

DETECTING THE EFFECTS OF ENVIRONMENTAL CHANGE ON ALASKA'S
SMALL MAMMAL FAUNA USING MACHINE-LEARNING-BASED GEOGRAPHIC AND
ISOTOPIC NICHE MODELING

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ABSTRACT

As anthropogenic climate change continues to alter biomes, ecosystems, and wildlife communities, determining how the niche spaces of species will respond is vital for determining appropriate conservation policy that promotes biodiversity and species persistence. In Alaska, quantifications of dietary patterns and geographic distributions of small mammals (rodents and shrews) are incomplete. As a result, wildlife managers are often ill-equipped to adequately account for these ecologically important taxa. I used stable isotopes, open-access occurrence records, and machine learning methods to model the dietary and geographic niche spaces of 17 species of small mammals in mainland Alaska. I also calculated the degree of niche overlap among species to estimate potential competition among conspecifics for both food and space. Using ‘bio-blitz’ sampling along two statewide megatransects, I documented small mammal species richness and collected stable isotope samples at 20 locations across Alaska. Stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) mixing models were used to define proportions of fungi, herbaceous plants, woody plants, lichens, and mosses in the diets of each species and to outline their fundamental and realized foraging niches. I created spatial distribution models for each species for the years 2010 and 2100 by applying machine learning methods to 4,408 unique occurrence records attributed with 27 and 33 environmental predictor variables, respectively. Spatial relationships between co-occurring species helped to determine the dominant structure of small mammal community assemblages for both time periods. Land change analyses identified regions of species loss, persistence, or gain over time. Stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of shrews, rodents, fungi, and herbaceous plants were also modeled spatially to create continuous baseline isoscape predictions for Alaska. Dietary niche models showed a high degree of fundamental niche overlap among species at the statewide scale, whereas realized niches were more segregated at the study area scale. This suggests that species may be plastic in their use of shared resources in order to avoid competition. Isoscape models highlighted mid-elevations in the Yukon-Tanana Uplands, Brooks Range foothills, and the Yukon-Kuskokwim Delta as isotopic ‘hot-spots.’ Isotope values were considerably higher than trophic baselines in these regions, indicating where small mammals may have been consuming more fungi than herbaceous plants. On average, 2010 distribution models accurately predicted the occurrence of species in the field 75% of the time,

and a composite species richness model highlighted biodiversity hotspots (11-13 species) across the Yukon-Tanana Uplands and western Brooks Range. Community assemblage analysis for 2010 parsed species into 5 main community groups: northern, cold-climate, interior, continental, and southern, but membership to these communities was predicted to remain largely unchanged by 2100. Individual distributions, however, were predicted to change dramatically by 2100 as members of the northern, cold-climate, and interior communities shifted northward, inland, and upward in elevation following moving climate envelopes. Regions such as southwest Alaska and the Seward Peninsula experienced projected declines in species richness, while the number of species inhabiting the western Brooks Range and Alaska Range were predicted to increase. Results indicated that while species assemblages were robust in their organization over time, evidence of dietary niche plasticity suggests that communities may remain amenable to the addition of new species as shifting distributions overlap in new and unexpected patterns. Mid-elevations in topographically diverse regions such as the Brooks Range, Alaska Range, and the Yukon-Tanana Uplands will likely be centers for increased species richness and contact zones for novel species interactions in the future. These models, intended for public use, describe baseline conditions and future projections of small mammal niche ecology, with far-reaching implications for terrestrial trophic systems. I recommend that wildlife conservation and management decisions consider these models as we seek to describe and conserve biodiversity and the persistence of small mammal species across Alaska in a future altered by climate change.

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CHAPTER 1. INTRODUCTION

1.1. CLIMATE AND ASSOCIATED LANDSCAPE CHANGE

Anthropogenic climate change is restructuring interactions among species and their environments in profound ways that have important implications for trophic communities and ecosystems (Lovejoy and Hannah 2005). In the circumpolar north, dominant weather patterns are shifting toward warmer conditions, especially in winter, with increasing, yet geographically variable precipitation across the region (Hinzman et al. 2013). At high latitudes, these effects are amplified by the increased concentration of atmospheric CO₂ near the poles (Holland and Bitz 2003; Chapin et al. 2005; Serreze and Francis 2006) resulting from positive feedbacks related to surface temperatures and decreased albedo (Pithan and Mauritsen 2014). In Alaska, mean temperatures have already risen as much 2.2°C annually (Wendler et al. 2014), driven by increases as high as 2.0°C in summer and 4.5°C in winter between 1949 and 1998 (Stafford et al. 2000). This warming trend has resulted in a decrease in fire-return intervals (Kelly et al. 2013) and altered habitat regimes across the state (Murphy et al. 2010). Precipitation in some regions like interior Alaska is decreasing, and in many areas, a higher percentage of precipitation is falling as rain instead of snow (Knowles et al. 2006). Both the product and an accelerant of climate change itself is the loss of arctic sea ice (Rogers et al. 2014; Vihma 2014). Over the past 30 years, the maximum area of autumn sea ice has been reduced by 50%, and by 2050 permanent sea ice is expected to disappear altogether (Vihma 2014). Sea ice loss is also resulting in further climate warming due to the decreased albedo of open water. The larger area of open water has also resulted in increased precipitation in many coastal regions as a result of its higher evaporation potential (Vihma 2014).

As a result of these changing environmental conditions, mean growing season has already increased by 10 days between 1970 and 2000 (Euskirchen et al. 2006), and with the extended growing season, habitat conditions are changing as well. Hardwood forests are projected to replace coniferous boreal forests in dry interior areas (Murphy et al. 2010), while wetlands and coastal and alpine tundra are drying and being invaded by shrubs and trees (Tape et al. 2012; Sweet et al. 2014) as permafrost melts and soils warm (Hinzman et al. 2006; Cable et al. 2014). In general, the ecosystems of continental North America appear to be moving northward and

displacing current arctic and boreal systems. As plant communities spread and ecosystems and biomes transition to new states, animal species associated with these habitats are predicted to follow climate envelopes. Species range shifts of 6.1 km per decade towards the poles and upward at a rate of 6.1 m/decade have already been documented (Parmesan and Yohe 2003).

In the Arctic, where climate effects are already especially pronounced (Serreze et al. 2000; Holland and Bitz 2003), species turnover rates are expected to exceed 40% by 2100 (Lawler et al. 2009). But whether species will move together in a predictable manner with other members of their community remains uncertain. In response to climate pressures, as species move at varying rates, adapt to new conditions, or fail to respond, a rearrangement of species resulting in novel community assemblages is predicted (Williams and Jackson 2007; Lurgi et al. 2012; Urban et al. 2012). This means that some current members of Alaskan wildlife communities may not persist and ecosystem services and trophic linkages maintained by these species may be lost in a climate-altered future.

1.2. SPECIES RESPONSES TO CLIMATE CHANGE

Species facing a moving climatic envelope have three main options to ensure persistence: dispersal, acclimation, or adaptation. For most species, dispersing with the climatic envelope will be the primary response, but this will depend on the ability of each species to move faster than the rate of climate change (Pearson and Dawson 2003; Schloss et al. 2012). For those species with indirect dispersal pathways or specialist needs not met by interim habitats, movement may prove difficult (Schloss et al. 2012). Adapting either intrinsically by acclimating to environmental conditions or adapting genetically to align physiological tolerances with environmental constraints may be an option for some species that are behaviorally or phenotypically plastic. But for most species, the rates of genetic adaptation in populations will be slower than the rate of climate change and will not benefit the persistence of a species (Hoffmann and Sgro 2011; Bellard et al. 2012). Barring the success of the first three options, the final outcome is extirpation. As such, global models have predicted the average extinction of 9.2% of species, and in some regions as much as 39% of species will not be capable of dispersing or adapting at rates consistent with climate change over the coming century (Schloss et al. 2012).

The arctic and boreal biomes are shrinking and receding northward, in many regions giving way to drier continental coniferous forests (Murphy et al. 2010; Hinzman et al. 2013). But what does this mean for the distribution of species, the structure of communities, and ultimately the functionality of ecosystems? I sought to address these questions by focusing on a diverse set of relatively easy-to-study, mammalian consumers.

Two dozen rodent (Rodentia) and shrew (Soricidae) species comprise the Alaskan small mammal fauna (MacDonald and Cook 2009), and they are well-suited for examining the effects of climate change on wildlife. Rodents and shrews are the most diverse taxa in the region, far outnumbering game species in population, yet garnering little research or funding despite their importance as primary prey for numerous avian and carnivoran predators in the arctic and boreal biomes (Krebs 2001). In addition to their value as prey, small mammals play important roles in seed dispersal, soil mixing, fungal inoculation, herbivory, and insectivory (Pank 1974; Maser et al. 1978; Hallett et al. 2003; Olofsson et al. 2012). They consume a diversity of foods including herbaceous plants, seeds, fungi, woody plants, lichens, mosses, carrion, and invertebrates (Carey et al. 1992; Hallett et al. 2003; Gough et al. 2007). However, the exact dietary proportion of these sources consumed by each species is not yet well understood.

Additionally, because small mammals are poorly studied, accurate, high-resolution maps detailing their current and predicted future distributions have not been published for Alaska. As such, predicting how many of these species will compete for food at local scales and for space at geographic scales in the context of a changing climate remains uncertain (Hope et al. 2013; Prost et al. 2013). Given their importance as the primary prey for numerous larger species in a variety of ecosystems, and for the ecological services they provide, small mammals should be valued more than they are for their roles in trophic cascades and their importance for ecosystem function and stability.

1.3. SMALL MAMMAL CONSERVATION AND MANAGEMENT

Given the extent of sweeping environmental changes, it is critical for the conservation of species to determine how the distribution and functionality of biotic systems may respond, especially in the North where changes are rapid and extensive (Serreze et al. 2000; Chapin et al. 2005). The consequences of climate-induced changes to Alaskan terrestrial food web systems remain one of the least-studied and understood fields of global change biology (Chapin et al.

2005; Hinzman et al. 2005). Although small mammals are often overlooked by managing entities, opportunities exist to monitor and conserve biodiversity hotspots with potentially beneficial ecological consequences throughout trophic systems.

In Alaska, several managing agencies and NGOs (non-government organizations) are tracking the conservation status of small mammals, although the degree to which populations are being monitored and actively conserved is limited. Currently, only the National Park Service conducts long-term monitoring of small mammals on a portion of the lands it manages in Alaska, although the U.S. Fish & Wildlife Service is preparing to conduct similar research in the near future. At the state level, plans that recognize the need to consider the diversity and trophic repercussions of non-game species as management objectives (as opposed to managing solely for consumptive purposes) are still in development. As such the State of Alaska Wildlife Action Plan specifically calls for the filling of data gaps pertaining in the distribution, life history, and long-term population monitoring of small mammal species throughout the state (Fritts et al. 2006).

The Alaska Natural Heritage Program (ANHP; <http://aknhp.uaa.alaska.edu/>) has developed a classification system for prioritizing the conservation status of species and subspecies, and these designations have helped to guide Alaska Department of Fish & Game (ADF&G) research and management. While an important first step, this system tends to overemphasize the status of island endemics while minimizing the ecological importance of more commonly distributed species, especially important prey species. The U.S. Fish and Wildlife Service, as well as the International Union for Conservation of Nature (IUCN; <http://www.iucnredlist.org>), and the Convention on International Trade of Endangered Species (CITES) also maintain similar conservation classification systems. Both the IUCN and the ANHP (in conjunction with the USGS-funded Gap Analysis Project; GAP) have created sets of spatial distribution maps for small mammal species. The IUCN range maps are global in coverage and thus coarse at the Alaska scale. However, the Alaska GAP models, created using MaxEnt and a large set of environmental covariates, represent a significant improvement in the documentation of current species distributions. In order to address many of the data needs identified in the Alaska Wildlife Action Plan, and to improve upon the accuracy of Alaska GAP models and to make predictions about the future, I selected 17 commonly detected small mammal species for this research. I used a combination of field sampling, open-access, archived

datasets, and machine-learning modeling to define both the dietary and geographic niche spaces of boreal and arctic small mammal species in Alaska.

1.4. ECOLOGICAL NICHE SPACE

The ecological niche, which defines the ecological and geographic constraints of a species, is well suited to assist in predicting the uncertain ecological outcome of new species interactions (Grinnell 1917). As conceptualized by Hutchinson (1957), the ecological niche is the space bounded by an n-dimensional hypervolume, such that no two species can occupy exactly the same space and where a species is able to persist indefinitely in the absence of competition (Holt and Gaines 1992; Araujo and Guisan 2006; McGill et al. 2006; Cushman 2010).

Dimensions include an infinite set of optimal temperatures, precipitation regimes, landcover, elevation, soil chemistry, and proximity to resources, for example.

At geographic scales, this is similar to the Grinnellian niche, a niche defined by the spatial distribution of the species (Grinnell 1917; Soberon and Peterson 2005; Soberon 2007). Biotic interactions like competition, predation, and symbiotic relationships also determine the portion of the fundamental niche that is ‘realized’, or occupied given biotic constraints (Pearson and Dawson 2003; Araujo and Guisan 2006; Soberon 2007; Cushman 2010; Evans et al. 2011). In quantifying the realized ecological niche of a species one can also calculate the degree to which species overlap ecologically with their competitors. The amount of inter-specific niche overlap allows us to predict how species may respond in a community context to a combination of altered nutrient availability and shifting species distributions (Wang et al. 2004).

The ensuing chapters use a range of approaches to describe both the fundamental and realized Hutchinsonian dietary niche spaces as well as the fundamental Grinnellian geographic niche space of 17 species of small mammals along two megatransects spanning Alaska (Fig. 1.1). Dietary niche spaces are outlined using stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) axes to determine dietary preference, trophic position, and competition potential. Fundamental geographic niche spaces are modeled using bioclimatic axes to map spatial distributions, biodiversity patterns, and to identify community structure. Together the quantifications of dietary and geographic niche spaces serve as a comprehensive means for predicting the consequences of climate change for an ecologically important group of Alaskan mammals.

1.5. CHAPTER 2 BACKGROUND: STABLE ISOTOPE ECOLOGY

Chapter 2 focuses on quantifying the dietary niche spaces of small mammals using stable isotopes. Stable isotope ratios, especially $\delta^{15}\text{N}$, and to a lesser degree $\delta^{13}\text{C}$, are useful for discerning a variety of biotic and abiotic relationships between organisms and their environments across space and time (Kelly 2000; Bearhop et al. 2004; Layman et al. 2007). Ecologists have employed stable isotope analyses with great success for tracing energy and nutrient flow through ecosystems (Gannes et al. 1998; Bearhop et al. 2004), identifying dietary sources (Fry 2006; Hobson and Wassenaar 2008), and clarifying trophic relationships within communities (Yi et al. 2006). Determining the amount of niche overlap between species is used as a means for estimating the potential for interspecific competition between emerging species interactions.

Stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) are ingested in diets and are assimilated into body tissues, such as hair, blood, muscle, or bone. Analyzing the stable isotope ratios in tissues allows for the use of stable isotopes as a marker to identify the origin of food sources. Nitrogen isotopes are useful for differentiating among specific food sources (Phillips and Gregg 2001; Crawford et al. 2008) and assigning trophic positions to species (Post 2002; Yi et al. 2006; Anderson and Cabana 2007). Carbon isotopes can identify marine versus terrestrial sources of carbon while providing a second dimension to complement $\delta^{15}\text{N}$ value when outlining isotopic niche spaces. Relative trophic positions of species indicate levels of omnivory and can help to indicate food web complexity (Post 2002). A better understanding of the niche spaces occupied by species and the competitive relationships between them will help to conserve ecosystem functionality in a changing environment.

1.6. CHAPTER 2 RESEARCH QUESTIONS

In this chapter, I address three main research questions:

1. What are the over-winter/spring proportions of fungi, herbaceous plants, woody plants, lichens, and mosses in the diets of small mammals?
2. How do the fundamental dietary niche spaces of small mammals overlap in Alaska?
3. How do realized dietary niche spaces of small mammals overlap at local scales and what are the implications for interspecific competition and coexistence?

1.7. CHAPTER 3 BACKGROUND: SPATIAL MODELING AND MACHINE-LEARNING

Whereas Chapter 2 focuses on the dietary niche of small mammals, Chapter 3 examines the geographic niche space by model-predicting the current distributions of small mammals in Alaska. Here, spatial modeling adds the dimension of landscape space to the quantification of ecological niche breadth (Kerr et al. 2011). Species distribution models, also termed ecological niche models, or bioclimatic models, are spatial models that use the environmental conditions underlying a set of known occurrence locations to predict the likely distribution of a species across unsampled space (Cushman 2010). Whether predicting the presence of a species, or isotopic values, point processes can be extrapolated across entire landscapes to create continuous predictive surfaces across large spatial extents (Wiersma et al. 2011).

Spatial models that use machine-learning programs such as RandomForests, TreeNet, CART, Mars, and MaxEnt in concert with GIS (Geographic Information System) software (e.g., ArcGIS) estimate species distributions by incorporating the geographic locations as well as a host of environmental predictor variables at those locations into predictions (Wiersma et al. 2011). Tree-based machine-learning programs use binary recursive decision tree rules to parse data points into terminal categories that minimize within-group variance. The program then writes a unique algorithm to encapsulate the set of rules describing patterns in terminal data categories with the highest possible accuracy.

Unlike other methods, limited by the number of variables that can be included in models, machine-learning processes can incorporate dozens if not hundreds of variables and their interactions as part of their predictive capacity (Hastie et al. 2001; Cutler et al. 2007; Kelling et al. 2009; Huettmann and Gottschalk 2010; Li et al. 2011). Each variable approximates one dimension of the n -dimensional hypervolume that constrains the fundamental niche space of a species. As such, machine-learning models are some of the best for deciphering the complex, confounding, and non-linear relationships among variables that drive ecological processes (Cutler et al. 2007). Documenting the spatial distributions of species, regions of overlap, and patterns of biodiversity adds the dimension of geographic space to the n -dimensional niche hypervolume as I seek to understand how communities and ecosystems may change over time.

1.8. CHAPTER 3 RESEARCH QUESTIONS

In this chapter I use the above methods to address three main research questions:

1. What are the current distributions of small mammals in mainland Alaska?
2. What are the dominant community arrangements for small mammals in Alaska?
3. Where are the current biodiversity hotspots in Alaska and who manages these lands?

1.9. CHAPTER 4 BACKGROUND: ISOSCAPES

Just as wildlife occurrences can be modeled across space as geographic distributions, so too can isotope values, in the form of landscape isotope models, or 'isoscapes' (West et al. 2010). Spatial patterns in the isotopic properties of systems are emerging as one of the leading analyses for understanding climate, biogeochemical and organismal biology (Hobson and Wassenaar 2008; Vachon et al. 2010; West et al. 2010). Applications of isoscapes include defining patterns in trophic interactions across landscapes (Hobson et al. 1999; Awkerman and Hobson 2007; Still and Powell 2010), identifying wildlife movement patterns (Hobson and Wassenaar 2008; Yerkes et al. 2008), and determining the spatial origins of nutrients or contaminants (Pardo and Nadelhoffer 2010) and their sources of error. Isoscapes that were model-predicted here describe a set of current biogeochemical baselines against which future conditions can be compared in order to identify regions undergoing ecological change.

Isoscapes in Chapter 4 depict the variation in isotope values for different trophic functional groups across the state including rodents, shrews, fungi, and herbaceous plants. Trophic group isoscapes were contrasted in ArcGIS to highlight broad spatial, biogeochemical patterns among trophic relationships. These models can also be used to highlight regional isotopic anomalies, where values deviate considerably from baselines as outliers. Such areas could indicate locales that are being influenced by atypical environmental factors either as a result of anthropogenic climate change or other human impacts. I also used the stable isotope values of small mammals and their food sources to calculate the relative trophic positions for rodents across Alaska. This was done in order to identify regions where higher levels of omnivory may be enriching rodent isotope values out of proportion to dietary baselines. Such ecologically relevant maps and spatial analyses have never been produced for Alaska. They can provide new utility for isotopic analyses as they are applied to wildlife conservation, community ecology, landscape assessment, and ecological health monitoring.

1.10. CHAPTER 4 RESEARCH QUESTIONS

In this chapter two main research questions are addressed:

1. What are the spatial isotopic patterns of Alaskan small mammals and their diets?
2. How do relative trophic positions of rodents vary across Alaska?

1.11. CHAPTER 5 BACKGROUND: FUTURE SCENARIO MODELS

The development of futures-scenario models for species distributions will provide a framework for predicting changes in species distributions and community structure over the coming century. Future models created here use downscaled climate projections from the International Panel on Climate Change (IPCC) A2 scenario as input variables to model species distributions in a manner similar to Chapter 3. These future models can be used to predict how species distributions and wildlife assemblage patterns are likely to shift over the coming century given significant anthropogenic climate change.

Just as maps of current species distributions were combined to create composite maps depicting species richness for 2010, future distribution maps can also be summed to show how biodiversity hot-spots are likely to move by 2100. As species distributions respond independently to transitioning habitats and biomes, dominant species assemblage patterns may also change complexion resulting in novel small mammal communities in the future. Comparing future species distribution and biodiversity maps with those in the present day using the Landscape Change Modeler (Clark Labs, Worcester, MA, USA) I quantify regions of species persistence, gains, and loss over time. These species-specific and spatially explicit maps can inform wildlife managers as to where the effects of climate change may be most dramatic, with the goal of inspiring more effective conservation measures that promote small mammal biodiversity and persistence throughout the coming century.

