountain.; ROND: Mitchell Co, Pisgah NF, Round Bald; JANE: Mitchell Co, Pisgah NF, Jane Bald; GRAS: Avery Co, Pisgah NF, Grassy Ridge Bald).

	All Sites	**SAM**	**BBK**	**PIS**	**ROND**	**JANE**	**GRAS**
Agromyzidae	Cdor 76%	Cdor 43%	*Cdor 69%	*Cdor 44%	Cdor 77%	Cdor 73%	Cdor 95%
Chloropidae	Rcar 39%	Apar 55%	Apar 56%	Isp2 20%	Rcar 78%	Rcar 47%	Rcar 50%
Sphaeroceridae	Lery 87%	Lery 68%	Lery 59%	*Lery 73%	Lery 61%	Latr 56%	Lery 59%

Species abbreviations: Apar *(Apallates particeps),* Cdor (*Cerodontha dorsalis),* Isp2 *(Incertella sp.2),* Lery *(Leptocera erythrocera),* Latr *(Lotophila atra),* Rcar *(Ropalopterum carbonarum).* *Less than 50 individuals in the family.

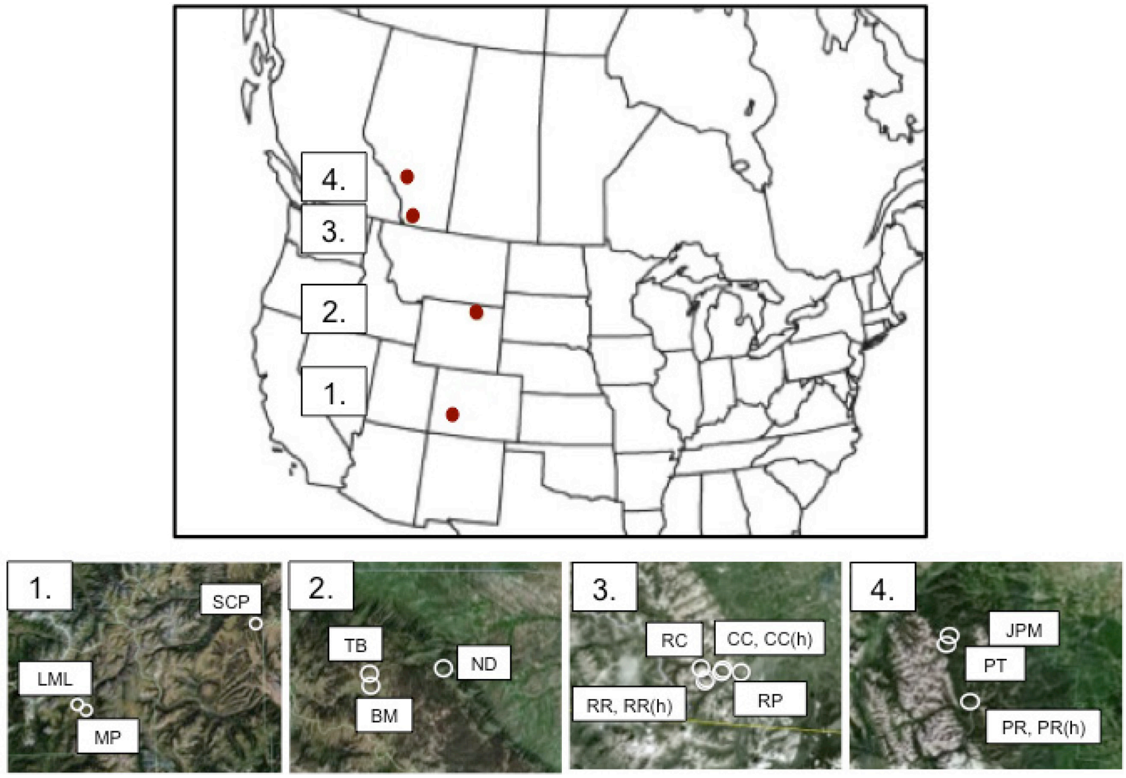


Figure 1. Location of study sites in the Rocky Mountains (1: Molas Pass, CO; 2: Bighorn Mountains, WY; 3: Waterton Lakes NP, AB; 4: Kananaskis region, AB). Bottom images show arrangement of sample areas within each site (LML: Little Molas Lake, MP: Molas Pass, SCP: Spring Creek Pass; BM: Bald Mountain, ND: Near Dayton, TB: Twin Buttes, CC: Coppermine Creek, CC(h): Coppermine Creek (higher), RC: Rowe Creek, RR: Ruby Ridge, RR(h): Ruby Ridge (higher), RP: Redrock Parkway; JPM: Jumping Pound Mountain, PR: Powderface Ridge, PR(h): Powderface Ridge (higher), PT: Powderface Trail).