1.12. CHAPTER 5 RESEARCH QUESTIONS

In this final research chapter, I use future spatial predictive models to answer the following questions:

1. What are Alaskan small mammal distributions projected to look like in 2100?
2. What will future small mammal community assemblages look like in 2100?
3. How are biodiversity patterns expected to change in Alaska by 2100?



Fig. 1.1. Photo of field sampling along the Yukon River megatransect
The author paddles a canoe filled with trapping equipment down-river from Marshall, AK
between field sampling points along a 750-mile megatransect of the Yukon River in 2012.

CHAPTER 2. QUANTIFYING TROPHIC NICHE SPACES OF RODENTS USING STABLE ISOTOPES ($\delta^{15}\text{N}$ AND $\delta^{13}\text{C}$) AT TWO SCALES ACROSS ALASKA¹

2.1. ABSTRACT

Changing climate conditions are causing shifts in global species distributions, resulting in altered food webs and novel species assemblages in terrestrial systems. How sympatric small mammal diets overlap and whether this may translate into competitive exclusion among new species interactions remains largely unknown. Monitoring niche overlap in changing arctic and boreal communities can assist in forecasting interspecific competition and species turnover. We quantified small mammal isotopic niche spaces, which may reflect dietary niche spaces, at study sites along two megatransects spanning Alaska. Field sampling resulted in the capture of 724 small mammals belonging to 12 species of rodent and six species of shrew. We created dietary mixing models based on hair samples for six rodent species using stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) analyses in R. We also modeled isotopic niche ellipses and quantified niche overlap among species at small and large scales. A varied combination of fungi and herbaceous plants composed the diets of most species. Fundamental niche spaces overlapped considerably between sympatric species of rodents statewide, but realized niche spaces were largely segregated at individual sites. We conclude that some degree of dietary plasticity served to partition niche spaces and minimize interspecific competition, allowing sympatric species to co-exist.

2.2. INTRODUCTION

The fundamental ecological niche as conceptualized by Hutchinson (1957) is the space bounded by an n -dimensional hypervolume, consisting of a range of climatic and biotic variables, wherein a species is able to persist indefinitely in the absence of competition (McGill et al. 2006). At geographic scales, this concept is closely aligned with the Grinnellian notion of a species' niche being defined by its spatial distribution (Soberon 2007). Yet, biotic interactions including competition, symbiotic relationships, and predation also play important roles in

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outlining the portion of the fundamental niche that is ‘realized’, or occupied given the influence of other species, such that no two species should occupy exactly the same space (Soberon 2007).

Outlining the realized isotopic niche spaces of species and quantifying the magnitude of interspecific niche overlap can provide a means of identifying potential competitors at local scales. The extent of isotopic overlap can aid in predicting interspecific dietary differences (Wang et al. 2004; Ercoli et al. 2014) as well as the potential for coexistence or competitive exclusion of new species interactions (Araujo and Guisan 2006). New species interactions (e.g., between boreal and arctic species) are likely to occur in Alaska and Canada in the future as the warming climate pushes communities northward and upward in elevation (Williams and Jackson 2007; Murphy et al. 2010; Chapter 5).

Theory indicates that co-occurring species compete along resource, predation, space, and time axes. Co-existence occurs because trade-offs among competitors along these axes provide each species with a unique set of advantages and disadvantages (Chesson 2000; Moll and Brown 2008). When the occupied space bounded by these axes are similar among species, competition and possibly exclusion will result (Chesson 2000). Determining how new species interactions will play out in this context of competition is important for predicting the consequences of shifting and overlapping wildlife distributions.

Yet, defining the dimensions of small mammal diets (one axis of the fundamental niche) has been problematic (Bearhop et al. 2004; Huettmann and Gottschalk 2010). Quantifying the feeding ecology of wildlife has traditionally focused on direct observations, and fecal or stomach content analysis, but these techniques likely do not adequately reflect the quantity of nutrients assimilated into tissues and observations of cryptic species can be difficult (Gannes et al. 1998; Bearhop et al. 2004; Crawford et al. 2008). More recently, ecologists have successfully employed stable isotope analyses ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) to define the dietary niche of species and to trace nutrient flow between trophic levels and through ecosystems (Fry 2006; Layman et al. 2007a; Layman et al. 2007b; Perkins et al. 2014). Nitrogen isotopes are especially useful for differentiating between specific food sources (Phillips and Gregg 2001; Crawford et al. 2008) and assigning trophic positions to species (Post 2002; Yi et al. 2006; Anderson and Cabana 2007). Increases in $\delta^{15}\text{N}$ between 2.0‰ and 3.4‰ (Post 2002; McCutchan Jr. et al. 2003) and in $\delta^{13}\text{C}$ between 0.4‰ and 0.8‰ (Post 2002; Caut et al. 2009) with each subsequent trophic level

have been documented, but vary by species, tissue, and location (DeNiro and Epstein 1981; Minagawa and Wada 1984; Caut et al. 2009).

This variability can be employed as a measure of foraging breadth and to define the boundaries of the realized isotopic niche (Layman et al. 2007a; Jackson et al. 2011; Ercoli et al. 2014). For example, populations with high densities that consume a wide range of prey or forage species will exhibit greater variation in isotopic values, and wider niche breadths than those consuming a narrow range of dietary items (Layman et al. 2007b; Syvaranta and Jones 2008; Ercoli et al. 2014). Ultimately, patterns of co-existence may depend on limiting niche overlap between competitors at local scales, despite fundamental niche spaces that may overlap considerably at geographic scales (Ryan 1986; Hallett et al. 2003; Araujo and Guisan 2006).

In terrestrial communities of the boreal forest and the Arctic, rodents are important components at the base of food webs and provide significant energy flow via predation to higher trophic-level animals, including raptors and mammalian carnivorans (Robinson et al. 2014). They also provide numerous ecological services including seed dispersal (Lichti et al. 2014), symbiosis with mycorrhizal fungi (Maser et al. 1978; Luoma et al. 2003; Frank et al. 2009), soil development and fertilization (McKendrick et al. 1980; Hallett et al. 2003; Eldridge and Whitford 2009), and herbivory (Luoma et al. 2003; Gough et al. 2007; Olofsson et al. 2012). Stomach content analyses of northern rodents have shown a spectrum of dietary sources that include some combination of grasses, seeds, berries, buds, lichen, moss, fungi, and in some cases arthropods (Lensink 1983; Bangs 1984; Batzli and Henttonen 1990; Bergman and Krebs 1993; Luoma et al. 2003).

Alaska's small mammal fauna is diverse and includes dozens of species of rodents and shrews (*Sorex* spp.). Among these, *Clethrionomys rutilus* (Pallas, 1779 (northern red-backed voles), we consistently use ITIS (Integrated Taxonomic Information System) names, but see Carleton et al. 2014 for taxonomy) is one of the most common species in the boreal forest (Krebs et al. 2014) and is ubiquitous across most of the state with the exception of arctic and coastal regions (MacDonald and Cook 2009). They are found at a range of elevations in boreal and tundra ecoregions, inhabiting a diversity of terrestrial habitats including forests, shrublands, meadows, bogs, and talus slopes (West 1977; Zuercher et al. 1999).

As climate conditions warm, precipitation regimes change, and biomes shift northward, the distribution of *C. rutilus* (and other species) is also likely to move northward and upward in

elevation, encroaching on cold-climate-adapted communities that include *Microtus oeconomus* (Pallas, 1776 (root voles)), *M. miurus* (Osgood, 1901 (singing voles)), and *Dicrostonyx groenlandicus* (Trail, 1823 (collared lemmings); Gilg, Sittler and Hanski 2009; Lawler et al. 2009; Chapter 5). The competitive outcome of these species interactions including with new species that may enter Alaska from Canada in the future (Chapter 5) remains a significant unknown in the prediction of species persistence following climate change.

The diets of *Microtus* spp. have been shown to contain higher proportions of grasses, sedges, and herbaceous plants than *C. rutilus*, largely due to differences in preferred habitat (Krebs et al. 2010). But the degree to which their niches overlap with *C. rutilus* and one another remains unquantified (Batzli and Jung 1980; Batzli and Henttonen 1990; Bergman and Krebs 1993). Additionally, no studies have used stable isotopes to quantify isotopic niche overlap between multiple small mammal species across broad regions.

As a tool for predicting the outcomes of new species interactions (coexistence or exclusion), we describe the fundamental and realized isotopic niches of small mammals by quantifying dietary composition, trophic breadth, and degree of niche overlap between co-occurring species at geographic and local scales across Alaska. We predict that species with overlapping fundamental isotopic niche spaces at the statewide scale will be more partitioned in realized space at individual study sites in the presence of competitors. The degree to which small mammal isotopic niche spaces overlap with one another will help to identify the potential for interspecific dietary competition among novel small mammal interactions. Results will assist in determining the outcomes of new boreal and arctic species encounters as these occur with increasing frequency in the future.

2.3. MATERIALS AND METHODS

2.3.1. Field Sampling

We trapped small mammals at 20 locations between elevations of 10m and 1132m along latitudinal and longitudinal megatransects across Alaska between 2010 and 2013. Sampling sites were located in a diversity of habitats and ecoregions across the state (Fig. 2.1). Most low-elevation sites were dominated by *Picea mariana* (Mill. (black spruce)) forests interspersed with ericaceous shrubs and *Sphagnum* spp. (peat-moss) wetlands. Mid-elevation sites were composed of a mixture of *P. glauca* ((Moench) Voss (white spruce)) and black spruce, as well as mixed

hardwoods, ericaceous shrubs and *Salix* spp. (willows). High elevation sites and the two northernmost sites were devoid of trees and dominated by ericaceous shrubs and graminoid (e.g., *Carex* spp., *Eriophorum* spp.) tussock tundra.

In order to maximize capture of a wide diversity of species at each site, we placed 300 traps (200 Sherman live-traps (7.6 x 8.9 x 22.9 cm), 50 Museum Special snap traps (7 x 14 cm) and 50 pitfall traps (d=10.2 cm, h=17.8 cm)) throughout the range of available habitats along three 1-km trapping loops emanating from the plot center. Sherman traps were baited with rolled oats, snap traps with peanut butter, and pitfall traps were unbaited and placed at 10-m intervals. Traps were checked twice daily and remained open for five days and nights. Locations of captured individuals were recorded using a Garmin GPS and voucher specimens were permanently archived in the Mammals Collection at the University of Alaska Museum of the North (Supplemental File A).

2.3.2. Isotope Analysis

Hair samples from 329 small mammals belonging to 15 small mammal species were collected at 19 sites. Hair was sampled by shaving a 1-cm² patch of hair from the rump and preserved dry in paper coin envelopes. Hair samples were cleaned using a 2:1 methanol/chloroform solution, dried in a Blue-M #OV-18A oven (Thermal Product Solutions, White Deer, PA, USA), and homogenized in a 6770 Freezer/Mill (Spex Sampleprep, Matuchen, NJ, USA). Available food sources of rodents were sampled opportunistically from among the dominant species available. Three to five samples from each of five vegetative groups (herbaceous plants, woody plants, lichens, mosses, and fungi) were collected from each site. Vegetation samples were stored dry in paper envelopes before being ground and homogenized in a BeadbeaterMini with 3.2 mm chrome/steel beads (Biospec Products, Inc., Bartlesville, OK, USA).

Approximately 300–800 µg of hair and vegetation were weighed into tin capsules, combusted, and analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ on a continuous flow mass spectrometry system at the University of Alaska Anchorage Stable Isotope Laboratory. The isotopic ratios were reported in units per thousand (‰) against the international standards of Vienna Pee Dee Belemnite for carbon and AIR for nitrogen. Internal standards (BWBII keratin, peach leaves, moose (Linnaeus,

1758 (*Alces alces*)), and three-spined stickleback (*Gasterosteus aculeatus* (Linnaeus, 1758)) were used to determine an accuracy of $\pm 0.3\%$ for both carbon and nitrogen.

Because rodents moult in a series of continuous waves over their body, it can be difficult to determine exactly when hair was grown and thus the time period for which isotope samples are representative of diet (Sare et al. 2005a). Adult voles generally molt once in early spring (late April or early May; Al-Khateeb and Johnson 1971), and in Alaska tend to grow their summer pelage during the month of May (Sealander 1979). They do not moult again until autumn (late September or early October), and so any hair collected during the summer should be representative of their spring diet during late April and May (Sealander 1979). Because of caching of fungi, seeds, and berries (Krebs et al. 2010), spring diet may include over-winter stores that were collected during the previous autumn.

2.3.3. Trophic Niche Analysis

We used the stable isotope analysis package in R (SIAR (Parnell et al. 2010) in R2.12.1 (R Core Team 2013)) to create five-source mixing models using $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for hair samples belonging to *C. rutilus*, *D. groenlandicus*, *M. miurus*, *M. oeconomus*, and *M. xanthognathus* (Leach 1815 (yellow-cheeked vole)) at 17 sites across Alaska. SIAR uses a Bayesian process to calculate all possible solutions to the model and provides the most likely solution among a range of potential dietary proportions (Parnell et al. 2010). This type of model is considered to be an improvement over previous mixing models (e.g., linear mixing models or IsoSource (Phillips and Gregg 2003)) in that it incorporates sources of uncertainty into posterior probability distributions of consumer and source isotopic values (Parnell et al. 2010; Ercoli et al. 2014). Models yield the most probable proportions of a consumer's diet based on mean and standard deviations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of each consumer, five dietary sources, and trophic enrichment factors. Mean and standard deviation of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were calculated for consumers and vegetation functional groups and used as source inputs to SIAR. The most appropriate mean diet-to-tissue trophic enrichment priors that were input to SIAR were selected from the literature: 2.7‰ ($\sigma = 1.67$) for $\delta^{15}\text{N}$ and 2.4‰ ($\sigma = 1.01$) for $\delta^{13}\text{C}$ (Parnell et al. 2010; Sare et al. 2005b). Datasets met model-assumptions for normal distributions and we used a non-informative dirichlet prior for source contribution. Samples for rodents and vegetation sources were pooled by species across study sites where taxa were present. Models were not constructed for other rodents or shrews because

of insufficient sample sizes ($n < 4$) and because invertebrate prey were not sampled for shrews.

Isotopic niche space was quantified for eight rodent species using the Stable Isotope Bayesian Ellipse package in R (SIBER). SIBER was used to plot species niche ellipses and convex hulls, and to quantify niche overlap between species at study-site and statewide scales (Jackson et al. 2011). Unlike convex hulls (Layman et al. 2007a), which are sensitive to sample size, ellipses generated by SIBER are unbiased with respect to sample size, allowing for more robust comparisons among communities (Jackson et al. 2011). The statewide analysis was pooled across all study sites and did not account for interspecific interactions, thus reflecting species' fundamental niche spaces, while study-site analyses were more reflective of realized patterns in niche occupancy. We adjusted $\delta^{15}\text{N}$ values to trophic position to account for site-to-site variations in baselines using the formula: $Tp = 1 + (\delta^{15}\text{N}_{\text{rodent}} - \delta^{15}\text{N}_{\text{baseline}})/\Delta n$, where Tp = continuous trophic position, and Δn = trophic fractionation between the consumer and the base, in this case 2.7‰ (Post 2002; Anderson and Cabana 2007). Herbaceous plants were used as the primary producer to represent the first order baseline because all species consumed them, they were present at all sites, and variation in stable isotope values was low across Alaska (Anderson and Cabana 2007; Ercoli et al. 2014). $\Delta^{13}\text{C}_{\text{rodent}}$ values were also corrected to account for differences in baselines using $\delta^{13}\text{C}_c = (\delta^{13}\text{C}_{\text{rodent}} - \delta^{13}\text{C}_{\text{baseline}})/\delta^{13}\text{C}_{\text{baseline}}$, where $\delta^{13}\text{C}_c$ was the corrected $\delta^{13}\text{C}$ value and herbaceous plants were used as the baseline (Ercoli et al. 2014). Trophic position was used to infer relative levels of omnivory (Anderson and Cabana 2007), and together with $\delta^{13}\text{C}_c$ these metrics composed the isotopic dimensions of species dietary niche space.

Statewide and site-specific core niche areas were calculated for each species based on an ellipse of one standard deviation centered on the mean, containing roughly 40% of the data (Jackson et al. 2011; Ercoli et al. 2014). Convex hulls included the full extent of the data and were included to delineate the full range of samples. We used SIBER to calculate the area of ellipse overlap between co-occurring species at both study-site and statewide scales. Areas of overlap were divided by the sum of ellipse areas for co-occurring species to determine the percentage of niche overlap between species (0–50%).

2.4. RESULTS

2.4.1. Isotopic Niche Space of Taxa

Over a period of 30,700 trap-nights, 724 small mammals belonging to 12 species of rodent and six species of shrew were captured at 20 locations across Alaska (Table 2.1). Stable isotope values varied among sites and ranged between -0.14‰ and 7.44‰ for $\delta^{15}\text{N}_{\text{hair}}$ and between -31.5‰ and -21.5‰ for $\delta^{13}\text{C}_{\text{hair}}$ (Supplementary File A). After correcting isotope values to account for differences in baselines, mean trophic position calculations ranged between 0.7 for *D. groenlandicus* and 2.8 for *M. pennsylvanicus* (Ord, 1815 (meadow voles), Table 2.2). Plotted in dual isotope space, trophically adjusted stable isotope means and 95% confidence intervals placed the pooled isotopic niche space of rodents between the regions occupied by fungi and herbaceous plants (Fig. 2.2). Shrews $\delta^{15}\text{N}$ was 2.1‰ greater and $\delta^{13}\text{C}$ was 0.9‰ greater than rodents. The trophically-adjusted isotopic space of shrews was closest to fungi, although invertebrates were not sampled (Fig. 2.2).

2.4.2. Dietary Composition of Rodents

Patterns in dietary composition calculated by mixing models varied extensively in the proportions and combinations of dietary sources preferred by rodents among study sites (Fig. 2.3). Herbaceous plants comprised the largest proportions of all diets with the exception of *D. groenlandicus* and *M. xanthoganthus*. The proportion of herbaceous plants was largest for *M. oeconomus* (0.52), which had the only diet with proportions of fungi significantly less than herbaceous plants. *Clethrionomys rutilus* consumed significantly more fungi (0.60) than all other species except *M. xanthognathus* (0.23), and also consumed the smallest average amount of lichen (0.12) and woody plants (0.03). The average diets of *D. groenlandicus* and *M. miurus* were the most diverse and were composed more of woody plants, mosses, and lichens than other species. Models for *C. rutilus* and *M. oeconomus* differentiated well between sources, with the exception of herbaceous plants and fungi in *C. rutilus*. Other models had more difficulty differentiating between herbaceous plants, woody plants, and moss and as such credible intervals were large in many cases for the pooled data.

2.4.3. Niche Overlap

Stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) varied substantially both among study sites for a given species and among species at the same location (Supplementary File A). Averaged across populations, a clear pattern of the consumption of sources with high $\delta^{15}\text{N}$ values was evident for *C. rutilus*, *M. oeconomus*, *M. miurus*, and *M. pennsylvanicus* (Table 2.2, Fig. 2.4). This is contrasted by the lower $\delta^{15}\text{N}$ values of *D. groenlandicus*, *M. longicaudus* (Merriam, 1888 (long-tailed voles)), and *M. xanthognathus* (Table 2.2, Fig. 2.4). $\delta^{15}\text{N}$ values varied extensively among sites from *D. groenlandicus* at the Canning River (0.6‰) to *C. rutilus* at Fox Point Island (4.3‰, Table 2.2, Fig. 2.4). The highest $\delta^{15}\text{N}$ value (7.1‰) occurred at Yukon Crossing in both *C. rutilus* and *M. oeconomus* (Table 2.2).

Plotted against trophic position, $\delta^{13}\text{C}$ added a second dimension for defining isotopic niche position and extent (Fig. 2.4). Most species demonstrated extensive overlap with sympatric species in their statewide fundamental niche ellipses. The *C. rutilus* ellipse overlapped substantially with that of *M. oeconomus* (29.7%), while overlap with other co-occurring species ranged from 0% to 17.2%. Trophic positions of *M. oeconomus* were elevated and similar to *C. rutilus*, but the former had slightly lower $\delta^{13}\text{C}$. *Microtus miurus* and *M. pennsylvanicus* occupied similarly high trophic positions and their niche spaces overlapped with *M. oeconomus* by 15.6% and 14.0%, respectively. *Dicrostonyx groenlandicus* occupied a low trophic position but also a space high in $\delta^{13}\text{C}$, whereas *Synaptomys borealis* (Richardson, 1828 (northern bog-lemmings)) trophic positions were highly variable and their $\delta^{13}\text{C}$ values were the lowest of any species. These were also the only two species whose niche ellipses did not overlap with any other species (Fig. 2.4). Niche ellipses of *M. xanthognathus* overlapped with those of *M. oeconomus* (8.8%), *M. pennsylvanicus* (8.7%), and *M. miurus* (8.6%), while *M. longicaudus* and *M. xanthognathus* intersected only slightly (5.1%).

Realized niche ellipses were more segregated from one another in isotopic space across Alaska; only limited overlap occurred between the niche spaces of co-occurring species at three of the eight surveyed sites (Fig. 2.5). The best example of niche segregation occurred at the biodiverse White Mountains site, where three species coexisted without any core intersection (Fig. 2.5h). The most significant overlap at the study-site scale occurred between *C. rutilus* and *M. miurus* at Isabel Pass, where 13.7% of the total niche area was occupied by both species (Fig.

2.5c). The other two intersections occurred between *C. rutilus* and *M. oeconomus* at Chandalar River (11.6%, Fig. 2.5b) and Kenai Lowlands (10.8%; Fig. 2.5d).

2.5. DISCUSSION

Alaskan small mammals differed slightly in the proportions of fungi and herbaceous plants they consume (Fig. 2.3), resulting in fine-scale partitioning of niche spaces at the site scale (Fig. 2.5). However, isotopic analyses indicated extensive fundamental niche overlap between species at the regional scale (Fig. 2.4). These results point to plasticity in the realized dietary niche spaces of small mammals (Soininen et al. 2014). This flexibility may act to preclude extensive competition between species, even as new community assemblages develop as a consequence of shifting species distributions resulting from climate change (McGill et al. 2006).

2.5.1. Dietary Composition by Species

Variations in proportions of fungi consumed versus herbaceous plants largely account for differences in trophic position and niche differentiation between species. *Clethrionomys rutilus* incorporated the highest percentage of fungi into their diets compared to all other species. Stomach content analyses have shown *Clethrionomys gapperi* (Hall and Cockrum, 1952 (southern red-backed vole)) to consume large amounts of mycorrhizal fungi (Maser et al. 1978; Luoma et al. 2003). Disproportionate uptake of an enriched food source like fungi would explain their elevated trophic position and high $\delta^{13}\text{C}$. Specialization on fungi could be one mechanism allowing them to minimize dietary overlap and interspecific competition with *Microtus* spp. Conversely, elevated trophic position may be an indication of omnivory (Post 2002; Anderson and Cabana 2007), and unanalyzed sources such as invertebrates, bird eggs, or carrion could have contributed to their higher niche position as well (Sealy 1982; Batzli 1985). Additionally, because of low nitrogen concentrations in berries (Phillips and Koch 2002), woody plants may be underrepresented in species like *C. rutilus* that consume berries, but not leaf or stem material (Krebs et al. 2010), as is more common for *D. groenlandicus* or *M. miurus* (Fig. 2.2, Rodgers and Lewis 1986; Bergman and Krebs 1993).

Herbaceous plants were also an important dietary component for all species, and their proportion was highest in *M. oeconomus*. Although this species also consumed fungi, its low ratio of fungi-to-herbaceous consumption differentiated them along this axis from *C. rutilus*.

Similar enrichment in $\delta^{15}\text{N}$ for these species resulted in comparable trophic positions, but the higher proportional use of herbaceous plants by *M. oeconomicus* shifted their core niche to a $\delta^{13}\text{C}$ space lower than that of *C. rutilus*. This supports stomach-content analyses, which found that *M. oeconomicus* typically consume more herbaceous material (monocots) than *C. rutilus* (Bangs 1984).

Such partitioning was also evident in habitat selection patterns along the Yukon River. Detections of *M. oeconomicus* occurred frequently on *Salix* spp. (willow) sandbars where *Equisetum* spp. (horsetail) was the most available food source. By contrast *C. rutilus* was found more often in upland forests, where fungi were common. The specialization of these two sympatric species on different primary food sources may explain the partitioning of niche space and allow for their co-existence in adjacent habitats (Krebs et al. 2010). The apparent tradeoff in habitat use between the two species suggests that their co-existence may be stable over the long-term, as each species is able to out-compete the other in preferred habitats (Grant 1972; Chesson 2000).

The fundamental dietary niche position of *M. miurus* also overlapped substantially with that of *M. oeconomicus*. Similar to *M. oeconomicus*, mixing models for *M. miurus* also indicated herbaceous plants to be marginally more important in their diet than fungi (Fig. 2.3). This is consistent with foraging studies conducted in Alaska that found while both species primarily consumed herbaceous plants, *M. miurus* was partial to dicots and *Equisetum* spp., whereas *M. oeconomicus* preferred monocots like *Eriophorum* spp. (cottongrass) and *Carex* spp. (true sedges (Batzli and Henttonen 1990)).

Dicrostonyx groenlandicus showed similar dietary patterns to *M. miurus* yet it occupied very different isotopic niche positions. Mixing models found that it consumed relatively high proportions of woody plants, mosses, and herbaceous plants during the winter. These results largely concur with prior diet analyses that showed *D. groenlandicus* to consume primarily dicots including *Dryas integrifolia* (Vahl (entireleaf mountain-avens)) and *Salix arctica* (Pall (arctic willow)) in summer (Batzli and Jung 1980; Rodgers and Lewis 1986; Bergman and Krebs 1993). Mosses and lichens were important components in winter, but comprised negligible proportions of the summer diet (Bergman and Krebs 1993). The higher proportional consumption of food sources with lower isotope values (e.g., woody plants, and mosses), and

low consumption of fungi and herbaceous plants by *D. groenlandicus* may be an explanation for its low trophic position and differentiated niche space.

Whereas $\delta^{13}\text{C}_{\text{hair}}$ and dietary proportions of *M. xanthognathus* were similar to that of *M. oeconomus* and *M. miurus*, the trophic position of *M. xanthognathus* was somewhat lower. Previous research has shown that *M. xanthognathus* frequently caches *Equisetum* spp. and *Epilobium* spp., which comprised over 90% of its over-winter consumption (Lensink 1983). The isotopic niche ellipse for *M. longicaudus* occurred in a region of low $\delta^{15}\text{N}$, similar to that of *M. xanthognathus*, suggesting similar diets. Although small sample sizes precluded mixing models from resolving dietary proportions for these species, van Horne (1982) found that *M. longicaudus* consumed high percentages of dicots, fruits, and seeds than monocots and other sources.

2.5.2. Interspecific Niche Competition

Isotopic niche spaces varied for each species among sites, demonstrating the shifting nature of the realized dietary niche (Fig. 2.5) versus the more broader fundamental niche (Fig. 2.4). The combination of intersecting dietary niches at the statewide scale, broad spatial variation, and a lack of realized niche overlap at most study sites suggests that species may be capable of adjusting their diets or preferred habitats locally in order to minimize foraging competition with sympatric species (Holt 1993; Soininen et al. 2013). This is consistent with what niche theory predicts for communities that compete for limited resources. When sympatric species are limited by a single resource, niche partitioning cannot occur, but where multiple resources or predators exist, local niche partitioning is possible (Amarasekare 2008). Additionally, smaller-bodied species (e.g., *C. rutilus*) that may consistently lose agonistic encounters over one resource (e.g., herbaceous plants) to larger-bodied species (e.g., *M. oeconomus*; Grant 1972; McGill et al. 2006) can find stabilizing advantage in another resource (e.g., fungi) allowing for co-existence.

The broad intersection of fundamental trophic niche space between *M. oeconomus* and *C. rutilus* indicates significant potential for strong competition between these species where they co-occur. But the dietary niche comprises only a single axis of the overall fundamental niche of a species, and other spatial and environmental constraints including variations in habitat and range extents must also be considered when quantifying the fundamental niche breadth species.

Analyses of the geographic overlap between species have indicated that distributions of *M. miurus*, *M. oeconomus*, and *D. groenlandicus* were correlated with one another, as were *C. rutilus* with *M. xanthognathus*, and *M. pennsylvanicus* with *S. borealis* (Baltensperger and Huettmann 2015). The dietary preferences of *D. groenlandicus* and *S. borealis* appear to be specialized enough to avoid competition with both similarly distributed specialist and generalist species (Morris 1996). In other cases even though fundamental dietary niches may overlap (e.g., *M. pennsylvanicus* and *M. oeconomus*), because species do not have sympatric distributions, competition is avoided. While all distributions overlap to some degree (especially with *C. rutilus*), the only species combination with both highly correlated distributions and similar fundamental isotopic niche spaces are *M. oeconomus* and *M. miurus*.

When *M. miurus* or *M. oeconomus* co-occur with *C. rutilus* (e.g., Figs 2.5b, c, d), realized niches overlap and competition for limited resources could exist. However, Batzli and Henttonen (1990) showed a finer preference for dicots and monocots, respectively, by these species. In this analysis, these sources were pooled together as a single functional group and so no distinction in consumption could be made. Our results show that *M. oeconomus* may also be more dependent on herbaceous plants than mosses, whereas these proportions are roughly equal in *M. miurus*. These dietary differences may be one mechanism for differentiating foraging habits between these species and thus for avoiding interspecific competition. A separation of preferred habitats has also been observed between these species, pointing to fine-scale spatial partitioning even in regions where they co-occur (Galindo and Krebs 1985; Batzli and Henttonen 1990).

2.5.3. Implications of Climate Change

As climate change acts to rearrange species distributions and community assemblages, the number of species combinations sharing similar dietary and geographic niche spaces may change (McGill et al. 2006; Williams and Jackson 2007). *Clethrionomys rutilus*, whose niche space currently overlaps with those of *M. oeconomus*, *M. pennsylvanicus*, and *M. miurus* is predicted to expand northward and upward in elevation (Williams and Jackson 2007; Chapter 5). If future distributions result in more frequent contact between these four species, even small intersections in their diets could lead to increased dietary competition and exclusion near niche boundaries where competitive disadvantages cannot be offset along other niche axes. As an

example, Bergman and Krebs (1993) concluded that dietary competition was minimal between wild *D. groenlandicus* and *M. oeconomus*, but that overlap increased when the two species were forced to select between a limited set of available plants.

In contrast, the isolation of the fundamental dietary niche of *D. groenlandicus* and *S. borealis* (Fig. 2.4) may serve to insulate them from competition with *C. rutilus* and other voles as the distributions of boreal species encroach into the Arctic. Whether *D. groenlandicus* can persist in the context of expanding boreal species will not only depend on interspecific competition, but also whether changes in tundra vegetation can adequately provide for the nutritional needs of healthy populations (Rose and Birney 1980). As tundra vegetation (e.g., *Dryas* spp. and *Carex* spp.) gives way to encroaching shrubs from the south (Tape et al. 2012), it is uncertain whether arctic and alpine species will be extirpated as their primary habitats and food sources dwindle, or if they will adapt to new conditions. If arctic species are able to adapt to a boreal ecosystem, they will encounter heightened competition from a host of vole species that have already established their own niches from a limited combination of available foods. Ultimately the composition of these new communities will depend on the degree of niche plasticity among competitors and the availability of unoccupied niche space.

2.6. ACKNOWLEDGEMENTS

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2.7. FIGURES

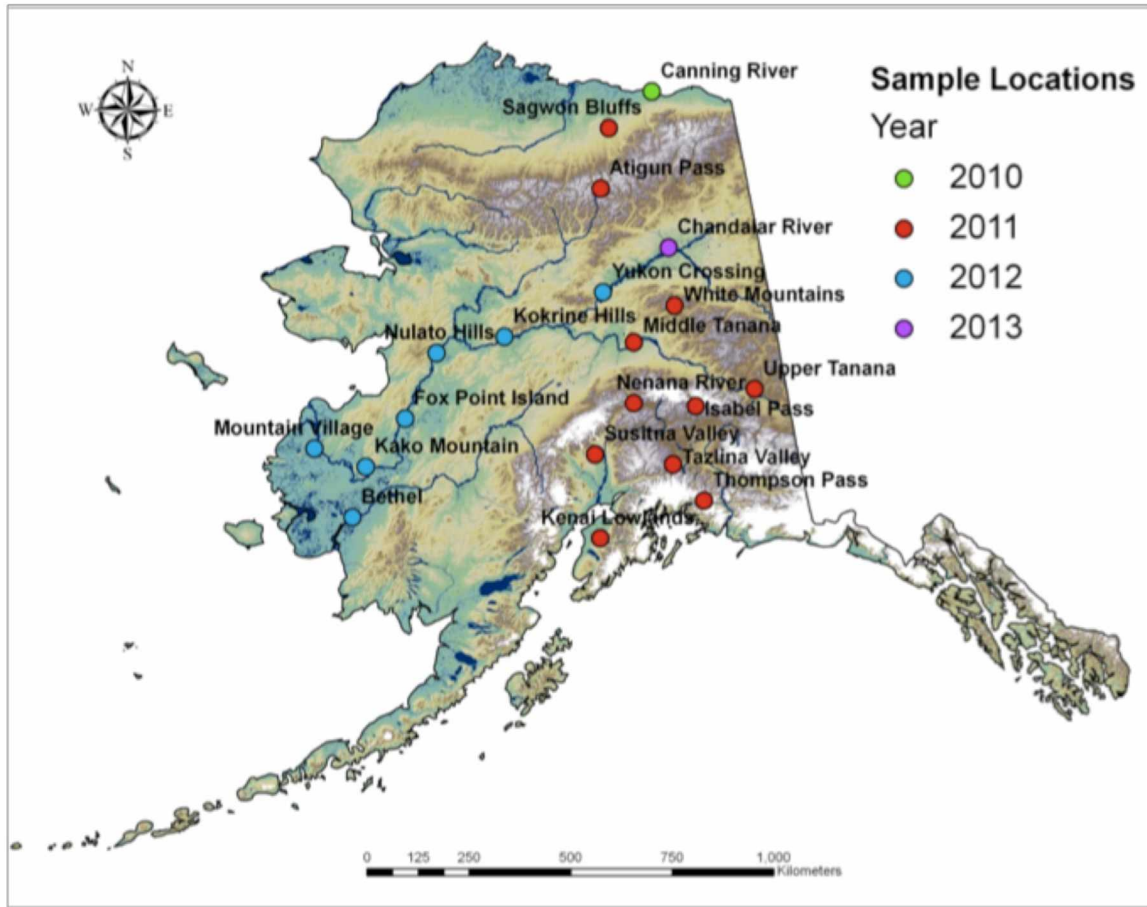


Fig. 2.1. Study area map
Shaded relief map of Alaska depicting 20 study-sites sampled along latitudinal and longitudinal megatransects according to year sampled.

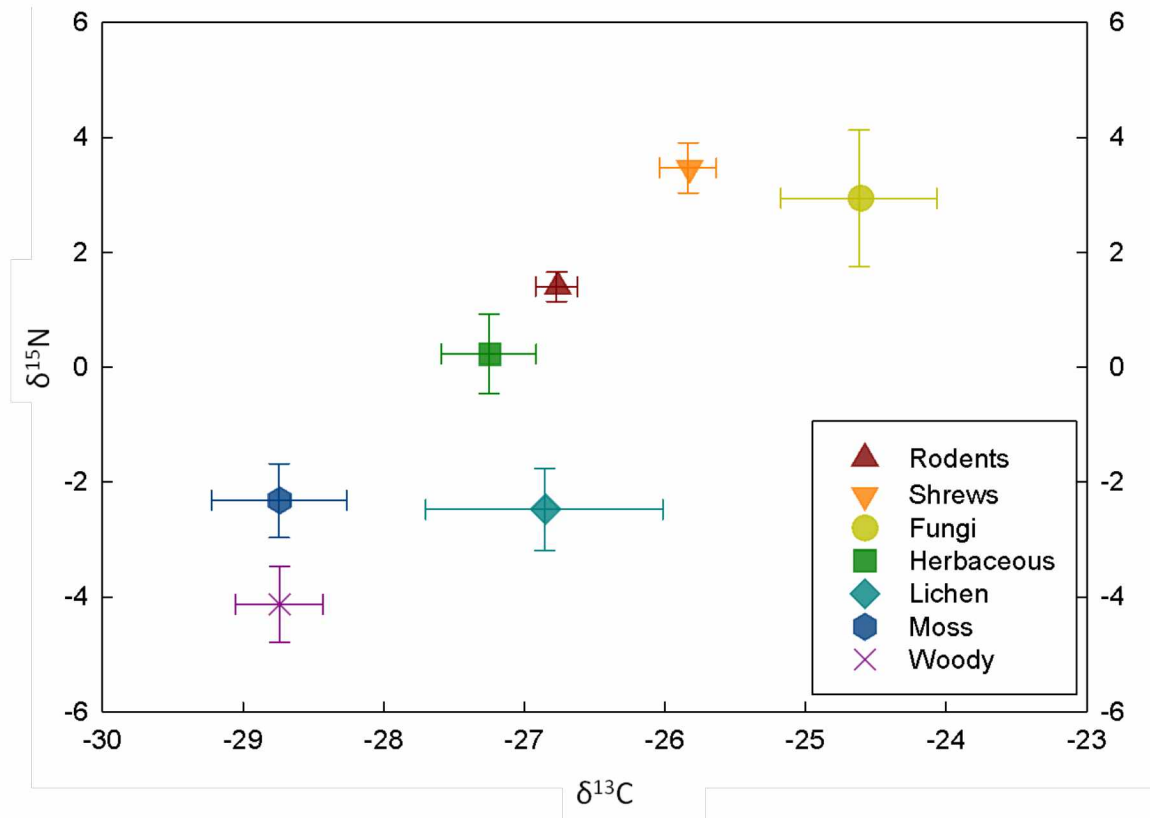


Fig. 2.2. Stable isotope biplot for rodents, shrews, and dietary components
 Dual isotope plot depicting means and 95% confidence intervals for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of rodents, shrews, and five vegetation functional groups pooled across 20 sample locations. Rodent and shrew $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were corrected downward 2.7‰ and 2.4‰, respectively to account for trophic enrichment.

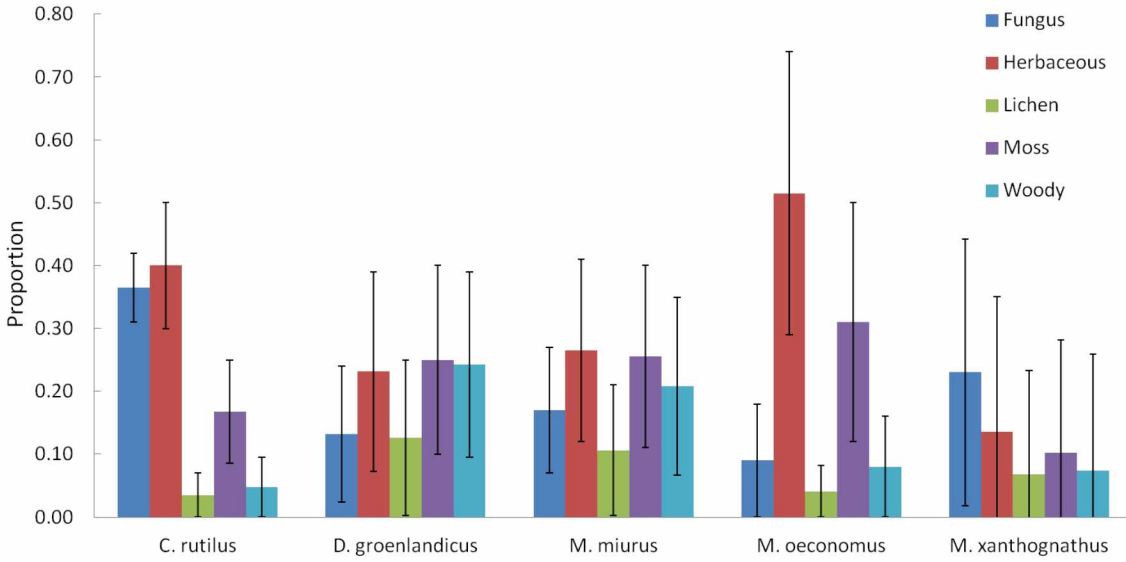


Fig. 2.3. Dietary mixing model proportions for five rodent species
 Pooled medians and 95% credible intervals of proportions of dietary sources for five species of rodent (voles and lemmings) as calculated by SIAR using five-member mixing models.

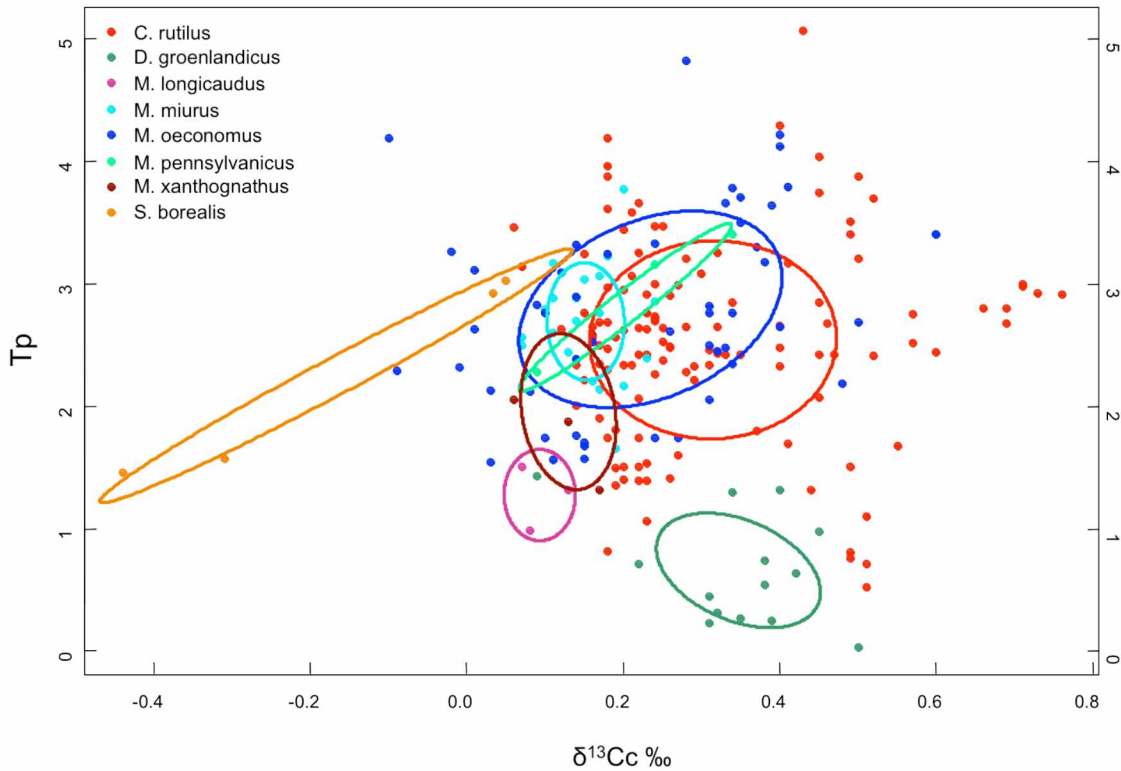


Fig. 2.4. Stable isotope niche space ellipses for eight rodent species
 Core isotopic niche ellipses, representing fundamental niches, calculated in SIBER for eight rodent species (voles and lemmings) across Alaska. Trophic position (Tp) is plotted against corrected $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_c$) values. Standard ellipses include 1 standard deviation of the mean, or roughly 40% of data.