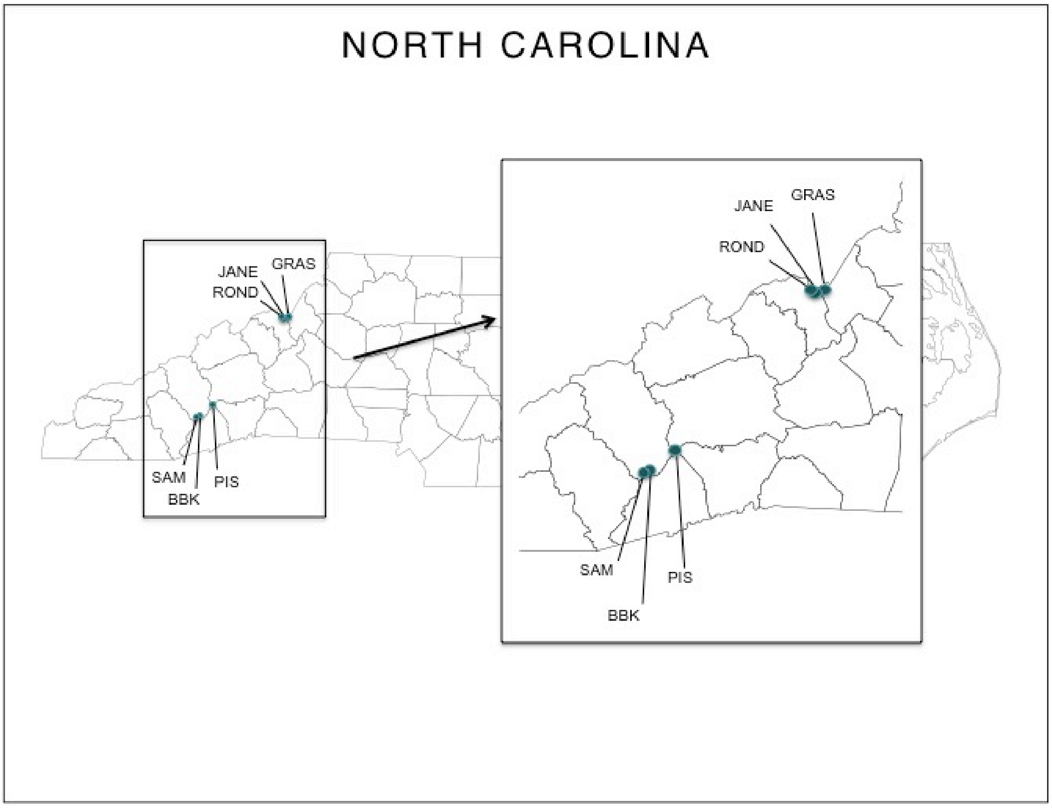


Figure 2. Location of study sites in the Appalachian Mountains of North Carolina (SAM: Haywood Co, Pisgah NF, Sam Knob; BBK: Haywood Co, Pisgah NF, Black Balsam Knob; PIS: Haywood Co, Pisgah NF, Little Pisgah Mountain.; ROND: Mitchell Co, Pisgah NF, Round Bald; JANE: Mitchell Co, Pisgah NF, Jane Bald; GRAS: Avery Co, Pisgah NF, Grassy Ridge Bald).

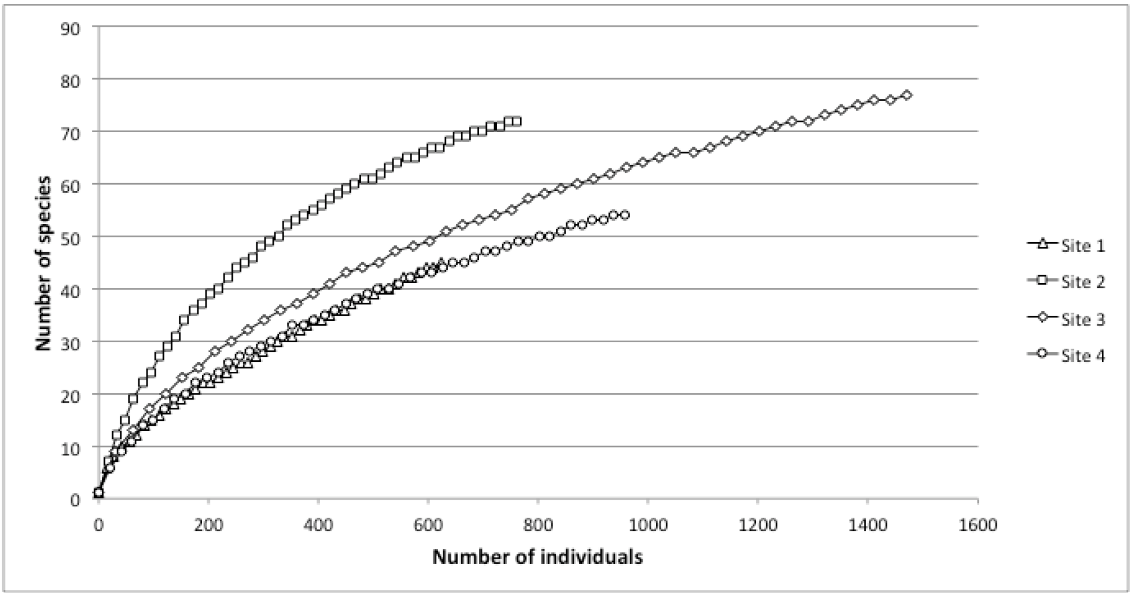


Figure 3. Individual-based rarefaction curve for Molas Pass, CO (Site 1), the Bighorn Mountains, WY (Site 2), Waterton Lakes NP, AB (Site 3) and Kananaskis, AB (Site 4).

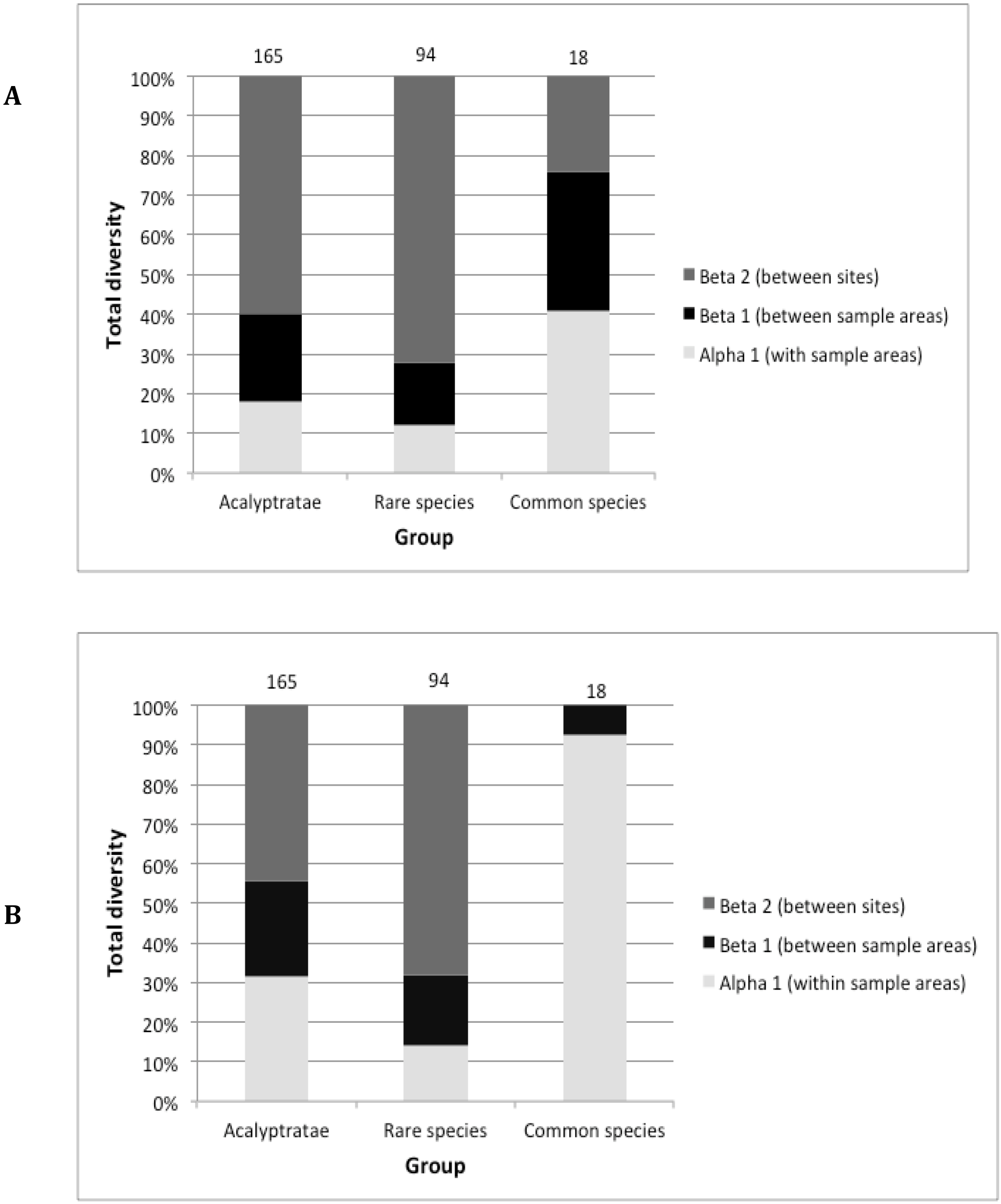


Figure 4. Observed (A) and expected (B) proportion of species richness for the Rocky Mountain data explained by alpha- and beta-diversities in the entire community, rare species, and common species. Total species richness for each group is shown at the top of each bar.