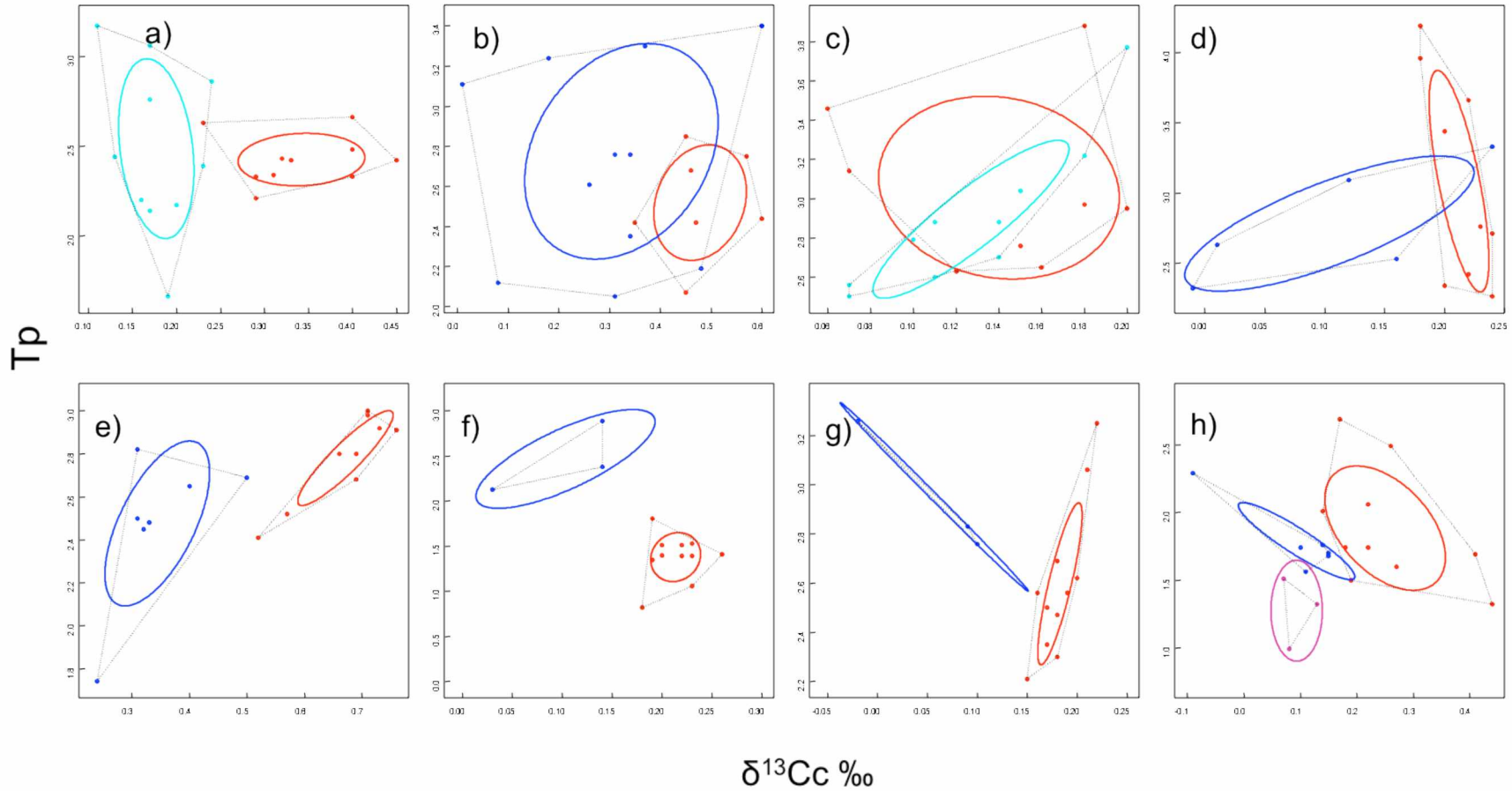


Fig. 2.5. Dietary niche overlap plots for co-occurring species at eight study sites

Standard niche ellipse (solid) and convex hull (dashed) isotopic niche areas calculated in SIBER for co-occurring species at eight study sites: a) Atigun Pass, b) Chandalar River, c) Isabel Pass, d) Kenai Lowlands, e) Mountain Village, f) Nenana River, g) Sagwon Bluffs, h) White Mountains. Species include *Clethrionomys rutilus* (northern red-backed voles; red), *Microtus miurus* (singing voles; light blue), *M. oeconomus* (root voles; dark blue), and *M. longicaudus* (long-tailed voles; pink). Trophic position (Tp) is plotted against corrected $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_c$) values.

2.8. TABLES

Table 2.1. Alaska small mammal species names and samples Integrated Taxonomic Information System (ITIS)-derived scientific names, common names, and Taxonomic Serial Numbers (TSN) for study species. The full list includes all species captured during field sampling, * denotes species for which niche ellipses were calculated, and † denotes species for which dietary mixing models were created.

Species	Common Name	TSN #	<i>n</i> Sites	<i>n</i> Samples
<i>Clethrionomys rutilus</i> *†	northern red-backed vole	180293	15	122
<i>Dicrostonyx groenlandicus</i> *†	northern collared lemming	180328	2	14
<i>Lemmus trimucronatus</i>	brown lemming	180320	1	1
<i>Microtus longicaudus</i> *	long-tailed vole	180299	1	3
<i>Microtus miurus</i> *†	singing vole	180309	2	20
<i>Microtus oeconomus</i> *†	root vole	180298	10	51
<i>Microtus pennsylvanicus</i> *	meadow vole	180297	2	4
<i>Microtus xanthognathus</i> *†	yellow-cheeked vole	180301	2	4
<i>Sorex cinereus</i>	cinereus shrew	179929	11	56
<i>Sorex hoyi</i>	pygmy shrew	179946	3	6
<i>Sorex monticolus</i>	montane/dusky shrew	179950	4	5
<i>Sorex tundrensis</i>	tundra shrew	179957	4	18
<i>Sorex ugyunak</i>	barren-ground shrew	552509	1	5
<i>Sorex yukonicus</i>	Alaskan tiny shrew	555663	1	1
<i>Synaptomys borealis</i> *	northern bog-lemming	180323	3	4
<i>Tamiasciurus hudsonicus</i>	red squirrel	180166	6	0
<i>Urocitellus paryii</i>	Arctic ground squirrel	930321	1	0

Table 2.2. Stable isotope values and calculations for seven rodent species
Means and 95% confidence intervals for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, corrected $\delta^{13}\text{C}$ ($\delta^{13}\text{Cc}$) and trophic position (derived from $\delta^{15}\text{N}$), from rodent hair for 7 species of rodent at sampling locations across Alaska.

Scientific		Hair $\delta^{13}\text{C}$ ‰		Hair $\delta^{15}\text{N}$ ‰		Hair $\delta^{13}\text{Cc}$ ‰		Trophic Position	
Name	<i>n</i>	Mean	95% CL	Mean	95% CL	Mean	95% CL	Mean	95% CI
<i>C. rutilus</i>	122	-24.47	-24.59 – -24.34	4.53	4.17 – 4.89	0.31	0.29 – 0.34	2.54	2.4 – 2.69
<i>D. groenlandicus</i>	14	-25.56	-25.77 – -25.35	1.57	0.92 – 2.22	0.35	0.29 – 0.40	0.66	0.4 – 0.92
<i>M. longicaudus</i>	3	-25.21	-25.79 – -24.61	2.04	0.28 – 3.80	0.09	0.01 – 0.18	1.27	0.62 – 1.93
<i>M. miurus</i>	20	-25.47	-25.70 – -25.24	2.29	1.75 – 2.82	0.15	0.13 – 0.18	2.69	2.47 – 2.91
<i>M. oeconomus</i>	51	-25.99	-26.29 – -25.69	4.37	3.88 – 4.86	0.24	0.19 – 0.28	2.79	2.57 – 3.01
<i>M. xanthognathus</i>	4	-25.99	-26.88 – -25.10	3.88	1.64 – 6.11	0.13	0.05 – 0.20	1.95	1.13 – 2.78
<i>S. borealis</i>	4	-28.51	-32.82 – -24.19	4.37	-0.19 – 8.94	-0.17	-0.55 – 0.22	2.24	0.9 – 3.59

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CHAPTER 3. PREDICTIVE SPATIAL NICHE AND BIODIVERSITY HOTSPOT MODELS FOR SMALL MAMMAL COMMUNITIES IN ALASKA: APPLYING MACHINE-LEARNING TO CONSERVATION PLANNING²

3.1. ABSTRACT

Context

Changing global environmental conditions, especially at northern latitudes, are threatening to shift species distributions and alter wildlife communities.

Objective

We aimed to establish current distributions and community arrangements of small mammals to provide important baselines for monitoring and conserving biodiversity into the future.

Methods

We used 4,408 archived museum and open-access records and the machine-learning algorithm, RandomForests, to create high-resolution spatial niche models for 17 species of rodents and shrews in Alaska. Models were validated using independent trapping results from 20 locations stratified along statewide megatransects, and an average species richness curve was calculated for field samples. Community cluster analyses (*varclus*) identified geographic patterns of sympatry among species. Species models were summed to create the first small-mammal species richness map for Alaska.

Results

Species richness increased logarithmically to a mean of 3.3 species per location over 1,500 trap-nights. Distribution models yielded mean accuracies of 71 % (45 % - 90 %), and maps correctly predicted a mean of 75 % (60 % - 95 %) of occurrences correctly in the field. Top predictors included Soil Type, Ecoregion, Landfire Land-cover, December Sea Ice, and July Temperature at the geographic scale. Cluster analysis delineated five community groups (3 - 4

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species/group), and species richness was highest (11 - 13 species) over the Yukon-Tanana Uplands.

Conclusions

Models presented here provide spatial predictions of current small mammal biodiversity in Alaska and an initial framework for mapping and monitoring wildlife distributions across broad landscapes into the future.

3.2. INTRODUCTION

The arctic and boreal biomes of the circumpolar North are undergoing dramatic changes in climate, geographic distribution, ecosystem function, and food web structure (ACIA 2005; Lovejoy and Hannah 2005; IPCC 2007; Lawler et al. 2009). Mapping the current extent of spatial overlap among sympatric species will be of important conservation concern as we monitor changes in the distributions of small mammal species in the future (Prost et al. 2013). In Alaska, small mammals are managed as non-game species under the Wildlife Action Plan (ADF&G 2006). This management plan recently called for the increased study of non-game and underrepresented species, especially birds and small mammals. Specific requests included efforts aimed at mapping species distributions, establishing spatial ecological system baselines, documenting biological diversity, and identifying lands vital for the conservation of wildlife in the face of increased human impacts in Alaska (ADF&G 2006).

In terrestrial communities, small mammals comprise a large portion of the primary consumer trophic level and represent the interface between fine-scale changes on the ground, including those related to water, soils, toxins, and micro-climate conditions (Hallet et al. 2003). Rodents are essential prey for a variety of carnivores and raptors, and also play invaluable roles in seed dispersal, nutrient cycling, plant growth, and herbivory (Newton 1979; Gough et al. 2007; Gilg et al. 2009; Olofsson et al. 2012). Insectivorous shrews, although less important as prey, are valuable in controlling invertebrate populations (Buckner 1964). Yet, despite the ecological importance of small mammals, high-resolution studies across the extent of Alaska are conspicuously lacking.

Most descriptions of small mammal distributions in Alaska have been coarse, non-quantitative, or incomplete, whereas spatially-explicit, GIS-based quantifications using modern statistical methods to analyze community composition and species richness patterns have not

been conducted for the state (MacDonald and Cook 2009; Gotthardt et al. 2013; Hope et al. 2013, www.natureserve.org, www.iucnredlist.org). Using a novel niche modeling technique, we provide such a detailed, quantitative, spatial analysis that addresses many of the regional management goals for small mammals. These products should prove beneficial for land managers as they act to promote ecological stability through species diversity (Lawler et al. 2003; Hooper et al. 2005).

The ecological niche, which encompasses the environmental constraints of a species, is best suited for predicting the uncertain ecological outcome of species interactions. As conceptualized by Hutchinson (1957), the ecological niche is the space bounded by an n -dimensional hypervolume such that no two species can occupy exactly the same space (Cushman 2010). Dimensions include an infinite set of abiotic and biotic variables including optimal temperatures, precipitation regimes, land-cover, elevation, soil chemistry, and resource proximities, to name a few. Only by quantifying the current dimensions of niche space and interspecific overlap will it be possible to correctly predict how species may respond in a community context to a combination of altered food availability and a shifting geographic arrangement of species (Wang et al. 2004; Williams and Jackson 2007; Hope et al. 2010; Murphy et al. 2011; Chapter 5).

Spatial modeling adds the multiple dimensions of landscape space to the quantification of ecological niche breadth (Kerr et al. 2011). Beyond general linear models, machine-learning algorithms such as RandomForests, TreeNet, Mars, CART, and MaxEnt are especially adept at estimating species distributions by incorporating the environmental conditions at species' detection locations into spatial predictions (Wiersma et al. 2011). Unlike resource selection functions, which only include a limited set of variables (e.g., Johnson et al. 2004) machine-learning can include hundreds of variables and all of their interactions to identify dominant signals in the data (Breiman 2001a, b; Cutler et al. 2007). RandomForests is therefore capable of incorporating many dimensions of the ecological niche simultaneously (Cutler et al. 2007; Booms et al. 2010, Evans et al. 2011). As such, machine-learning modeling techniques are some of the newest and most comprehensive methods for deciphering complex, confounding, and non-linear relationships among variables that drive ecological processes (Breiman 2001b; Cutler et al. 2007; Kelling et al. 2009; Huettmann and Gottschalk 2010; Li et al. 2011).

To outline the potential for inter-specific competition in small mammal assemblages, we focus on the construction of detailed niche-based distribution maps for 17 species (Table 1), using them to identify the current arrangement of small mammal communities and to create a species richness map for small mammals in Alaska. This research, in concert with subsequent analyses of dietary niche overlap using stable isotopes (Chapter 2) and future projections of species distributions (Chapter 5) will quantify the multi-metric ecological niche spaces occupied by small mammals, and provide projections as to how the roles of organisms are likely to shift in a future dominated by changes in climate and land-use (Wang et al. 2004).

3.3. METHODS

3.3.1. Study Area

Alaska covers an area of 1.7 million km² and extends from 71.4° N latitude at Pt. Barrow to 54.2° N at Amatignak Island, and 130.0° W longitude in Portland Canal in the Alexander Archipelago to 172.4° E on Attu Island in the Aleutian Archipelago. The state contains a diversity of geographic features including several mountain ranges—notably the Alaska, Brooks, Coastal, Aleutian, and Chugach Ranges—and elevations up to 6,036 m. Alaska's vast land area contains hundreds of glaciers and thousands of lakes that are drained by several large river systems (Molina 2001). Extreme variations in climate and geography have resulted in diverse ecosystems that include: arctic sedge tundra, boreal forest, deciduous hardwoods, peat wetlands, temperate rainforest, coastal grasslands, alpine tundra, shrub-lands, and others (Viereck et al. 1992).

3.3.2. Data Collation

We compiled records of small mammals from digital georeferenced collections totaling over 112,000 occurrence records in Alaska. A subset of these was used as training data to create distribution models for 17 species of rodents and shrews in mainland Alaska (Table 3.1). Data were collated from archived occurrence datasets, primarily from the Global Biodiversity Information Facility (GBIF; www.gbif.org), but also from a variety of natural history museum collections that do not necessarily serve their data to GBIF. This compiled set of presence-only records was filtered to remove duplicates, coincident detections of species at the same location, and those records without geographic precision to at least five decimals (sub-1-m accuracy).

Because of the presence-only nature of archived datasets that lack a geographically stratified design, we aimed to minimize the effects of sampling bias by using only one record per species within a 2-km radius of any given location. After manually removing these inaccurate or duplicate records, a total of 4,408 unique georeferenced small mammal records collected between 1900 and 2012 remained and comprised the final model training dataset (Supplementary File B).

3.3.3. Field Collection

As part of a larger effort to expand wildlife occurrence databases in Alaska, and to sample small mammal tissues for stable isotope analyses, we conducted 20 small mammal inventories along two megatransects (Assogbadjo et al. 2005) across the state between 2010 and 2013 (Fig. 3.1). During 2011, we sampled small mammal diversity along a 1,500-km latitudinal transect between the Arctic Ocean and the Gulf of Alaska. In 2012, we completed small mammal biodiversity sampling at seven locations along a longitudinal transect of the Yukon River during a 1,250-km canoe expedition from the Dalton Highway to Mountain Village. Additional sampling was conducted at the mouth of the Canning River on the Arctic coast during 2010 and near the mouth of the Chandalar River in 2013.

At each location we attempted to detect rodents and shrews using 200-300 traps (Sherman live traps, Museum Special snap traps, and pitfall traps) set at 10-m intervals along two or three trap-loops throughout available habitats within 1 km of the plot center. Traps remained open for five nights at each site (10 nights at Canning River) so that all sites were sampled with at least 1,500 trap-nights (number of traps * number of nights). Different trap types have different detectability rates, but the diversity of traps allowed for the sampling of a variety of taxa; Sherman live-traps primarily captured rodents, Museum Special traps captured rodents and some shrews, and pitfall traps captured only shrews. We received International Animal Care & Use (IACUC) approvals (172650-2, 172650-16) and Alaska Department of Fish and Game (ADF&G) Collection Permits (10-135, 11-114, 12-106, 13-162) for all field protocols, and specimens were archived at the University of Alaska Museum of the North.

We recorded the species detected at sampling locations for each day and plotted the accumulated species richness against the cumulative number of trap-nights. Linked with predictive modeling, this mobile, low-impact sampling scheme was designed as an efficient and

cost-effective means of independently sampling biological diversity across a large geographic extent. Detections of small mammals in these surveys were later used to independently validate the accuracy of species distribution models created from the small mammal training dataset.

3.3.4. Model Development

We used RandomForests (Salford Systems, Inc., San Diego, CA, USA; www.salford-systems.com) to create spatial distribution models for each of the 17 species of mainland small mammals in Alaska. RandomForests is a machine-learning software that uses binary recursive decision trees to parse data points into terminal categories that minimize within-group variance (Cutler et al. 2007; Elith et al. 2008; Appendix 3A). Machine-learning methods are non-parametric, and are especially adept at incorporating multi-variate interactions to analyze large, datasets without consistent sampling protocols (Prasad et al. 2006; Cutler et al. 2007; Elith et al. 2008; Evans et al. 2011). As such, they are an effective means to describe and predict the complexity of ecological systems (De'ath and Fabricius 2000; Prasad et al. 2006; Evans et al. 2011; Baltensperger et al. 2013). Results are data-driven and not fit to *a priori* assumptions as would be the case using frequentist, Bayesian, or maximum entropy (MaxEnt) methods (Breiman 2001a, Cutler et al. 2007, Elith et al. 2008; Phillips et al. 2006).

Presence points as well as 'pseudo-absence' points for each species were attributed with 33 environmental predictor layers (Table 3.2) using the intersect (*isectpntrst*) command in the free software, Geospatial Modeling Environment 7.2 (GME; H. Beyer; www.spataleecology.com/gme). Environmental predictor variables included continuous raster (60-m accuracy) and categorical polygon layers, all of which had the potential to affect the biogeography of small mammals. These effects may occur directly at the ecosystem or landscape scales (e.g., habitat, proximity to resources, topography, etc), or indirectly at landscape or regional scales (e.g., climate, ecoregion, etc.; Table 3.2).

Because this was a presence-only dataset, lacking available absences, it was necessary to generate a set of pseudo-absences to represent areas where target species weren't likely to be found. Random sets of pseudo-absences resulted in inaccurate models, so pseudo-absences were instead derived from the presence locations of all other non-target species (Elith and Leathwick 2007; VanDerWal et al. 2009). We assumed that a presence of any of the non-target species, without the coincident occurrence of the target species within a 1-km radius, represented a

pseudo-absence for the target species (Elith and Leathwick 2007). Although not ideal, given potential differences in sampling among other collection efforts, this was the best available option given the limitations of presence-only datasets and has been shown to perform as well as or better than other pseudo-absence scenarios (Breiman 2001a; Elith and Leathwick 2007; VanDerWal et al. 2009).

The combined presence/pseudo-absence datasets for each species were then modeled in RandomForests. We grew each model to 1,000 trees and used all other software default settings. RandomForests then created a coded model called a ‘grove,’ containing the algorithm quantifying patterns in the training dataset. Aspatial performance was assessed using a set of ‘out-of-bag’ training points (a subset of points automatically left out of model construction; Breiman 1996). Using this out-of-bag dataset, predictive performance of each model was calculated using the area under the curve (AUC) based on the receiver-operating characteristic (ROC), which quantified the percentages of correctly-predicted presences and absences in each model (Zweig and Campbell 1993; Fielding and Bell 1997; Huettmann and Gottschalk 2010). RandomForests was also used to rank the relative importance of environmental variables in models.