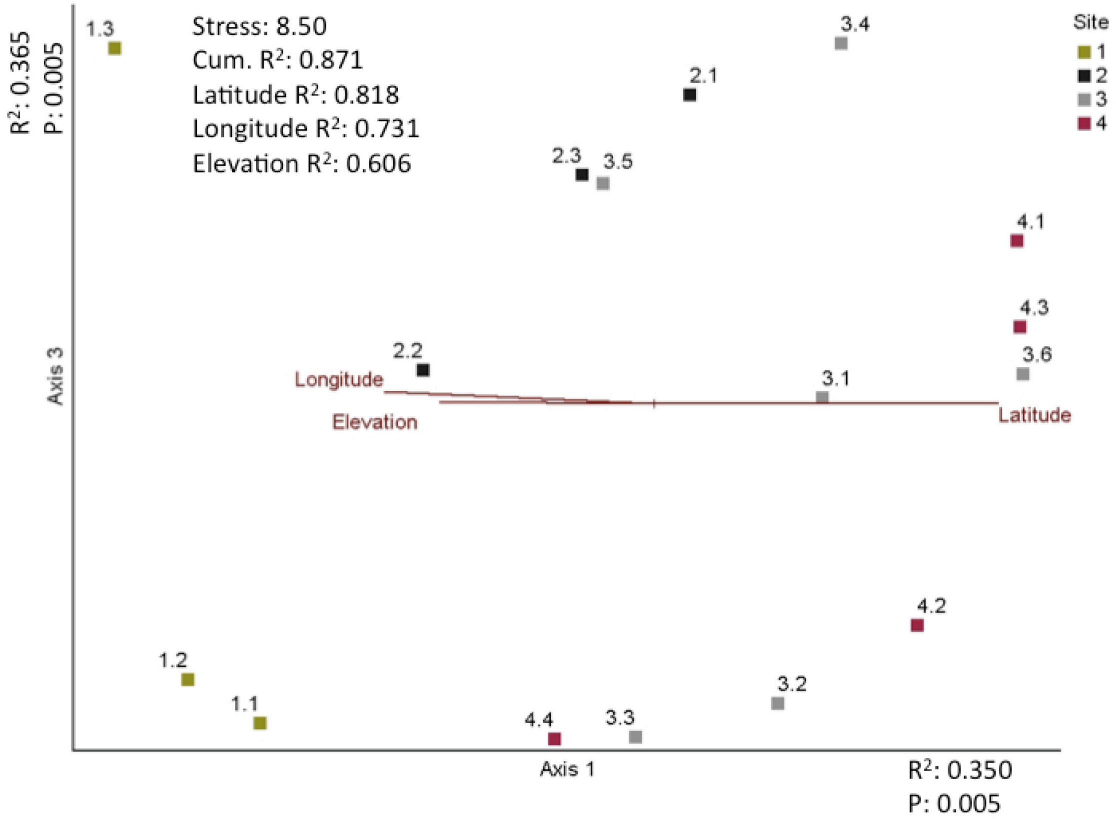


Figure 5. Non-metric multidimensional scaling ordination of Acalyptratae species composition of the 16 sample areas at Molas Pass, CO (1), the Bighorn Mountains, WY (2), Waterton Lakes NP, AB (3), and Kananaskis, AB (4). The two strongest axes of the three-dimensional solution are shown with the *P*-value and R^2 of each axis. Joint plot analysis reveals the main factors in composition.

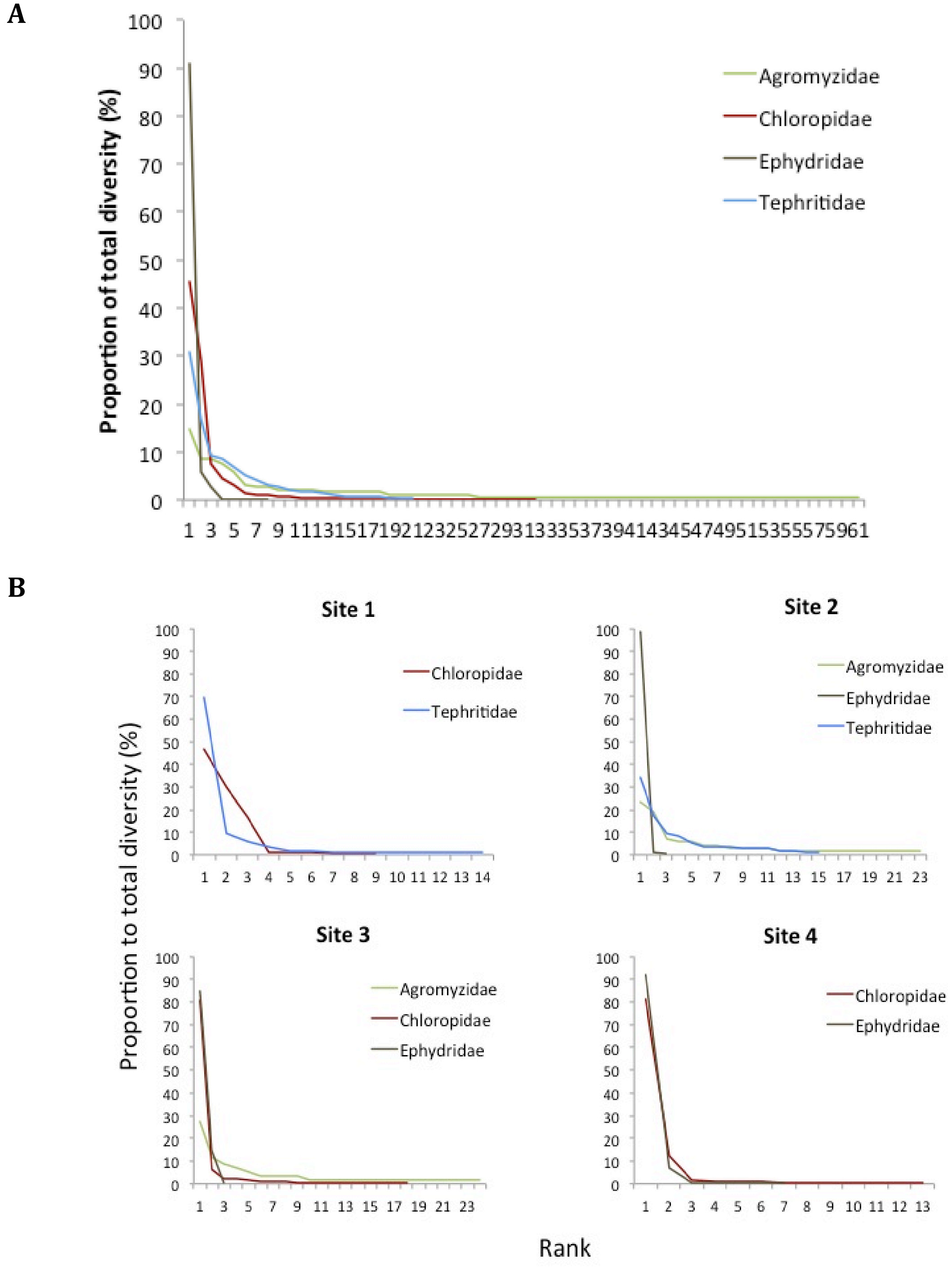
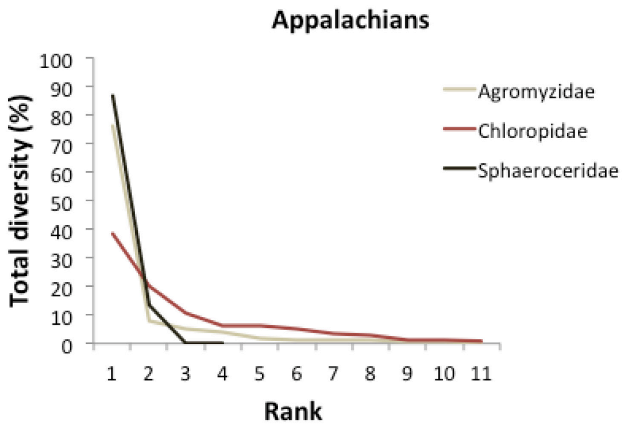