The grove files generated by RandomForests, containing the predictive algorithm, were then applied to a regular lattice of points (also attributed with the environmental variables) spaced at 5-km intervals across Alaska. Model outputs generated relative indices of occurrence (RIO; a ranking of pixels from 0 to 1 representing the likelihood of belonging to the ‘presence’ class) for each point in the regular lattice based on its underlying environmental variables. For better continuous spatial visualization, RIO values were smoothed between neighboring points across the extent of the study area using the *Inverse Distance Weighting* tool with 300-m resolution in ArcGIS 10.0 (ESRI, Inc., Redlands, CA, USA) and clipped to the state coastline, yielding a spatially continuous predictive distribution raster map of each small mammal species for Alaska. All GIS models and predictor layers were archived and are freely available on the online data repository dSpace (www.dspace.org) at the University of Alaska Fairbanks Elmer E. Rasmuson Library.

3.3.5. Model Validation

One advantage of our predictions is that they carry known accuracy estimates since they come from a consistent, testable, and transparent prediction process. We used independent field data sampled at 20 locations across Alaska to validate the spatial predictive accuracy of all maps. Observed presences and absences of species in the field were compared with model-predicted values at field locations for each species. We used a symmetric threshold of $\text{RIO} = 0.5$ for differentiating between model-predicted presences and absences and calculated the percentage of field points correctly predicted as presences and those correctly predicted as absences by each model. Using these accuracy percentages, we calculated Cohen's kappa (a statistical measure of agreement between modeled and observed values) for each species (Cohen 1960; e.g., Baltensperger et al. 2013).

3.3.6. Community Composition Analysis

In order to identify the degree of spatial niche overlap between species, we created a set of 50,000 random points across Alaska and attributed each point with the RIO values from the 17 species models. We used the *chart.correlation* command from the *Hmisc* package (F. Harrell; <https://github.com/harrelfe/Hmisc>) in R 2.12.1 (R Core Team 2013) to create a correlation matrix between species. This function yielded Pearson correlation coefficients (ρ^2) for all interspecific relationships. Species-pairings with correlation coefficients ≥ 0.5 were considered to be positively correlated and likely to co-occur in space, whereas pairings with a coefficient < -0.5 were negatively correlated and unlikely to co-occur. Coefficients between 0.5 and -0.5 were regarded as uncorrelated. Clusters of correlated species were visualized in tree form using the *varchus* command in *Hmisc*, so that we could easily identify groups of sympatric species. Using binary reclassified distribution models we also produced maps depicting the regions of Alaska where these communities are predicted to occur.

3.3.7. Biodiversity Hotspot Analysis

A composite biodiversity map was created for small mammals in Alaska by summing individual species models of known accuracies to create an implied predictive species richness map. Continuous species models were reclassified in a binary format so that cells with $\text{RIO} < 0.5$ (indicating the predicted absence of a species) were assigned an absolute absence value of 0,

whereas cells with $RIO \geq 0.5$ were assigned an absolute presence value of 1. The reclassified binary species models were summed in ArcGIS *Raster Calculator* to yield a raster whose cells indicated the total number of species predicted to occur there. We also calculated Pearson's correlation coefficient (Zar 2010) to assess the agreement between species richness values predicted by the composite biodiversity model and the number of species observed in the field.

We highlighted regions where ≥ 11 species ($\geq 85\%$ of maximum predicted species richness) were predicted to occur and arbitrarily designated these as biodiversity hotspots. The resultant biodiversity map was intersected with a land ownership map of Alaska to determine which government agencies and Native corporations are responsible for managing lands on which the highest levels of small-mammal species richness occur. Ownership of biodiversity hotspots was further parsed into individual management units for each managing entity and land areas were calculated for each species total.

3.4. RESULTS

3.4.1. Field Sampling

Over the course of 30,700 trap-nights (Fig. 3.2), we captured 624 small mammals belonging to 18 species at 20 locations along two geographic megatranssects spanning Alaska (Fig. 3.1). Only one species (American water shrew; *Sorex palustris*) of mainland Alaskan small mammals was not detected at any location (MacDonald and Cook 2009; Fig. 3.2). We documented several species in regions of the state where they had not previously been identified, representing range extensions for some. These new records included the capture of the rare and understudied Alaska tiny shrew (*S. yukonicus*; but see Hope et al. 2010 for taxonomy) in the Yukon-Tanana Uplands for the first time, as well as the documentation of the westernmost occurrences of yellow-cheeked voles (*Microtus xanthognathus*) near the village of Russian Mission, and long-tailed voles (*M. longicaudus*) in the White Mountains north of Fairbanks (MacDonald and Cook 2009).

Northern red-backed voles (*Clethrionomys rutilus*; but see Carleton et al. 2014 for taxonomy) were the dominant species at all but five locations near the geographic limits of their distributions where root voles (*Microtus oeconomus*), singing voles (*M. miurus*), and northern collared lemmings (*Dicrostonyx groenlandicus*) were caught in greater abundance (Fig. 3.2). The

dominant shrew species at most sites was the cinereus shrew (*Sorex cinereus*), except at Mountain Village where only tundra shrews (*S. tundrensis*) were captured.

Species richness curves averaged across all sites showed a roughly logarithmic increase in the number of species detected over the standard sampling period (Fig. 3.3). After just 300 trap-nights, a mean of 1.9 species was detected, but an additional 1,200 trap-nights resulted in the detection of fewer than two additional species and a mean total of 3.3 species per plot. However, no asymptote for species detection was attained after 1,500 trap-nights, indicating that the extent of total species richness had not been sampled.

3.4.2. Model Accuracy

Distribution maps created from each of the 17 species models (Appendix 3B, Supplemental File C) demonstrated high degrees of accuracy when evaluated a)spatially within each model using OOB cross-validation methods in RandomForests (Table 3.3), as well as spatially using the independent field-derived validation dataset (Table 3.4). Areas under the ROCs were greater than or equal to 0.90 for all species with the exceptions of water shrews and cinereus shrews (Table 3.3). All but two models (northern collared lemmings and northern bog-lemmings; *Synaptomys borealis*) demonstrated overall a)spatial accuracies greater than 50 %. The percent of training presence points correctly identified as presences in the models (sensitivity) exceeded 90 % for 14 of the 17 species, whereas the percentages of absences correctly identified (specificity) were somewhat less accurate but nevertheless exceeded 50 % for all but two species (Table 3.3).

3.4.3. Model Validation

Field validations of model predictions indicated the accurate spatial performance of most predictive models. Sensitivities and specificities were greater than or equal to 50 % for all models with the exception that just 11.1 % of cinereus shrew absences in the field were correctly identified as such by the model (Table 3.4). In general, sensitivities exceeded specificities, but sample sizes of presences for several species were small, making meaningful interpretation of validations difficult. A more conservative performance measure, Cohen's kappa, for long-tailed voles and singing voles was between 0.6 and 0.8, indicating 'substantial' agreement between models and field observations (Table 3.3; Landis and Koch 1977), whereas kappas for northern

collared lemmings, root voles, montane shrews (*Sorex monticolus*), and barren-ground shrews (*S. ugyunak*) were between 0.4 and 0.6 and demonstrated ‘moderate’ agreement. Validations between model predictions and field detections for six other species yielded kappas between 0.2 and 0.4, and less than 0.2 for an additional four species indicating ‘fair’ and ‘poor’ agreement, respectively (Table 3.4). Nevertheless all models performed better than random.

3.4.4. Species Distributions and Community Compositions

Predicted distribution models of small-mammal species were grouped by *varchus* analysis into five communities of similarly-distributed species (Fig. 3.4). The first community group, referred to hereafter as the ‘cold-climate community’, was composed of species found at high latitudes as well as high elevations mainly across the North Slope and throughout the Brooks Range (Figs 3.4, 3.5a). None of the four species in this cluster were predicted to occur with any certainty in the center of the state throughout the central portions of the Yukon and Kuskokwim River valleys, where members of the interior and southern communities were concentrated. The second cluster, or ‘northern community,’ was composed of species that occurred across much of the region north of the Alaska Range (Figs 3.4, 3.5b). These species were distributed patchily in a metapopulation arrangement across a variety of regions. Members of the third group, or ‘continental community’, included species occurring primarily near the Canadian border and apparently near the latitudinal extents of more southerly ranges (Figs 3.4, 3.5c). The fourth, or ‘interior community,’ included two species that were both primarily restricted to a narrow swath of dry boreal forest between the Brooks and Alaska Ranges (Figs 3.4, 3.5d). Northern red-backed voles were predicted to belong to this community, even though their range was much more expansive. The fifth species cluster, or ‘southern community,’ was composed of species predicted to occur mainly south of the Brooks Range (Figs 3.4, 3.5e). Top variables were largely consistent among models and on average were ranked in the order of *Soil Type*, *Ecoregion*, *Landfire Landcover* (vegetation), *December Sea Ice*, and *June Sea Ice*.

3.4.5. Regional Biodiversity Hotspots

A composite biodiversity map derived from the summation of 17 binary species models identified four main small-mammal species richness hotspots in Alaska (Fig. 3.5f). Model predictive accuracy, assessed using Pearson’s correlation coefficient, indicated moderate positive

correlation ($r = 0.6$) between modeled and observed species richness values for Alaska. Statewide, the majority of lands coinciding with biodiversity hotspots (> 10 species) are managed by the State of Alaska (20,199 ha), and the Bureau of Land Management (BLM) and Regional Native Corporations maintain an additional 7,271 ha and 5,587 ha, respectively (Table 3.5). The largest and most diverse of these hotspots occurred across the Yukon-Tanana Uplands near the Canadian border. Most of this area is managed by the State of Alaska, including the largest area predicted to contain the highest statewide level of small mammal diversity (13 species) in Game Management Unit 25 (Table 3.5). We detected 6 species in 1,500 trap-nights nearby at the Upper Tanana site in 2011 (Fig. 3.2). A significant portion of the Yukon-Tanana Uplands hotspot also occurs on land managed by the BLM, including in the Steese National Conservation Area, where we detected 7 species in 1,500 trap-nights at the White Mountains site in 2011 (Fig. 3.2). Doyon Regional Native Corporation, the National Park Service, and the U.S. Fish and Wildlife Service also maintain thousands of hectares containing high small mammal diversity in this region (Table 3.5).

The second small mammal hotspot occurred in the mountainous region between the headwaters of the Koyukuk, Kobuk, and Noatak Rivers in the central Brooks Range. Most of this land is managed by the National Park Service and the State of Alaska (Fig. 3.5f). A third hotspot cluster was located east of Kotzebue Sound in the Selawik National Wildlife Refuge, and on BLM and State of Alaska lands. Other diversity hotspots included several areas to the northwest of the Alaska Range in Denali National Park and on nearby BLM and State of Alaska lands (Fig. 3.5f). Regions predicted to contain low small mammal diversity included the North Slope, lower Yukon River, Yukon-Kuskokwim Delta, and Bristol Bay. Independent field results largely support these predictions. For example, we detected only northern collared lemmings at the Canning River site on the North Slope, just two species in the Nulato Hills along the lower Yukon, and three species at Mountain Village on the Yukon-Kuskokwim Delta (Fig. 3.2).

3.5. DISCUSSION

The goals of this research were to compile species occurrence records, predict species distribution and richness patterns, and to delineate the geographic community structure of small mammals in Alaska, while providing a modeling framework for other multi-species systems. We found that the distributions of the mainland small mammal species of Alaska can objectively be

structured into five main community groups (Fig. 3.4), each with a unique set of geographic patterns (Fig. 3.5) but similar ecological predictors that depict the influence of climate, soils, and vegetation on the arrangement of species across the state. We have created fine-resolution, statewide distribution maps for 17 mainland small mammal species in Alaska that represent the most accurate continuous depictions of occurrences to date. We also created species richness curves for sampling locations (Fig. 3.3), objective delineations of small mammal community structure (Figs 3.4, 3.5) and a small-mammal species richness map that is the first of its kind for small mammals in Alaska (Fig. 3.5f). The moderate to high accuracy of these models attests to the efficiency of machine-learning techniques when applied to archived datasets not collected using consistent methods.

3.5.1. Species Richness Sampling

The style of rapid assessment or ‘bio-blitz’ (Wilson 2006) sampling employed here allowed for small, mobile trapping teams to efficiently sample a geographically significant portion of Alaska in just two main field seasons. The detection of all but one of the small mammal species in the region is a testament to the efficacy of this design. Sampling efforts also added a large number of records to the statewide species occurrence dataset, expanding known species ranges and filling in training datasets gaps.

Trapping efforts detected roughly half of the model-predicted number of species occurring in most regions. The under-sampling of total species diversity at the plot level was perhaps the trade-off of a geographic megatranssect strategy designed to maximize diversity detection at the statewide scale. Despite a variety of trap styles aimed at detecting a diversity of species, and higher than average trap-nights, some species may have been especially trap-shy and remained undetected despite this intense effort. Because the number of species detected continued to increase with additional trap-nights, studies aiming to detect levels of species richness at the study site scale would be served well to trap in excess of 1,500 trap-nights.

3.5.2. Model Progress and Accuracy

All models performed remarkably well given their ability to correctly identify species presences. The models created here represent improvements in detail and accuracy over other maps for small mammals in Alaska including NatureServe and the International Union for

Conservation of Nature (IUCN; www.iucnredlist.org) range maps, deductive and inductive distribution models by the Alaska Gap Analysis Project (AKGAP; <http://gapanalysis.usgs.gov/species/data>) models (Gotthardt et al. 2013), and other recent species niche models (Hope et al. 2013). Commonly-used range maps are coarse in scale and reflect only basic minimum convex polygon outlines of the extents of species occurrences without accounting for the influence of environmental variables in defining niche space.

The AKGAP deductive models were derived solely from habitat suitability associations and these models tended to over-predict wildlife distributions (Gotthardt et al. 2013). Although inductive AKGAP models incorporated 20 environmental variables into predictive models, this is 13 fewer than used here, and inductive models tended to under-estimate distributions. Nearly all of our species models had higher overall accuracies than models for the same species generated by AKGAP (Gotthardt et al. 2013). Our models had AUC values similar to those of AKGAP and exceeded those for the five species modeled by Hope et al. (2013).

Nevertheless, all of these ecological niche-modeling approaches provide valuable species distribution predictions that likely fall on a spectrum between depictions of the fundamental and realized niche spaces. Models that over-predict distributions represent more of a fundamental niche versus our models, which likely depict a more restricted realized niche. Because ecological niche models often do not include parameters to account for the details of physiology, movement, and adaptation (Bush 2002), real distributions are probably closer to some combination of these models. Future distribution mapping efforts should focus on combining several modeling approaches into a single ensemble model framework that utilizes the best components of each to produce the most accurate spatial models (Elith and Leathwick 2007; Hardy et al. 2011).

The improved accuracy of our models can be attributed to the use of more accurate presences and more representative pseudo-absence datasets based on the locations of non-target-species where target species did not also occur. This practice is an improvement over the common alternative of using randomly generated pseudo-absences or Maxent-generated absences, and resulted in more accurate models that generalized well without fitting too tightly to the training data (Elith and Leathwick 2007, Gotthardt et al. 2013). Our emphasis on correctly predicting presences may have come at the cost of reduced absence prediction, as many specificity values and consequently some overall accuracies were rather low in comparison. This

effect may be a necessary detriment of using pseudo-absences in lieu of ‘true absences’ recorded in the field. Nevertheless, given the complexity of archived datasets, we have created models representing accurate predictions of species occurrence. We recommend using non-target surveys to aid in generating appropriate pseudo-absence scenarios for the creation of other multi-species, presence-only, distribution models.

3.5.3. Environmental Predictors

The top three predictors, *Soil Type*, *Ecoregion*, and *Landcover*, were similar for all species, and along with some climate-related layers were consistently the most important predictors used in model algorithms. Their prevalence demonstrates a consistent bottom-up effect of climate and soils interacting to produce habitats that drive biodiversity and community assemblage patterns. These results suggest that shifting habitat conditions resulting from changes in climate will likely have strong influence in determining distributions of wildlife and inter-specific relationships at northern latitudes.

Although these were the most important predictors on a geographic scale, their values may be overestimated at finer scales in the field. We should also note that the top three predictors are all categorical variables. Because of their categorical structure, RandomForests can easily utilize stark differences between categories to partition data points, effectively inflating the importance of these variables in the models. Nevertheless, these results provide data-mining-based foundations for more detailed hypothesis-driven analyses aimed at identifying mechanisms driving patterns of wildlife distribution.

3.5.4. Community Structure

Small mammal species in Alaska can be organized into five main community groups that reflect their current distributions and potential for interactions with other species. *Varchus* provides a repeatable method for outlining large-scale spatial relationships among wildlife species and for documenting changes in community arrangement over time. For example, the spatial pattern for the cold-climate community is an approximate inverse prediction of the interior community’s distribution, and members of these two communities do not often co-occur. As the membership of communities and the spatial arrangement between them changes with the warming climate, a consistent analysis such as *varchus* will be useful for documenting specific

changes in the community composition and overlapping distributions of wildlife species around the world.

Although *varchus* community clusters indicate the most common arrangement of species at a geographic scale, they do not reflect the extent of species assemblages that may occur across different habitats. The statewide species richness map depicts overlapping distributions of ≥ 6 species over a large portion of the state, clearly demonstrating frequent cross-over between community clusters on the landscape (Fig. 3.5f). Correlations between species within each cluster were high, but in some cases inter-cluster correlations for some species combinations were also large. The tightest geographic relationships occurred in the southern community, and indeed all of these species were frequently detected together in the field (Fig. 3.2).

Trapping records included several instances in which species belonging to different community groups co-occurred at a single location. For example, northern red-backed voles, root voles, and cinereus shrews—members of three different communities—occurred together at three sampling locations (Fig. 3.2), indicating wider geographic niche breadths and more generalist distribution patterns. Dominant species like northern red-backed voles and cinereus shrews are increasingly being found beyond their historical distributions, leading to the higher likelihood of novel species contacts and newly emerging interspecific relationships (Hope et al. 2013). Recent stable isotope analyses have shown that in areas where species distributions overlap, dietary plasticity and niche partitioning may allow dominant and secondary species to coexist without significant competition (Chapter 2). Monitoring how changes in the extent of geographic overlap between species may alter community membership can serve to identify the landscape-level effects of environmental change on wildlife persistence (Hope et al. 2013).

3.5.5. Regional Biodiversity Patterns

The region with the highest level of small mammal diversity was the Yukon-Tanana Uplands, where a maximum of 13 species were predicted to co-occur. This region appeared as a major biodiversity hotspot for several reasons. First, it is closest to the North American interior both geographically and ecologically. It is an extension of the interior Canadian boreal ecoregion and represents the farthest reach of many species that may be slowly expanding their ranges northward from the contiguous United States and Canada (Parmesan and Yohe 2003; Root et al. 2005). This includes members of the continental community, as well as members of the interior

and southern communities. Many of these species are also not usually found outside of the interior and historically did not occur in Alaska prior to the last glacial maximum (MacDonald and Cook 2009; A.G. Hope, personal communication).

Second, this region contains a wide range of elevations and habitats, resulting in a variety of available niches. With the diversity of habitats, it is likely that more common species such as northern red-backed voles, cinereus shrews, root voles, and other members of the northern community such as brown lemmings and tundra shrews would be found there. Because of the high elevations, the models predict that singing voles should also occur there. The only mainland species not predicted to live in this region are all three of the cold-climate species, whose distributions are far removed from this area. A similar geographic ecotone containing a variety of habitat types may also account for the hotspot in the Central Brooks Range between the headwaters of the Koyukuk, Kobuk and Noatak Rivers, as well as the hotspot cluster on the lee side of the Alaska Range. Such small mammal biodiversity hotspots occurring at the ecological crossroads along biome boundaries support the notion of these areas as important biodiversity reservoirs worthy of conservation in a changing climate (Neilson 1991).

3.5.6. Management Implications

The conservation of biodiversity is important for a number of reasons. Although many of these species occur together across the state and appear to fill similar ecological roles, our understanding of the mechanistic functions and niche overlap of animals in ecosystems is limited (Churchfield et al. 1999; Hooper et al. 2005; ADF&G 2006; Prost et al. 2013). Nevertheless, apparent ecological redundancy has the benefit of insuring against the uncertainty of climate change. Maintaining a range of species that provide different ecological services and that may respond differently to environmental disturbances can have a stabilizing effect on food webs and ecosystems as they evolve (Aarssen 1997; Hooper et al. 2005; Duffy et al. 2007). Maximizing diversity also increases the likelihood that species that have disproportionately large effects on ecosystem functionality will persist (Aarssen 1997, Hooper et al. 2005). Furthermore, active conservation of a diversity of prey species occupying a variety of niches is an essential part of conserving predator diversity, and ultimately for maintaining ecosystem-wide trophic structure and functionality (Noss 1990, Lawler et al. 2009).

Because two-thirds of the land in Alaska is public, the vast majority of small-mammal hotspots occur on federal and state lands, granting an opportunity to pursue biodiversity conservation on a large scale. For land managers, the results of these types of analyses should provide them with the spatially-explicit tools and knowledge to prioritize species richness as a conservation management goal. Documenting current distribution and baseline community patterns of primary consumers at a geographic scale is the first step towards identifying the effects of impending environmental changes on the bottom-up flow of nutrients into wildlife communities (Noss 1990). Of course, species responses will not be uniform, but will depend on the capacity of each to tolerate, adapt, or disperse given rapid, large-scale ecological change (Parmesan and Yohe 2003, Williams and Jackson 2007, Hope et al. 2013).