Figure 6. Rank abundance curves in the Rocky Mountains for four distinct trophic groups (Agromyzidae, Ephydridae, Chloropidae, Tephritidae). All sites combined (A) and each site individually (B) (1: Molas Pass, CO; 2: Bighorn Mountains, WY; 3: Waterton Lakes, AB; 4: Kananaskis, AB).

A


Appalachians
Total diversity (%)
100
90
80
70
60
50
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10 11
Rank
Agromyzidae
Chloropidae
Sphaeroceridae

B

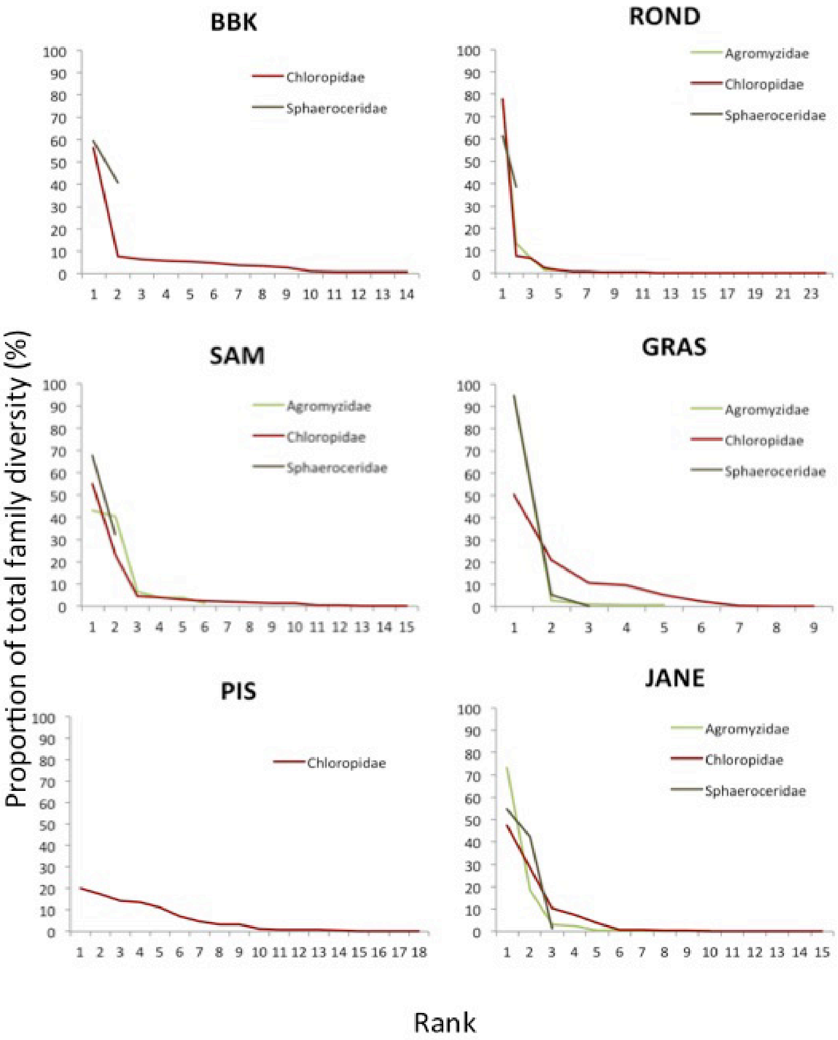

BBK
Chloropidae
Sphaeroceridae
RONDThe
Agromyzidae
Chloropidae
Sphaeroceridae
SAM
Agromyzidae
Chloropidae
Sphaeroceridae
GRAS
Agromyzidae
Chloropidae
Sphaeroceridae
PIS
Chloropidae
JANE
Agromyzidae
Chloropidae
Sphaeroceridae
Proportion of total family diversity (%)
Rank

Figure 7. Rank abundance curves in the Appalachian Mountains for three trophic groups. All sites combined (A) and each site individually (B) (SAM: Sam Knob; BBK: Black Balsam Knob; PIS: Little Pisgah Mountain; ROND: Round Bald; JANE: Jane Bald; GRAS: Grassy Ridge Bald).

Appendix 1: Acalyptrate species and morphospecies collected in the Rocky Mountains at Molas Pass, CO (1), the Bighorn Mountains, WY (2), Waterton Lakes NP, AB (3), Kananaskis, AB (4).

Family	**Species**	**Abundance**				**Total**
		1	**2**	**3**	**4**	
Agromyzidae	*Agromyza ?potentillae*	0	2	0	0	2
	Agromyza albertensis	0	4	7	0	11
	Agromyza fragariae	0	4	0	0	4
	Agromyza sp.1	0	1	2	0	3
	Agromyza sp.2	1	0	0	0	1
	Agromyza sulfuriceps	0	0	0	2	2
	Amauromyza angulicornis	0	3	0	0	3
	Amauromyza nevadensis	0	0	1	0	1
	Amauromyza scleritica	0	0	3	0	3
	Aulagromyza n.sp.	0	1	0	0	1
	Cerodontha (Butomomyza) parvella	0	0	0	1	1
	Cerodontha (Poemyza) sp.1	0	1	0	0	1
	Cerodontha (Poemyza) ?inconspicua	0	0	1	0	1

	Cerodontha (?Poemyza) sp.2	0	1	0	0	1
	Liriomyza ?n.sp. nr. nigrissima or *togata*	0	2	0	0	2
	Liriomyza artemisiae	1	0	0	0	1
	Liriomyza eboni	0	0	2	0	2
	Liriomyza elevate	0	16	0	0	16
	Liriomyza lathyri	0	0	1	0	1
	Liriomyza n.sp. nr. archbaldi	1	5	0	0	6
	Melanagromyza ?martini	0	0	0	2	2
	Melanagromyza sp.1	0	1	0	0	1
	Melanagromyza viridis	2	1	0	0	3
	Metopomyza interfrontalis	0	0	2	0	2
	Napomyza ?nugax	0	1	0	0	1
	Ophiomyia ?labiatarum or *sexta*	0	0	4	0	4
	Ophiomyia ?pulicaria or *pulicaroides*	0	0	1	0	1
	Ophiomyia ?sp. nr. levata	1	0	0	0	1
	Ophiomyia banffensis	0	0	1	0	1
	Ophiomyia malitiosa	0	0	2	0	2
	Ophiomyia nasuta	22	0	0	5	27
	Ophiomyia sp.1	1	0	0	0	1
	Ophiomyia sp.2	0	0	1	0	1
	Ophiomyia sp.3	0	1	0	0	1
	Ophiomyia sp.4	1	0	0	0	1
	Phytoliriomyza ?arctica	0	1	0	0	1
	Phytoliriomyza consulta	0	1	0	0	1
	Phytoliriomyza n.sp.1	0	0	1	0	1
	Phytomyza ?cineracea	0	0	1	0	1
	Phytomyza ?erigerophila	0	1	0	0	1
	Phytomyza ?n.sp. nr. spondylii + sii	0	2	0	0	2
	Phytomyza arnicicola	0	3	0	0	3
	Phytomyza gregoria	0	0	0	1	1
	Phytomyza lupini	0	13	0	0	13
	Phytomyza lupinivora	0	0	1	0	1
	Phytomyza misella	0	0	0	1	1
	Phytomyza n.sp. nr. pedicularicaulis	0	0	1	0	1
	Phytomyza saskatoonensis	0	2	0	3	5
	Phytomyza subalpina	0	0	0	4	4
	Phytomyza trivittata	0	0	5	0	5
	Phytomyza sp.1	0	0	0	1	1
	Phytomyza sp.2	0	0	1	0	1
	Phytomyza sp.3	0	0	0	1	1
	Phytomyza sp.4	1	0	0	0	1
	Phytomyza sp.5	0	0	1	0	1
	Phytomyza sp.6	0	0	0	1	1
	Phytomyza sp.7	0	0	16	0	16
	Phytomyza sp.8	0	0	0	4	4
	Phytomyza sp.9	0	0	1	0	1

	Phytomyza sp.10	0	0	1	0	1
	Pseudonapomyza atra	0	0	1	0	1
Anthomyzidae	*Anthomyza sp.1*	0	0	0	2	2
Carnidae	*Hemeromyia sp.1*	0	0	2	0	2
	Meoneura flavifacies	0	2	3	3	8
	Meoneura lamellata	0	1	0	1	2
Chamaemyiidae	*Chamaemyia polystigma*	332	18	189	33	572
	Leucopis (Leucopis) sp.1	9	2	17	2	30
	Leucopis (Ocellaris) sp.1	0	0	1	0	1
	Leucopis (Ocellaris) sp.2	2	0	0	0	2
	Plunomia obtusa	1	0	1	0	2
	Pseudodinia varipes	1	5	3	0	9
Chloropidae	*Apallates coxendix*	0	1	0	4	5
	Apallates particeps	0	2	0	0	2
	Aphanotrigonum scabrum	0	0	5	0	5
	Biorbitella hesperia	0	1	0	0	1
	Chlorops sp.1	1	0	0	0	1
	Chlorops sp.2	1	0	0	0	1
	Conioscinella sp.1	0	0	5	0	5
	Dasyopa sp.1	0	2	0	0	2
	Dicraeus ingratus	0	3	0	0	3
	Elachiptera decipiens	1	0	0	0	1
	Elachiptera knowltoni	1	0	0	0	1
	Incertella incerta	25	0	445	50	520
	Malloewia n.sp.1	0	0	4	0	4
	Malloewia neglecta	0	6	6	1	13
	Meromyza columbi	0	0	1	0	1
	Meromyza pratorum	0	0	9	0	9
	Meromyza sp.1	0	0	1	4	5
	Meromyza sp.2	0	0	3	0	3
	Meromyza sp.3	2	0	0	1	3
	Meromyza sp.4	45	1	1	5	52
	Neodiplotoxa pulchripes	1	9	0	0	10
	Olcella difficilis	0	0	35	1	36
	Olcella parva	0	0	14	1	15
	Olcella Pygmaea	0	0	2	0	2
	Oscinella frit group	2	2	0	327	331
	Oscinella sp.1	0	0	5	0	5
	Oscinella sp.2	2	0	0	0	2
	Siphonella oscinina	0	0	0	1	1
	Thaumatomyia glabra	0	2	0	0	2
	Thaumatomyia pulla	70	10	1	6	87
	Thaumatomyia pillipes	1	0	0	0	1
	Tricimba cincta	0	0	1	0	1
	Tricimba melancholica	0	0	1	0	1
Drosophilidae	*Drosophila sp.1*	0	2	0	0	2
Ephydridae	*Athyroglossa glaphyropus*	0	0	0	1	1
	Hyadina furva	1	0	0	0	1
	Hydriella griseola	0	2	87	2	91
	Lamproscatella sibilins	1	5	3	32	41