Monitoring shifts in individual species distributions over time will provide tangible accounts of how species are responding across space, and will be vital for assessing the temporal stability and adaptive capacity of natural systems (Hooper et al. 2005, Hope et al. 2013). Based on other predictive modeling efforts (Magness et al. 2008) we advocate for the establishment of a permanent network of small mammal survey sites, distributed across the state, but especially in the areas of highest diversity (e.g., Yukon Tanana Uplands), and checked at annual or decadal intervals to serve as the foundation for such long-term monitoring efforts (Noss 1990, Hope et al. 2013). Not only could a network of stations monitor species richness, but using a consistent trapping grid protocol would also allow for the calculation of species densities. These could also be modeled across space to create detailed maps of population status for multiple species. Both would be sound applications of the best professional research practices to wildlife management across a continually changing landscape.

Although species distributions and community compositions are likely to shift with the climate over time, providing wildlife with the opportunity to disperse to new areas within their niche envelope will be paramount for their persistence into the future (Bush 2002, Williams and Jackson 2007). Even as the climate, soils, and habitat conditions change, if land managers can promote the continued connectivity of important refugia along latitudinal and elevational corridors, then species incapable of coping with new environmental conditions can disperse to unexploited areas of their fundamental geographic niche (Bush 2002; Hope et al. 2013). Predicting where and how the environment will change, determining how species are likely to

respond, and conserving these areas for the future are the biggest challenges currently facing species diversity conservation worldwide.

3.6. ACKNOWLEDGEMENTS

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3.7. FIGURES

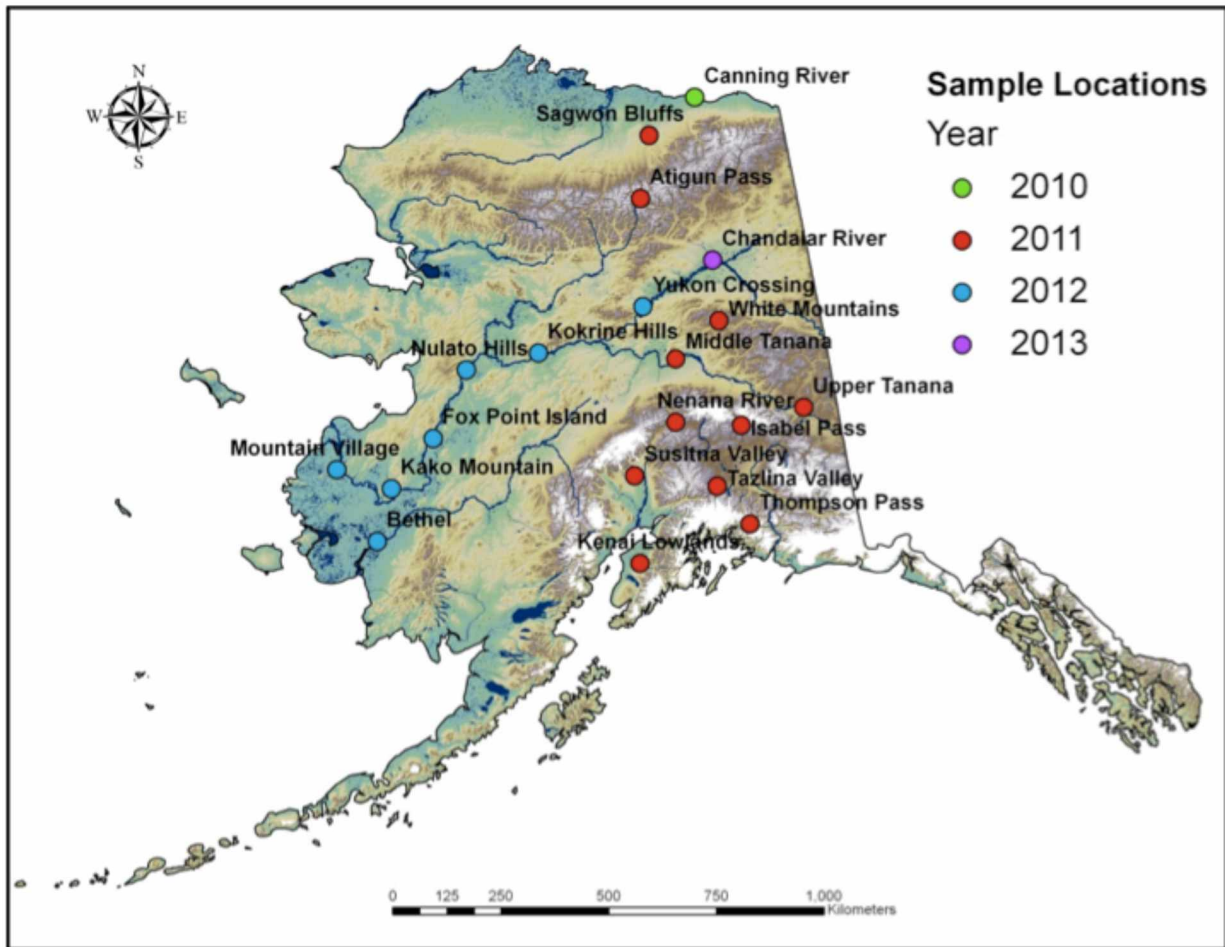


Fig. 3.1. Study area map
Depiction of small mammal sampling locations between 2010 and 2013. Locations are organized along latitudinal and longitudinal megatranssects across the state.

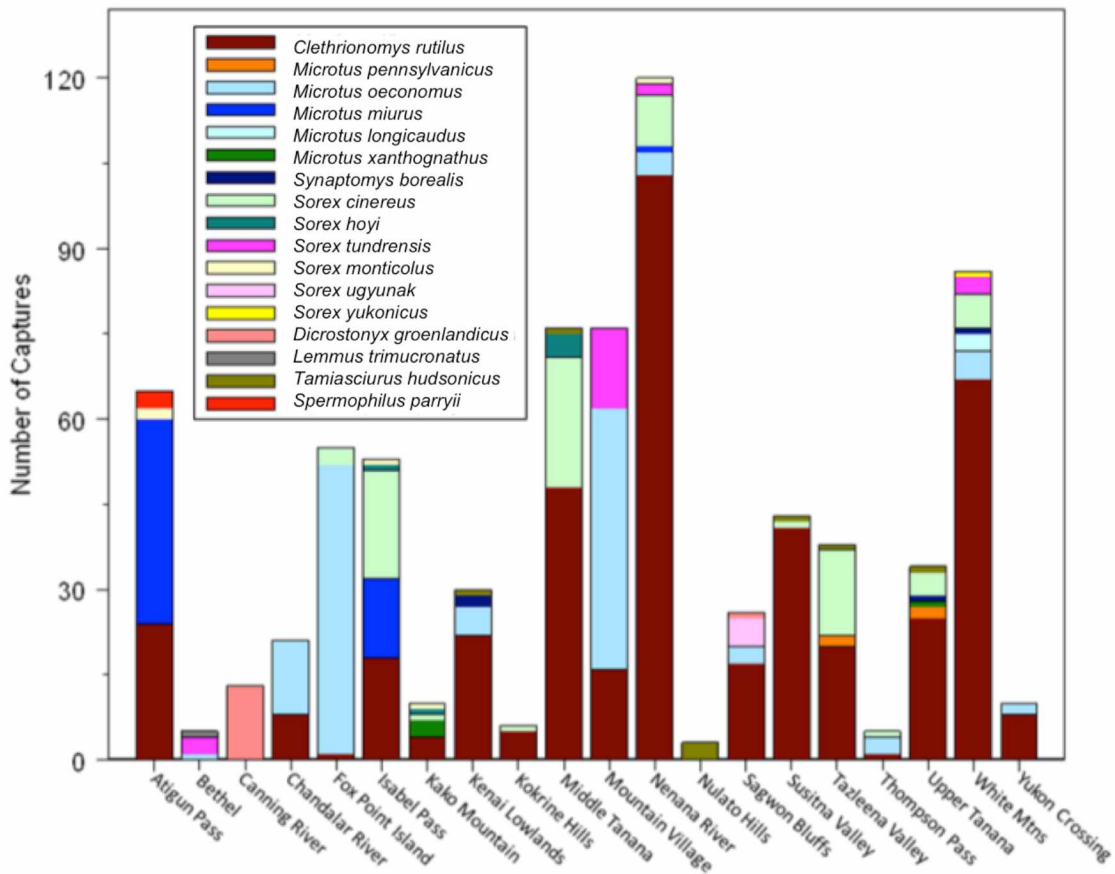


Fig. 3.2. Histogram of small mammal trapping detections
 Composite histogram of all species detected at 20 sampling locations between 2010 and 2013.
 Each location was sampled with 1,500 trap-nights.

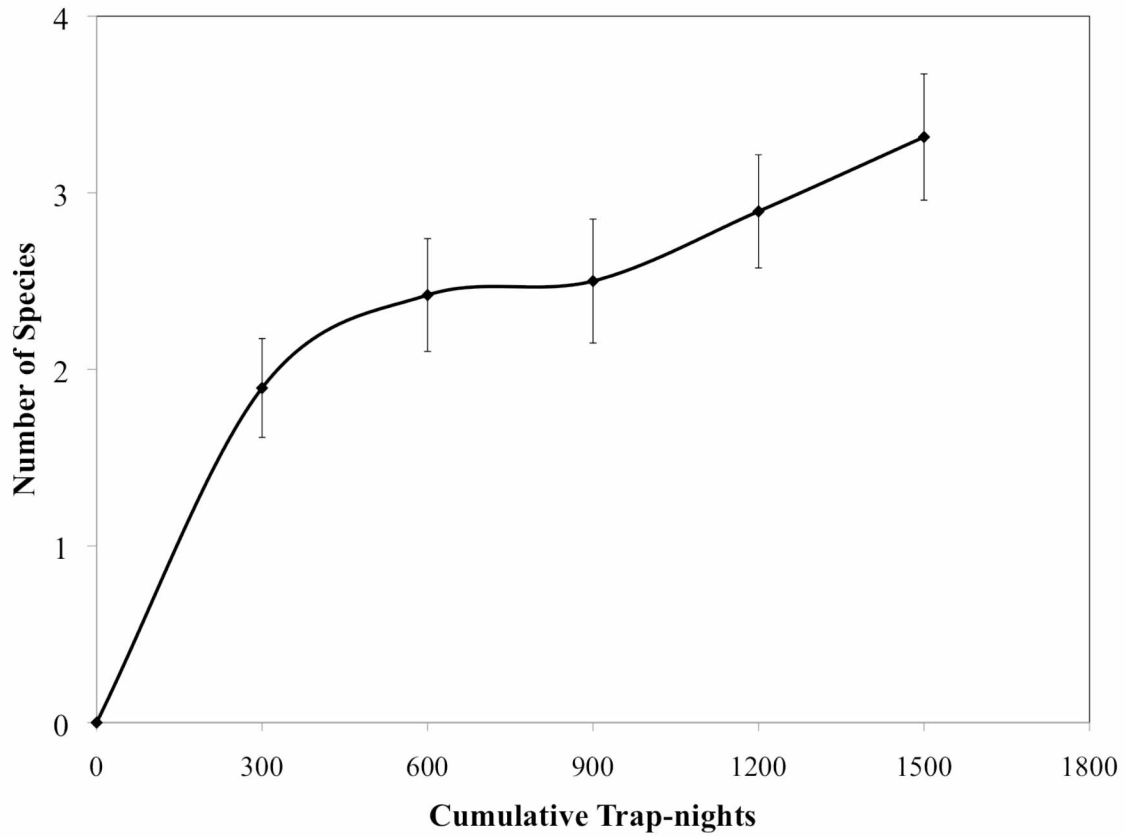


Fig. 3.3. Small mammal species accumulation curve
Mean number of species detected at sampling locations after cumulative number of trap-nights.
Error bars denote 95% confidence intervals.

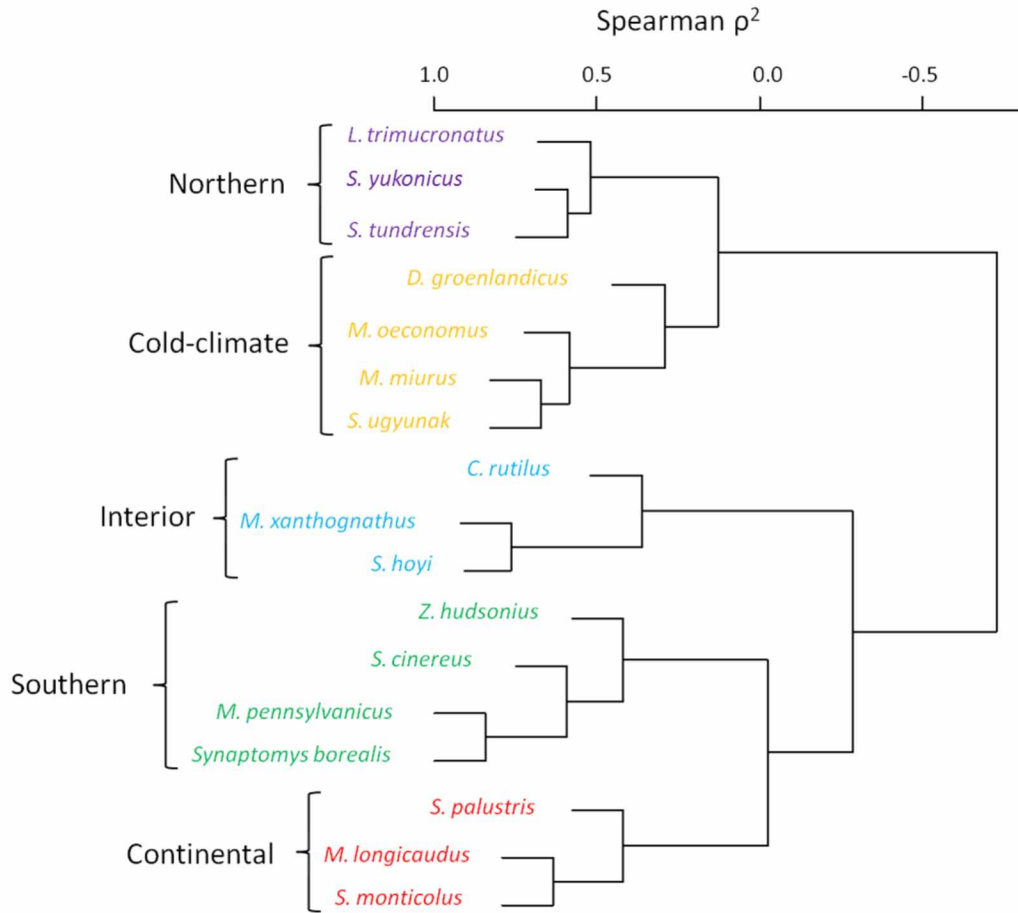


Fig. 3.4. *Varclus* analysis tree of small mammal community clusters
 Species pairs with root node correlation coefficients > 0.25 are considered to be part of the same community and have the same color. Species pairs with root node correlation coefficients < 0 are negatively correlated.

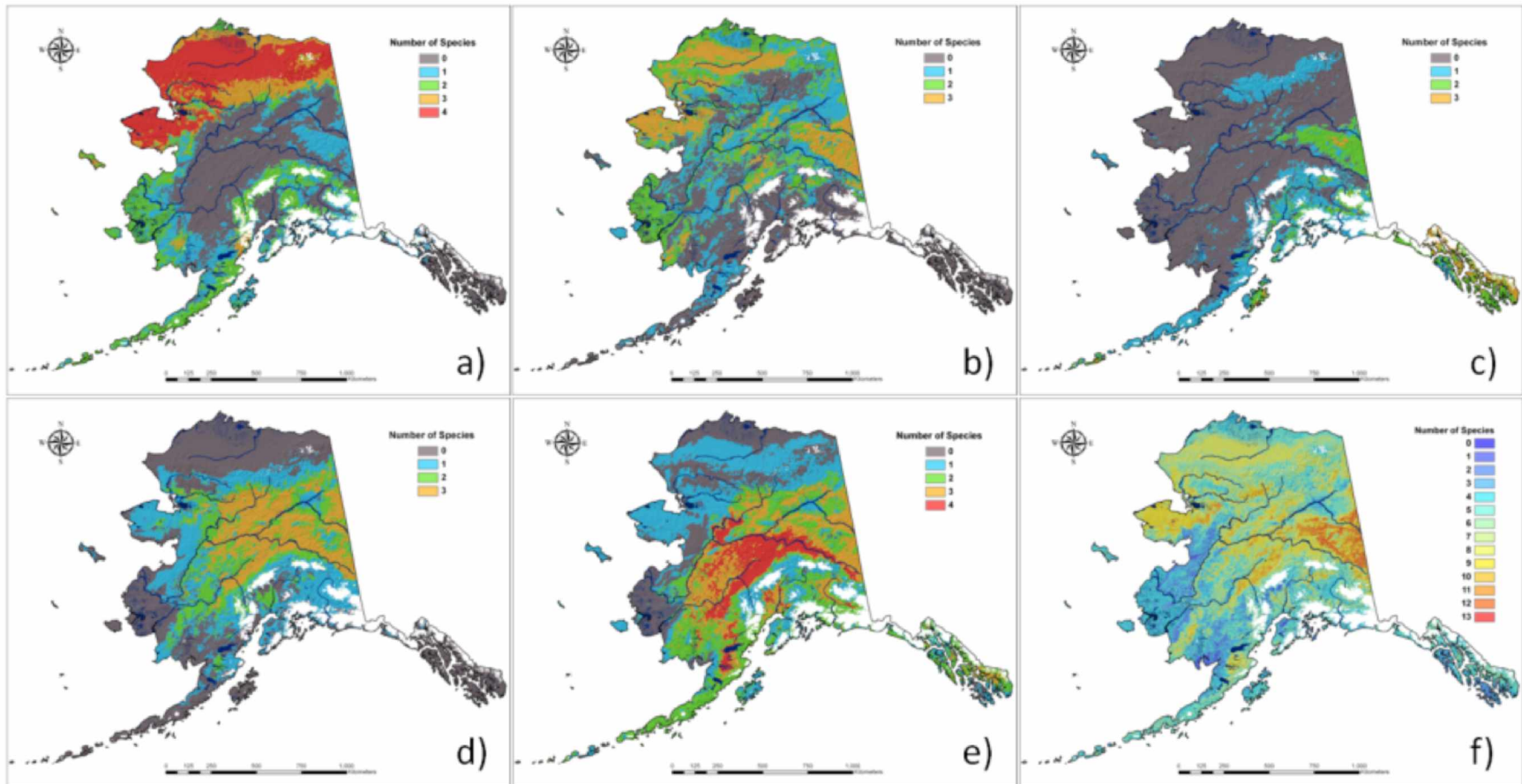


Fig. 3.5. Small mammal biodiversity hotspot maps

Maps depicting model-predicted small mammal species richness values for five geographic community clusters: a) cold-climate, b) northern, c) continental, d) interior, e) southern, and f) composite species richness map for Alaska. Maps are summations of individual species maps (Fig. 3.A.1) converted to binary maps using RIO (relative index of occurrence) = 0.5 as a threshold to differentiate between the presence or absence of each species at each pixel.

3.8. TABLES

Table 3.1. Small mammal species list

Integrated Taxonomic Information System (ITIS)-derived scientific names, common names, and Taxonomic Serial Numbers (TSN) for modeled species.

Species	Common Name	TSN #
<i>Clethrionomys rutilus</i>	northern red-backed vole	180293
<i>Dicrostonyx groenlandicus</i>	northern collared lemming	180328
<i>Lemmus trimucronatus</i>	brown lemming	180320
<i>Microtus longicaudus</i>	long-tailed vole	180299
<i>Microtus miurus</i>	singing vole	180309
<i>Microtus oeconomus</i>	root/tundra vole	180298
<i>Microtus pennsylvanicus</i>	meadow vole	180297
<i>Microtus xanthognathus</i>	yellow-cheeked/taiga vole	180301
<i>Sorex cinereus</i>	cinereus/ masked shrew	179929
<i>Sorex hoyi</i>	pygmy shrew	179946
<i>Sorex monticolus</i>	montane/dusky shrew	179950
<i>Sorex palustris</i>	American water shrew	179933
<i>Sorex tundrensis</i>	tundra shrew	179957
<i>Sorex ugyunak</i>	barren-ground shrew	552509
<i>Sorex yukonicus</i>	Alaska tiny shrew	555663
<i>Synaptomys borealis</i>	northern bog-lemming	180323
<i>Zapaterus hudsonius</i>	meadow jumping mouse	180386

Table 3.2. List of model variables

List of predictor variables used in models, type of data (raster or polygon), and their online sources. Raster layers have a 60-m resolution.

Variable Name	Data Type	Source
Aspect	Raster	http://ned.usgs.gov/
Distance to Coastline	Raster	http://dnr.alaska.gov/SpatialUtility/SUC?cmd=vmd&layerid=56
Distance to Contaminated Sites	Raster	http://dec.alaska.gov/spar/csp/db_search.htm
Distance to Fire	Raster	http://forestry.alaska.gov
Distance to Glaciers	Raster	http://dnr.alaska.gov/SpatialUtility/SUC?cmd=extract&layerid=27
Distance to Infrastructure	Raster	http://www.snap.uaf.edu/data.php
Distance to Insect Damage	Raster	http://forestry.alaska.gov
Distance to Lakes	Raster	http://nhd.usgs.gov/
Distance to Mean December Sea Ice	Raster	http://nsidc.org/data/nsidc-0051.html
Distance to Mean June Sea Ice	Raster	http://nsidc.org/data/nsidc-0051.html
Distance to Permafrost	Raster	http://agdcwww.wr.usgs.gov/agdc/agdc.html
Distance to River	Raster	http://nhd.usgs.gov/
Distance to Village	Raster	http://www.adfg.alaska.gov/index.cfm?adfg=maps.data
Distance to Wetlands	Raster	http://www.fws.gov/wetlands/data/
Ecoregion	Polygon	http://agdc.usgs.gov/data/usgs/erosafo/ecoreg/
Elevation	Raster	http://ned.usgs.gov/
Fire Year	Raster	http://forestry.alaska.gov
Insect Damage Year	Raster	http://forestry.alaska.gov
Landfire land cover	Polygon	http://www.landfire.gov/vegetation.php

(Table 3.2 continued)

Mean Annual Precipitation	Raster
Mean Annual Temperature	Raster
Mean December Precipitation	Raster
Mean December Temperature	Raster
Mean First Day of Freeze	Raster
Mean First Day of Thaw	Raster
Mean July Precipitation	Raster
Mean July Temperature	Raster
Mean Number of Grow Days	Raster
NLCD land cover	Polygon
Slope	Raster
Soil Type	Polygon
Surficial Geology	Polygon
Terrain	Raster

<http://www.prism.oregonstate.edu/>
<http://www.snap.uaf.edu/data.php>
<http://www.prism.oregonstate.edu/>
<http://www.prism.oregonstate.edu/>
<http://www.snap.uaf.edu/data.php>
<http://www.snap.uaf.edu/data.php>
<http://www.prism.oregonstate.edu/>
<http://www.prism.oregonstate.edu/>
<http://www.snap.uaf.edu/data.php>
<http://www.mrlc.gov/nlcd2006.php>
<http://ned.usgs.gov/>
<http://www.nrcs.usda.gov/wps/portal/nrcs/site/ak/home/>
<http://agdc.usgs.gov/data/usgs/geology/metadata/beikman.html>
<http://ned.usgs.gov/>

Table 3.3. Small mammal model performance metrics

Model training dataset sample sizes and aspatial (internally cross-validated) model performance metrics for 17 species of small mammals in Alaska. AUC ROC (area under the receiver operating curve) is a measure (0.00 to 1.00) of performance describing how well presences and absences are correctly predicted as such. Sensitivity and specificity are individual measures of correctly identified presences and absences, respectively, and accuracy is a combined measure of sensitivity and specificity.

Species	n Training Presences	n Training Absences	AUC ROC	Sensitivity	Specificity	Accuracy %
				% Presences Correct	% Absences Correct	Overall Correct
<i>Clethrionomys rutilus</i>	949	1157	0.96	91.15	86.34	88.51
<i>Dicrostonyx groenlandicus</i>	35	2539	0.95	100.00	45.33	46.08
<i>Lemmus trimucronatus</i>	142	2098	0.95	99.30	54.19	57.05
<i>Microtus longicaudus</i>	191	2292	0.99	100.00	87.30	88.28
<i>Microtus miurus</i>	183	2153	0.98	98.91	71.44	73.59
<i>Microtus oeconomus</i>	612	1029	0.94	93.95	79.20	84.70
<i>Microtus pennsylvanicus</i>	244	1725	0.96	99.18	63.30	67.75
<i>Microtus xanthognathus</i>	88	2377	0.99	100.00	70.55	71.60
<i>Sorex cinereus</i>	818	267	0.88	70.05	85.77	73.92
<i>Sorex hoyi</i>	97	1370	0.95	97.94	63.72	65.99
<i>Sorex monticolus</i>	566	507	0.90	80.04	83.43	81.66
<i>Sorex palustris</i>	13	1701	0.77	69.23	66.20	66.22
<i>Sorex tundrensis</i>	195	1071	0.94	99.49	67.13	72.12
<i>Sorex ugyunak</i>	37	1634	0.99	100.00	90.33	90.54
<i>Sorex yukonicus</i>	34	1610	0.98	100.00	69.88	70.50
<i>Synaptomys borealis</i>	142	1986	0.91	98.59	45.92	49.44
<i>Zapus hudsonius</i>	72	2348	0.95	100.00	53.58	54.96

Table 3.4. Small mammal model validation metrics

Sample sizes and validation statistics for the independent field validation dataset compared to model predictions for 17 species of small mammals in Alaska. Sensitivity and specificity are individual measures of correctly identified presences and absences, respectively, and accuracy is a combined measure of sensitivity and specificity. Cohen's Kappa is an alternate metric that evaluates the success of observed versus modeled value agreement between -1.0 (perfect disagreement) to 1.0 (perfect agreement; Cohen 1960). Only specificity could be calculated for *Sorex palustris* because it was not detected in the field.

Species	<i>n</i> Validation Presences	<i>n</i> Validation Absences	Sensitivity	Specificity	Accuracy %	Cohen's Kappa
			% Presences Correct	% Absences Correct	Overall Correct	
<i>Clethrionomys rutilus</i>	18	2	61.11	100.00	65.00	0.24
<i>Dicrostonyx groenlandicus</i>	2	18	100.00	83.33	85.00	0.50
<i>Lemmus trimucronatus</i>	1	19	100.00	57.89	60.00	0.12
<i>Microtus longicaudus</i>	1	19	100.00	94.74	95.00	0.64
<i>Microtus miurus</i>	3	17	100.00	88.24	90.00	0.69
<i>Microtus oeconomus</i>	10	10	70.00	80.00	75.00	0.50
<i>Microtus pennsylvanicus</i>	2	18	50.00	72.22	70.00	0.12
<i>Microtus xanthognathus</i>	2	18	50.00	61.11	60.00	0.05
<i>Sorex cinereus</i>	11	9	100.00	11.11	60.00	0.12
<i>Sorex hoyi</i>	3	17	66.67	76.47	75.00	0.31
<i>Sorex monticolus</i>	4	16	75.00	81.25	80.00	0.47
<i>Sorex palustris</i>	0	20	--	75.00	--	--
<i>Sorex tundrensis</i>	4	16	75.00	56.25	60.00	0.20
<i>Sorex ugyunak</i>	1	19	100.00	89.47	90.00	0.46
<i>Sorex yukonicus</i>	1	19	100.00	73.68	75.00	0.22
<i>Synaptomys borealis</i>	3	17	66.67	76.47	75.00	0.31
<i>Zapus hudsonius</i>	1	19	100.00	78.95	80.00	0.27

Table 3.5. Biodiversity hotspot land management calculations
 Land ownership status and area (ha) for biodiversity hotspots in Alaska containing at least 11 species of small mammal. Public lands are parsed into management subunits for geographic specificity.

Land Status	Number of Species			Total
	11	12	13	Area (ha)
<u>State of Alaska</u>	11,937.4	8,225.3	36.7	20,199.4
Game Management Unit 20	9,340.9	7,471.9	4.3	16,817.1
Game Management Unit 25	887.2	705.7	32.4	1,625.3
Game Management Unit 12	666.4	87.3	0.0	753.7
<u>Bureau of Land Management</u>	4,953.7	2,304.9	12.1	7,270.7
Steese Conservation Area	2,515.1	1,305.8	4.7	5,089.2
Upper Black River Subunit	372.5	767.5	7.5	1,147.5
Forty-mile Planning Subunit	468.3	97.8	0.0	566.1
<u>Native Corporations</u>	3,611.1	1,937.5	38.8	5,587.4
Doyon Ltd	3,581.3	1,937.5	38.8	5,557.6
N.A.N.A Regional Corp	28.1	0.0	0.0	28.1
<u>National Park Service</u>	2,022.6	1,078.9	15.5	3,117.0
Yukon-Charley Rivers NP	1,306.2	1,013.0	12.4	2,331.6
Denali National Park	436.2	0.4	0.0	436.6
Gates of the Arctic National Park	258.7	10.4	0.0	269.1
<u>U.S. Fish and Wildlife Service</u>	1,697.8	164.9	0.0	1,862.7
Arctic National Wildlife Refuge	124.0	1.9	0.0	125.9
Yukon Flats National Wildlife Refuge	109.7	155.1	0.0	264.8
Tetlin National Wildlife Refuge	159.8	0.0	0.0	159.8
Military	15.4	23.4	2.8	41.6
Private	2.6	0.0	0.0	2.6

3.9. APPENDIX 3

Appendix 3A. A short primer on the functionality and application of RandomForests for analyzing landscape GIS datasets (*sensu* Breiman 2001a, b; Drew et al. 2011)

Traditional frequentist statistics apply a probabilistic framework that usually begins with testable hypotheses that are evaluated against an *a priori* model (Zar 2010; Burnham and Anderson 2002). For that, a mathematical model such as a general linear or logarithmic one is assumed and then parameters of this model are individually estimated from the fitted data, often in a stepwise fashion (Zar 2010; Breiman 2001b; Cutler et al. 2008). For correct inference this assumes independence, a normal distribution of errors, no interactions, and precise model fits (Burnham and Anderson 2002, Johnson et al. 2004).

In contrast, machine-learning is non-parametric. It operates without a pre-assumed, underlying distribution model, and instead uses a very flexible algorithm to ‘learn,’ or describe generalizable patterns extracted from the ‘training,’ or input dataset that can consist of many dozens of predictors (Cutler et al. 2008). The machine-learning approach is generic, but it also works rather well when the system of interest is complex and unknown. It acts by extracting dominant signals from the data for the purpose of creating accurate predictions. Many machine-learning algorithms exist (Hastie et al. 2001; Elith et al. 2006) including popular algorithms like classification and regression Trees (CARTs), TreeNet, RandomForests, GARP, and Boosted Regression Trees. Because of the robust performance of such algorithms (Elith et al. 2006; Drew et al. 2011 for landscape ecology applications), here we focus on the mechanics of the RandomForests algorithm (Breiman 2001a) for generating generalizable, predictive models based on a set of wildlife occurrence training points (see Baltensperger et al. 2013 for an application).

One aspect of RandomForests is that it uses binary recursive decision trees to group training points into similar categories, called ‘nodes’, that together outline general patterns in the training dataset. Growing a tree successfully involves using the most powerful binary ‘splits,’ or partitions, to categorize data points. Much how a dichotomous taxonomic identification key identifies taxa based on a series of yes/no criteria and decision rules, each data point is evaluated by RandomForests against a set of ‘splitting rules’ dictated by distinct predictor variables in the model. For a simple tree model containing just two predictor variables, elevation and temperature for example, each data point is evaluated in sequence against both variables.

Conceptually, RandomForests might evaluate whether each point occurs at an altitude greater or less than a 2000 m threshold, for example. If greater than 2000 m, the point is placed in one group, or 'node', and if less than 2000 m, the point is placed in a different node. Subsequently, RandomForests evaluates points within these nodes based on a second, recursive splitting rule (e.g., whether the average temperature at the point is greater or less than 0° C let's say, or whether the elevation is greater or less than 4000 m). This generates a second set of nodes, partitioned into more detailed categories based on additional splitting rules than the first set. Nodes then continue to be split into smaller and smaller categories based on thresholds in predictors until the highest level of homogeneity within each node has been met (Cutler et al. 2007; Elith et al. 2008). The nodes in this final set are called 'terminal nodes', and these rules are fit with constants and finally contribute to an algorithm that describes the structure of the larger tree (Cutler et al. 2007).

Another powerful aspect of RandomForests is that it doesn't use just a single tree, only two predictors, or even all of the data points in a single training dataset. In most cases, RandomForests grows hundreds or even thousands of trees using different random subsets of predictors, and data points (Breiman 1996; Cutler et al. 2007). This randomized subsetting of data points (rows) and predictors (columns) is termed 'bagging'. It is essentially a bootstrapping technique to create many alternate trees based on a sampled subset of the dataset (both rows and columns) each with its own descriptive algorithm (Breiman 1996; Breiman 2001a). The complete data set is never used and thus RandomForests rarely overfits the data. Points not used in the growth of a tree are called 'out-of-bag' (OOB) samples and are used to evaluate each tree's predictive accuracy through cross-validation (Breiman 2001a; Elith et al. 2008). Because predictor variables (columns) are also randomly bagged, RandomForests is able to determine the importance of variables in model creation based on their frequency of use at node splits (Breiman 2001a). Because of the inherent hierarchical structure within trees, each node is dependent on splits higher in the tree based on recursive predictors. This allows RandomForests to automatically incorporate interactions among variables into the actual development of the model (Hastie et al. 2001; Elith et al. 2008).

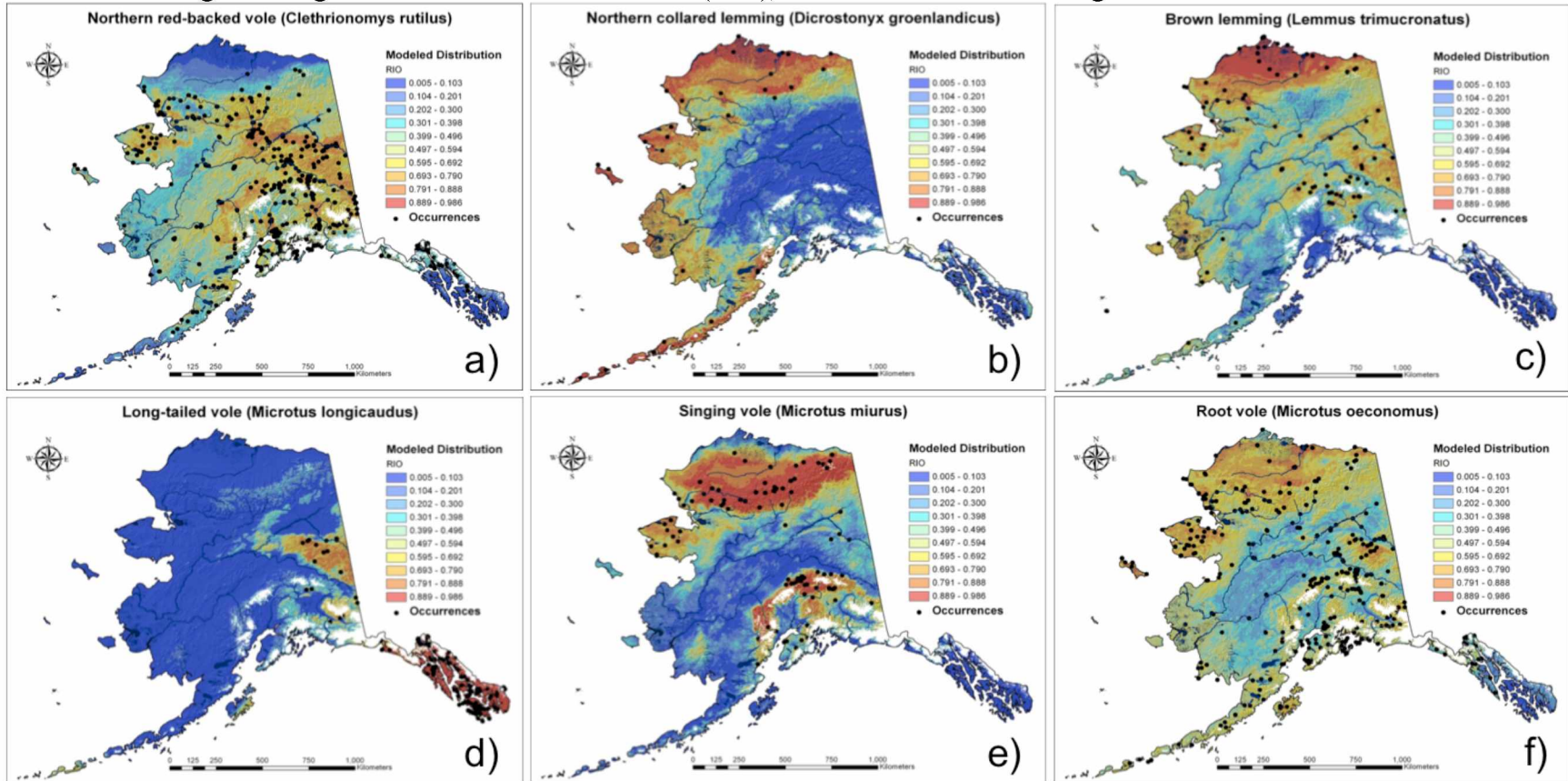
Usually, very detailed trees are also 'pruned,' or scaled back, by collapsing the weakest links identified through cross-validation (Hastie et al. 2001); this allows for optimizing among predictors in order to find the best predictive tree. Together with bagging, this makes for a

powerful model selection method. Ultimately, individual trees are weighted based on their OOB classification rates through ‘voting’ and get combined to create a final ‘forest’ algorithm that most accurately describes the dominant patterns in the training dataset (Cutler et al. 2007). This final algorithm is saved as a ‘grove’ file. A grove is a binary file that contains the best-fit set of statistical rules that predict the relative index of occurrence (RIO) for a species at a location in space. This grove algorithm can be ‘scored,’ or applied, to a regular grid of points (rows and their attributes) spanning the study area of interest. Based on the combination of predictor values present at each point, the grove algorithm calculates the appropriate RIO value at that location as an outcome of the applied rule set from the trained ‘forest.’

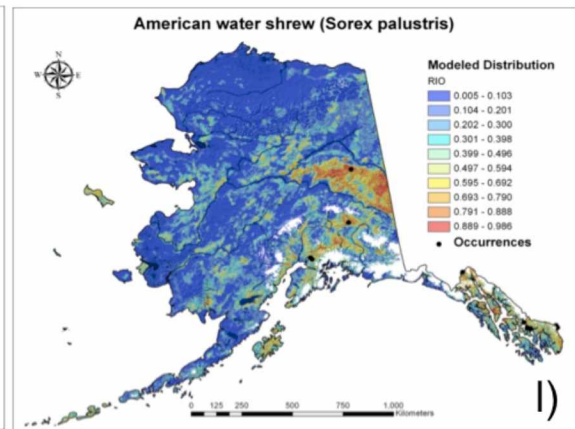
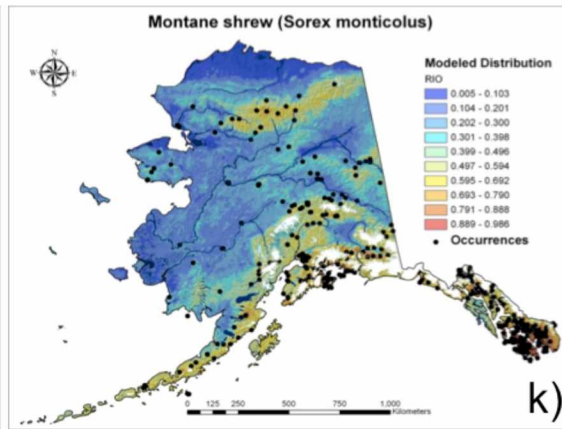
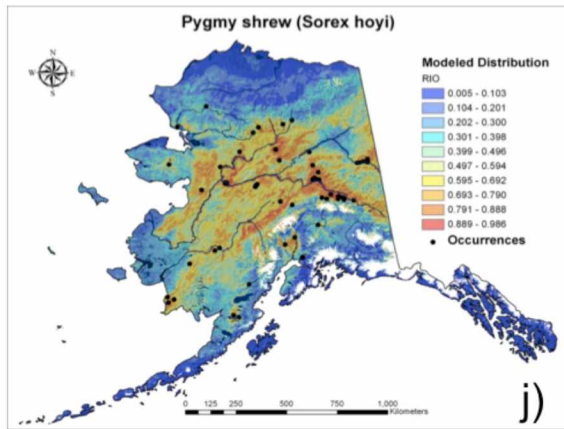
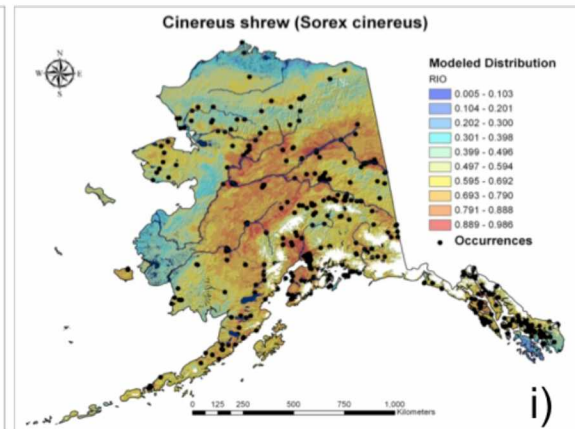
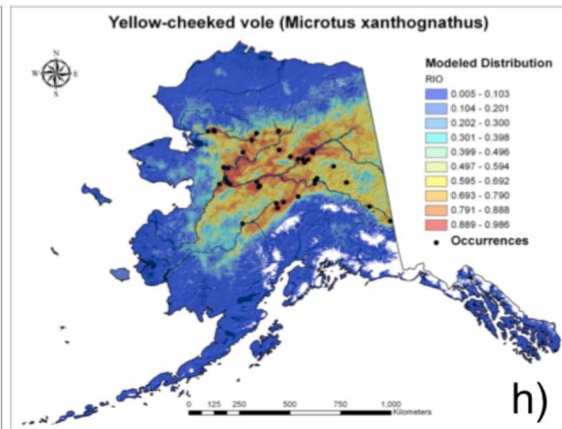
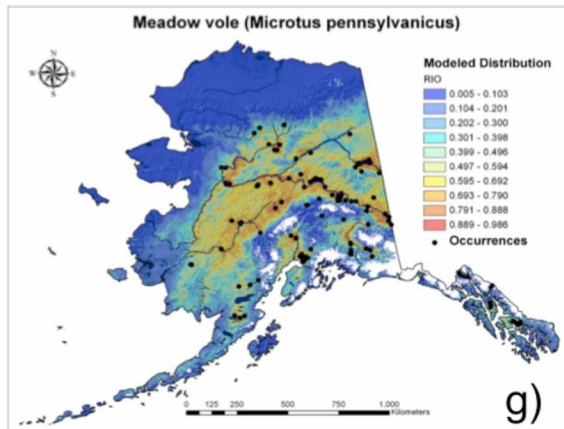
It should be noted that these are the general steps used in the construction of a RandomForests model for landscape applications like ours (see Ohse et al. 2010 for a GIS-based conservation example). Several software implementations, specific settings, and optimization steps exist and these will determine the exact performance of RandomForests. Implementations in R and SAS (Carey, NC, USA), for instance, lack some features that exist in the Salford Systems (San Diego, CA, USA), which can result in performance differences. RandomForests, and machine-learning as a discipline, remains dynamic and continues to improve as computing power and knowledge increase. We believe that there are many benefits that machine-learning can provide to ecology, conservation, and landscape research due to RandomForests’ ability to handle many more predictors, its classification power, and non-parametric framework.