	Nostima approximata	0	0	0	1	1
	Philygria debilis	0	465	506	426	1397
	Philygria nigriscens	0	0	0	1	1
	Scatella (Scatella) obsoleta	0	0	0	1	1
Heleomyzidae	*Pseudoleria similis*	1	2	0	0	3
	Trixoscelis flavida	0	0	1	0	1
	Trixoscelis fumipennis	0	0	29	0	29
Lauxaniidae	*Homoneura ornatipes*	0	0	2	2	4
	Lauxania shewelli	0	0	0	8	8
	Minettia lupulina	0	0	3	0	3
Lonchaeidae	*Chaetolonchaea americana*	0	2	0	0	2
	Protearomyia cordillerensis	1	1	0	0	2
Milichiidae	*Madiza sp.1*	0	0	1	0	1
	Phyllomyza securicornis	0	0	0	1	1
Piophilidae	*Mycetaulus nigritellus*	0	0	0	1	1
Psilidae	*Psila astrata*	0	20	0	1	21
Sepsidae	*Sepsis biflexuosa*	0	1	1	2	4
	Sepsis neocynipsea	1	26	1	10	38
Sphaeroceridae	*Coproica sp.1*	0	0	1	0	1
	Ischiolepta scabra	1	0	0	0	1
	Leptocera erythrocera	0	2	2	10	14
	Limnosininae *sp.1*	0	0	0	1	1
	Limnosininae *sp.2*	0	0	0	1	1
	Limnosininae *sp.3*	0	0	1	0	1
	Limnosininae *sp.4*	0	1	0	0	1
	Limnosininae *sp.5*	0	2	0	0	2
	Limnosininae *sp.6*	0	2	0	0	2
	Lotophila atra	0	4	1	4	9
	Spelobia ochripes	0	0	1	0	1
	Spelobia sp.1	0	2	1	4	7
	Spelobia sp.2	1	3	1	0	5
Tephritidae	*Dioxyna sororcula*	0	3	4	1	8
	Dioxyna thomae	0	0	2	0	2
	Euarestoides acutangulus	79	2	1	0	82
	Neaspilota footei	1	4	0	0	5
	Paroxyna dupla	0	0	1	0	1
	Paroxyna farinata	2	6	3	0	11
	Paroxyna footeorum	1	0	1	0	2
	Paroxyna genalis	11	3	0	0	14
	Paroxyna murina	0	2	1	1	4
	Paroxyna pygmaea	0	37	3	5	45
	Paroxyna sabroskyi	1	9	15	0	25
	Paroxyna snowi	1	0	5	0	6
	Paroxyna variabilis	0	3	0	0	3
	Tephritis signatipennis	1	1	0	0	2
	Trupanea bisetosa	1	4	0	0	5
	Trupanea californica	1	0	0	0	1
	Trupanea eclipta	0	1	0	0	1
	Trupanea jonesi	4	19	0	0	23
	Trupanea nigricornis	7	10	0	1	18

	Trupanea radifera	2	4	1	0	7
	Xanthomyia platyptera	1	0	0	1	2
Tethinidae	*Pelomyiella melanderi*	1	0	0	0	1
Ulidiidae	*Curranops apicalis*	0	0	7	0	7
	Homalocephala sp.1	0	1	0	0	1
	Tritoxa cuneata	0	0	2	0	2
	Tritoxa sp.1	0	1	0	0	1

Appendix 2: Selected acalyptrate species and morphospecies in target families collected in North Carolina at Haywood Co, Pisgah NF, Sam Knob (SAM), Haywood Co, Pisgah NF, Black Balsam Knob (BBK), Haywood Co, Pisgah NF, Little Pisgah Mountain (PIS), Mitchell Co, Pisgah NF, Round Bald (ROND), Mitchell Co, Pisgah NF, Jane Bald (JANE), Avery Co, Pisgah NF, Grassy Ridge Bald (GRAS).

Species	**Abundance**						**Total**
	BBK	**GRAS**	**JANE**	**PIS**	**ROND**	**SAM**	
Agromyzidae							
Calycomyza solidaginis	3	1	0	2	2	2	6
Cerodontha dorsalis	9	166	184	4	58	32	453
Cerodontha magnicornis	0	5	6	0	10	3	24
Cerodontha (*Dizygomyza*) *?aristosa or fasciata*	0	0	0	0	5	0	5
Japanagromyza viridula	0	0	1	0	0	0	1
Liriomyza ?zinniae	0	0	1	0	0	5	6
Liriomyza trifoliearum	0	0	5	0	0	0	5
Liriomyza trifolii	0	1	3	0	0	0	4
Melanagromyza caerulea	0	0	1	0	0	0	1
Meopomyza sp.1	0	0	0	0	1	0	1
Ophiomyia nasuta	0	0	0	0	0	30	30
Phytoliriomyza arctica	0	0	47	0	0	1	48
Phytomyza compta	0	2	1	0	0	0	3
Phytomyza crassiseta	0	0	0	2	1	3	6
Phytomyza sp.1	0	0	1	0	0	0	1
Phytomyza sp.2	1	0	1	0	0	0	2
Phytomyza sp.3	0	0	0	1	0	0	1
Chloropidae							
Apallates dissidens	38	80	250	9	36	204	617
Apallates montanus	40	0	0	45	0	1	86
Apallates neocoxendix	20	157	32	31	111	15	366
Apallates particeps	398	71	64	144	24	483	1184
Ceratobarys eulophus	0	0	0	0	2	0	2
Chlorops sp.4	0	0	0	175	11	0	186
Conioscinella sp.1	0	0	0	0	0	2	2
Conioscinella sp.2	0	0	0	1	0	0	1
Conioscinella sp.3	0	0	1	0	1	0	2
Elachiptera costata	0	0	0	0	10	0	10
Incertella bispina	0	0	0	0	5	0	5
Incertella dorsata	0	0	0	0	2	0	2
Incertella minor	0	0	3	0	2	0	5
Incertella ovalis	0	0	0	1	2	0	3
Incertella sp.1	33	0	2	222	4	26	176
Incertella sp.2	46	1	5	201	4	40	297
Liohippelates pallipes	0	0	4	0	1	0	5

Meromyza americana	5	0	0	0	0	3	8
Olcella trigramma	7	0	0	8	0	20	35
Oscinella frit group	55	1	5	1	1	12	75
Parectecephala maculiceps	0	0	0	0	1	0	1
Pseudopachychaeta approximatonervis	0	18	2	0	2	0	22
Rhopalopterum carbonarum	27	374	417	137	1266	35	2256
Rhopalopterum luteiceps	0	0	0	2	0	0	2
Rhopalopterum painteri	6	0	1	13	2	3	25
Rhopalopterum soror	4	2	2	34	6	2	50
Rhopalopterum umbrosum	0	0	0	10	0	0	10
Thaumatomyia glabra	24	41	92	72	127	19	375
Thaumatomyia grata	0	0	0	0	1	0	1
Thaumatomyia pulla	5	0	1	4	3	12	24
Sphaeroceridae							
Copromyza equina	0	3	0	0	0	0	3
Leptocera erythrocera	54	1546	31	19	140	44	1834
Lotophila atra	37	86	40	7	88	21	279
Sphaerocera curvipes	0	0	1	0	0	0	1

CHAPTER 3: GENERAL CONCLUSION

This study has provided baseline data on Rocky and Appalachian Mountain alpine acalyptrate Diptera that will help to build a framework for future ecological, and systematic work. Alpine areas are important targets for conservation efforts in light of climate change. Biodiversity in these sensitive habitats is at risk, and it is quite possible that species will disappear before we even know they were there.

This study builds upon the small body of research on alpine Diptera to contribute baseline data that will be essential for addressing more focused ecological questions about the structure of the Diptera community. Assessing the effect of climate change on elevational and latitudinal gradients of Diptera diversity, the predictability of alpine Diptera assemblages for given regions and/or habitats or the suitability of alpine Diptera species as environmental indicators will require a comprehensive baseline dataset, likely at the species-level of taxonomic resolution. This is the first study to assess terrestrial alpine acalyptrate Diptera diversity patterns across scales and to look at species abundance distributions of particular trophic groups. This project provides baseline data for future studies of alpine Diptera ecology, by presenting patterns as various scales and proposing factors that influence the species assemblages.

The results have undrelined the usefulness of rarefaction to compare species patterns, especially when sampling effort was low. NMDS showed a definite latitudinal turnover in species richness with all sites significantly different except the two in Alberta, which were relatively close in distance and similar in elevation and plant composition. Bray-Curtis similarities revealed possible effects on alpine acalyptrate distribution of the Wyoming Basin, a large, low-elevation short-grass prairie that affects dispersal of other species (e.g. plants, butterflies, and beetles). Further assessment, based on population genetic studies, of the impact of the Wyoming Basin on Diptera distributions would be fruitful.

Patterns were not random at all scales and were variable between scales. For the most part, beta-diversity was higher than expected, especially in common species, probably as a result of the broad spatial scale of the study. Co-occurrence analysis showed non-random patterns only at Waterton Lakes, AB. Here co-occurrence was significantly less than expected, possibly reflecting a competitively structured community. Higher habitat heterogeneity may have been a factor at this site.

Abundance patterns at first seemed predictable in the Rocky Mountains, but when compared to Appalachian data were much more variable. Therefore, abundance patterns may not be predictable solely on a family's trophic roles. Although agromyzids are a frequently host-specific group, this may not necessarily reduce interspecific competition within the family, depending on host plant distribution, as shown with meadows in North Carolina, where *Cerodontha dorsalis* was by far the most dominant agromyzid species.

This work could be considered a pilot study, because of the broad geographic extent and short sampling period. Research should continue in alpine areas in order to learn more about the patterns and processes governing Diptera assemblages. A larger dataset of sites, species and individuals would allow finer-scale analysis of latitudinal and elevational gradient patterns. Analysis of additional trophic guilds (predators, parasites, etc.) is also advisable to expand our knowledge of species abundance patterns in this habitat and their influence on community structure. This research does, however, provide a baseline on diversity of previously underappreciated alpine Diptera that can be built upon to document changes in these habitats over time.