Appendix 3B. Predicted 2010 distributions of 17 small mammal species

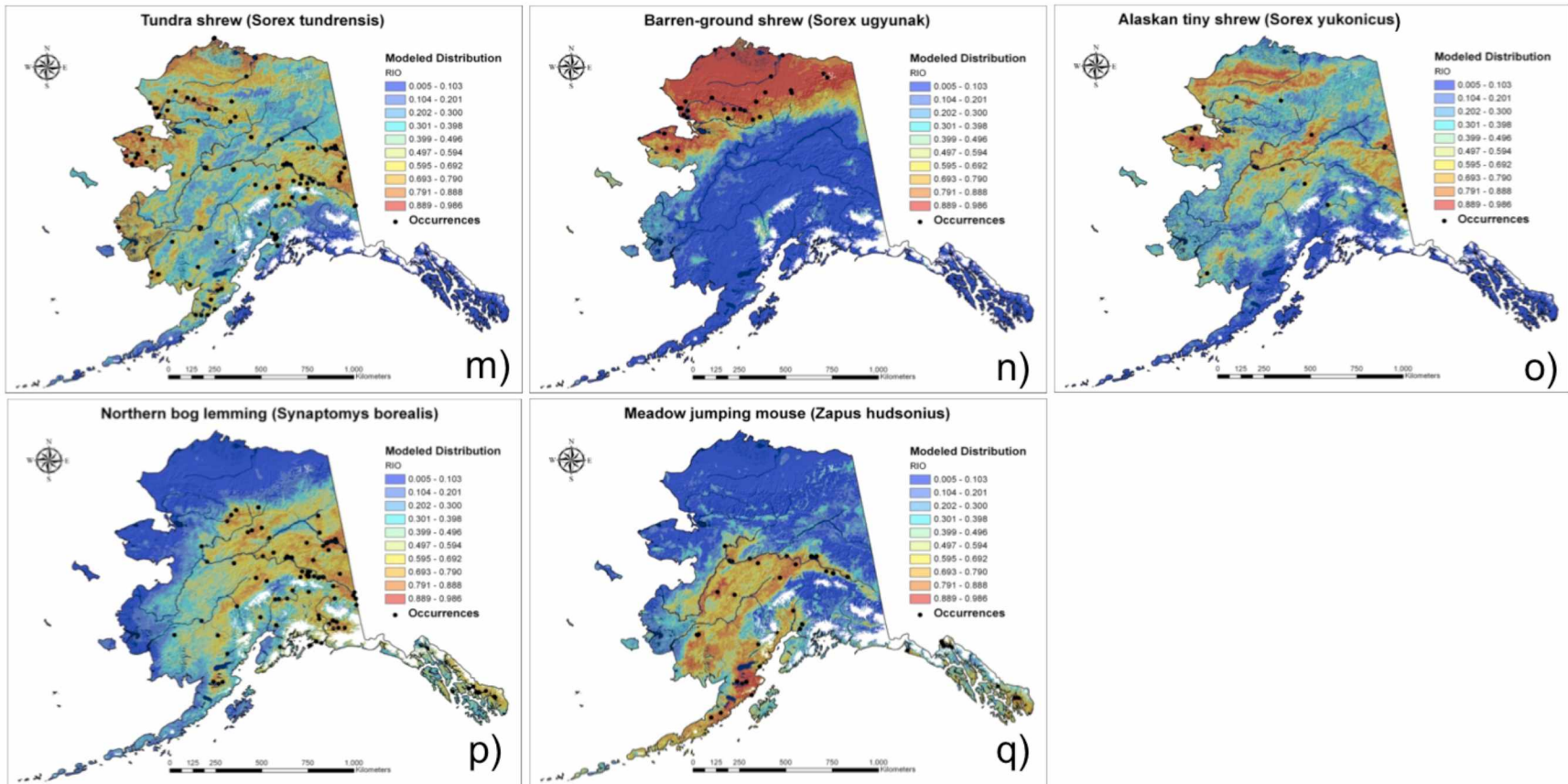
Predicted distributions species and their training points modeled across Alaska for 2010: a) northern red-backed vole (*Clethrionomys rutilus*), b) northern collared lemming (*Dicrostonyx groenlandicus*), c) brown lemming (*Lemmus trimucronatus*), d) long-tailed vole (*Microtus longicaudus*), e) singing vole (*Microtus miurus*), f) root vole (*M. oeconomus*), g) meadow vole (*M. pennsylvanicus*), h) yellow-cheeked vole (*M. pennsylvanicus*), i) cinereus shrew (*Sorex cinereus*), j) pygmy shrew (*S. hoyi*), k) montane shrew (*S. monticolus*), l) American water shrew (*S. palustris*), m) tundra shrew (*S. tundrensis*), n) barren-ground shrew (*S. ugyunak*), o) Alaska tiny shrew (*S. yukonicus*), p) northern bog-lemming (*Synaptomys borealis*), q) meadow jumping mouse (*Zapus hudsonius*). Warm colors indicate region of high relative indices of occurrence (RIO), and cool colors indicate regions of low RIO.



(Appendix 3B continued)



(Appendix 3B continued)



3.10. REFERENCES

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CHAPTER 4. IDENTIFYING SPATIAL PATTERNS IN SMALL MAMMAL DIETS ACROSS ALASKA USING MACHINE-LEARNING AND STABLE ISOTOPE RATIOS OF CARBON ($\delta^{13}\text{C}$) AND NITROGEN ($\delta^{15}\text{N}$)³

4.1. ABSTRACT

Trophic ecology has traditionally focused on defining diet-consumer interactions in individual systems at specific locations. Stable isotope ratios of nitrogen and carbon (expressed as $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, respectively) have been used to characterize diet and food web structure. Recently, maps depicting stable isotope variation across large regions (isoscapes) have emerged as useful tools to delineate spatial patterns and monitor changes in nutrient pathways through ecosystems. We used grass, fungi, rodent (Rodentia) and shrew (Soricidae) tissue samples collected throughout Alaska, USA and the Yukon Territory, Canada to create isoscape models for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values using machine-learning methods. We also produced the first map of modeled trophic positions for rodents across Alaska. Nitrogen isoscapes identified mid-elevations in the Yukon-Tanana Uplands, Brooks Range foothills, and the Yukon-Kuskokwim Delta as isotopic ‘hot-spots’ exhibiting relatively high $\delta^{15}\text{N}$ values. High-elevation alpine areas in the Brooks Range and Yukon-Tanana Uplands were predicted as ‘cold-spots’ exhibiting relatively low $\delta^{15}\text{N}$ values for all taxa. Carbon isoscapes were less variable without consistent spatial patterns among taxa. Predicted trophic positions were highest in the Middle Yukon Valley, and lowest on the Beaufort Sea Coast. Soil geology, landcover, ecoregion, and other interrelated variables were most influential in developing models. We conclude that trophic hotspots in interior Alaska may identify regions where rodents are more omnivorous than elsewhere in the region. These isoscapes can serve as isotopic baselines for future studies examining trophic position, food web complexity, niche overlap, and paleo-ecological conditions, and for identifying and monitoring regions undergoing environmental change.

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Identifying spatial patterns in small mammal diets across Alaska using machine learning and stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$).

4.2. INTRODUCTION

Trophic or food web ecology has become an increasingly important part of ecological research as it provides a means to understand the complexity of competition, resource partitioning, predatory-prey interactions, and the diets of individuals, populations and communities (Paine et al. 1980; Polis and Holt 1992; Schmitz et al. 2000; Dunne et al. 2002; Cardinale et al. 2006). In terrestrial ecosystems, food webs are structured with a diversity of plants comprising the base of the food web that provide primary production, which is utilized by primary consumers, secondary carnivores, and top predators (Batzli et al. 1980; McNaughton et al. 1989). However, while this suggests a rather linear flow of energy, there are nuances that disrupt this model, including secondary forage resources such as fungi for herbivores (Johnson 1996; Luoma et al. 2003), variation in diets of omnivores depending on size and mobility (Holyoak 1998; Cohen et al. 1993) and the abundance of large and small predators such as owls (Strigiformes), weasels (Mustelidae), wolves (*Canis lupus*), bears (Ursidae), and humans (Korpimäki and Nordahl 1989; Berger 1999; Hooper et al. 2005; Estes et al. 2011). Understanding the structure of food webs is of increasing importance in the face of rapid changes in climate, especially in northern latitudes where these changes are magnified (Hinzman et al. 2013) because of the importance of intact, sustainable food webs to subsistence hunting and harvesting in Alaska and other northern communities (Wenzel 2009).

Small mammals (Arvicoline rodents (Rodentia) and shrews (Soricidae)) fill important niches as herbivores and insectivores, respectively, in terrestrial ecosystems, and together they constitute the majority of prey for a variety of raptors and meso-carnivores (Carey et al. 1992; Hallet et al. 2003). In mainland Alaska these include 13 species of rodent and eight species of shrew (MacDonald and Cook 2009). Diets of rodents include a range of grasses, seeds, berries, buds, lichen, moss, fungi, and in some cases arthropods (Lensink 1954; Bangs 1984; Batzli and Hentonen 1990; Bergman and Krebs 1993; Luoma et al. 2003). Shrews are thought to be generally insectivorous, preying on a variety of terrestrial and aquatic invertebrates (Buckner 1964; Ryan 1986; Churchfield et al. 1999). Dietary mixing models determined that a mixture of grasses and fungi comprised the diets of most rodents in Alaska (Chapter 2).

Stable isotope analyses have been used to describe and quantify ecological systems and processes at site-specific scales. Nitrogen isotope ratios (expressed as $\delta^{15}\text{N}$ values) have been used to differentiate between dietary sources, assign species to trophic levels, and quantify niche

overlap within communities (Post 2002; Anderson and Cabana 2007; Layman et al. 2007; Crawford et al. 2008; Symes et al. 2013). Stable carbon isotope ratios (expressed as $\delta^{13}\text{C}$ values) have also been used to differentiate between marine and terrestrial inputs (Drever et al. 2000; Roth 2002; Fry 2006). However, these applications have traditionally focused on describing site-specific phenomena, and inference has generally not been extended to describe spatial trends over broad regions.

Interpolative isotopic maps, or isoscapes, have been used to provide spatially continuous representations of isotopic variation across space and time (Hobson et al. 1999; Craine et al. 2009; Still and Powell 2010; West et al. 2010; Hobson et al. 2012). Geo-referenced point samples of stable isotope values can be modeled using sets of environmental covariate predictors to create isoscapes that serve a variety of purposes (Bowen et al. 2010; Wunder 2010). Most commonly, these have been generated to depict variation in the stable isotopic composition of oxygen and hydrogen (expressed as $\delta^{18}\text{O}$ and δD respectively) composing meteoric water and biological samples. For example, isotopic monitoring networks such as the United States Network for Isotopes in Precipitation (USNIP; Welker 2012) have provided a framework to delineate the spatial and temporal patterns of monthly averages of $\delta^{18}\text{O}$ and δD values of precipitation at continental (Vachon et al. 2010; Welker 2012) and global scales (Rozanski et al. 1993; Bowen et al. 2005b). These maps have subsequently been used to trace the dispersal and migratory dynamics of species (Hobson et al. 1999; Greenberg et al. 2007; Hobson and Wassenaar 2008; van Wilgenburg et al. 2012) and to determine the spatial origin of food and water resource inputs into populations (Hobson and Wassenaar 1999; Wunder et al. 2005). Other applications have included forensic investigations to identify origins of illegally trafficked wildlife (Bowen et al. 2005a), marijuana (*Cannabis* spp.) cultivation (Booth et al. 2010), and to aid in missing persons identification (Ehrlinger et al. 2010). However, most of these rely on large-scale, consistent geographic trends in $\delta^{18}\text{O}$ or δD values (Dutton et al. 2005; Vachon et al. 2007; Liu et al. 2014).

In contrast, few isoscapes have been generated for $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values, due to the lack of an established sample collection network (Welker 2012), the more heterogeneous patterns of these isotopes at fine scales (Sullivan and Welker 2007; Werner et al. 2012), and complicated and interacting trends across larger regions (Pardo and Nadelhoffer 2010). Nevertheless, research aimed at illustrating patterns in plant and soil $\delta^{15}\text{N}$ and foliar $\delta^{13}\text{C}$ values have been conducted at

individual study sites (Rascher et al. 2012) as well as at both continental (Still and Powell 2010) and global scales (Amundson et al. 2003; Craine et al. 2009). These studies have demonstrated geographic patterns in $\delta^{13}\text{C}$ values driven by trends in available moisture (Lajtha and Marshall 1994; Männel et al. 2007), and the distribution of C3 and C4 plants (Still and Powell 2010). Additionally, soil $\delta^{15}\text{N}$ values and ultimately foliar $\delta^{15}\text{N}$ values display broad-scale variability with elevation, mean annual precipitation and mean annual temperature (Amundson et al. 2003; Rubenstein and Hobson 2004; Männel et al. 2007; Craine et al. 2009). These patterns have also been shown to manifest themselves in the tissues of herbivores foraging on plant sources along these geographic gradients (Kelly et al. 2000; Männel et al. 2007).

Stable isotopes can provide more sensitive indicators of ecological perturbations than more direct but less quantifiable observations of wildlife (Williams et al. 2007). The creation of taxon-specific isoscapes from individual georeferenced samples can allow us to detect spatially-explicit biological responses and integrate them with changes in environmental conditions (Williams et al. 2007). Comparing isoscapes of consumers to baseline vegetation isoscapes, it may be possible to identify areas where isotope values diverge from expected patterns based on known or inferred diets. Such anomalies may indicate aberrations in food web structure and function, highlighting areas of significant geochemical, physiological, ecological, or environmental change (Williams et al. 2007; Verdade et al. 2014). The combination of stable isotope analyses with other ecological monitoring practices has been termed ‘isotopic biomonitoring’ and can serve to identify where and how natural processes are being affected by anthropogenic activity (Williams et al. 2007; Verdade et al. 2014).

Despite numerous applications of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values to wildlife systems and the increasing prevalence of isoscapes, we are unaware of examples of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isoscapes based on terrestrial wildlife samples. Because predictions of $\delta^{18}\text{O}$ or δD values may follow more consistent trends than $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values across large spatial extents, spatial modeling of $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values may have been less appealing using standard regression or basic spatial interpolation techniques (Pardo and Nadelhoffer 2010). However, the implementation of machine-learning software that utilizes large, diverse sets of environmental covariate predictors in combination with georeferenced point samples (Elith et al. 2006; Craig and Huettmann 2009; Wiersma et al. 2011) offers new opportunities to construct isoscapes for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for wildlife and their diets.

Here we use machine-learning modeling methods to create isoscapes of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for the primary dietary components (grasses and fungi) of common small-bodied rodents in Alaska to serve as baselines for research of terrestrial consumers diets. Accordingly, we have also created the first known isoscapes for voles and shrews, as a demonstration of how relationships between consumers and diets can be used to model trophic position and to identify spatial dietary patterns and isotopically anomalous regions that deviate from expected trophic relationships (Williams et al. 2007).

4.2.1. Study Area

Alaska contains 1.7 million km^2 and extends from $54^\circ 40'$ N to $71^\circ 50'$ N latitude, and 130° W to 173° E longitude from the easternmost point in the Alexander Archipelago to Pt. Barrow on the Arctic Coast to the Aleutian Island Archipelago extending nearly to Asia. The state contains a diversity of geographic features including several mountain ranges—notably the Alaska, Brooks, Coastal, Aleutian, and Chugach Ranges—and elevations up to 6,036 m. Alaska's vast land area contains hundreds of glaciers and thousands of lakes. There are also several substantial river systems including the Yukon, Tanana, Koyukuk, Kuskokwim, Susitna, Copper, Noatak, Kobuk, and Colville Rivers (Molina 2001). Extreme variations in climate and geography have resulted in very diverse ecosystems that include: arctic sedge tundra, boreal forest, deciduous hardwoods, peat wetlands, old-growth temperate rainforest, coastal grasslands, alpine tundra, shrub-lands, and many others (Viereck et al. 1992).

4.3. MATERIALS AND METHODS

4.3.1. Field Collection

Leaf samples of modern grasses (162 samples) from across Alaska and Yukon Territory were collected from specimens held at the Herbarium of the University of Alaska Museum of the North (Supplemental File D). Grasses were chosen as they are ubiquitous to Alaska, compared with other plant groups that have more limited distributions (e.g., tree species). Caution was taken to avoid incorporation of material with herbarium glue attached (Wooller et al. 2007).

We also conducted 20 inventories of small mammals along two statewide megatransects (Assogbadjo et al. 2005) between 2010 and 2013 and collected 326 tissues for stable isotope analyses (Fig. 4.1). During 2011, we sampled small mammal diversity along a 1,500-km

latitudinal transect between the Arctic Ocean and the Gulf of Alaska. In 2012, we completed small mammal sampling at seven locations along a longitudinal transect of the Yukon River during a 1,250-km canoe expedition from the Dalton Highway to Mountain Village. Additional sampling was conducted at the mouth of the Canning River on the Arctic coast during 2010 and near the mouth of the Chandalar River in 2013.

At each site we placed 300 traps (200 Sherman live-traps (7.6 x 8.9 x 22.9 cm), 50 Museum Special snap traps (7 x 14 cm) and 50 pitfall traps (d=10.2 cm, h=17.8 cm) throughout the range of available habitats along three 1-km trapping loops emanating from the plot center. Sherman traps were baited with rolled oats, Museum Specials with peanut butter, and pitfall traps were left unbaited. Traps were checked twice daily and remained open for five days and nights at each site. Captured individuals had a 1-cm² patch of hair shaved from their hind quarters and samples were preserved dry in paper coin envelopes. Locations of captured individuals were recorded using a Garmin GPS and specimens were measured, processed, and preserved according to University of Alaska Museum of the North and Institutional Animal Care and Use Committee standards (#172650). Voucher specimens were permanently archived in the Mammals Collection at the University of Alaska Museum of the North (Supplemental File A). A total of 54 unidentified epigeal fungal cap samples were also collected opportunistically from sample sites and stored dry in paper bags. Herbaceous plants, lichens, mosses, and woody plants were sampled for separate analyses and to serve as dietary baselines (Chapter 2).

4.3.2. Isotope Analyses

Plant samples were prepared for stable isotopic analysis according to Wooller et al. (2007) where an aliquot (~300 to 500 µg) of freeze-dried samples of leaf fragments were weighed into tin capsules, which were sealed and introduced into the autosampler (A2100) of an ECS 4010 elemental analyzer (Costech Analytical Technologies, Inc., Valencia, CA, USA) interfaced via a Finnegan Conflo III to a Thermo Delta+XP IRMS (Thermo Electron Corp., Bremen, Germany) at the Alaska Stable Isotope Facility, University of Alaska Fairbanks. The results are presented in standard delta (δ) notation in per mil (‰). For δ¹³C and δ¹⁵N values, analytical precision was determined by conducting multiple analyses (n = 50) of a homogenous peptone standard during the analytical runs. The stable carbon isotope ratio of the combustion gas (CO₂) from each sample was analyzed using continuous-flow, stable isotope ratio mass

spectrometry. Carbon isotope compositions of samples are expressed relative to Vienna Pee Dee Belemnite and nitrogen relative to atmospheric nitrogen.

Fungi samples were ground and homogenized in a BeadbeaterMini with 3.2 mm chrome/steel beads (Biospec Products, Inc., Bartlesville, OK, USA). Hair samples from 329 small mammals belonging to 15 small mammal species were analyzed from 19 of the 20 sites surveyed. Hair samples were cleaned using a 2:1 methanol/chloroform solution, dried in a Blue-M #OV-18A oven (Thermal Product Solutions, White Deer, PA, USA), and homogenized in a 6770 Freezer/Mill (Spex Sampleprep, Matuchen, NJ, USA). Approximately 300–800 µg of hair and fungi were weighed into tin capsules, combusted, and analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values on a continuous flow mass spectrometry system at the University of Alaska Anchorage Stable Isotope Laboratory.

4.3.3. Trophic Position Calculation

In order to create a spatial model of continuous modeled trophic position for rodents across Alaska relative to vegetation baseline data, we calculated the trophic position for individuals according to the formula: $\text{TP} = 1 + (\delta^{15}\text{N}_{\text{rodent}} - \delta^{15}\text{N}_{\text{baseline}})/\Delta n$, where TP = continuous trophic position and Δn = trophic fractionation between the consumer and the base, in this case 2.7‰ (Post 2002; Sare et al. 2005; Anderson and Cabana 2007). Herbaceous plants, collected at each site, were used as the first order baseline because all rodents consumed them, they were present at all study sites, and isotopic variation was low across the study area (Anderson and Cabana 2007; Ercoli et al. 2014).

4.3.4. Model Development

We used the TreeNet algorithm in SPM 7.0 (Salford Systems, Inc., San Diego, CA; www.salford-systems.com) to create statewide isoscape models for grasses, fungi, rodents, and shrews. Using continuous trophic position calculations for individual rodents, we also modeled relative trophic position in relation to an herbaceous plant baseline across Alaska. TreeNet is a machine-learning software that uses binary recursive decision trees in sequence to parse data values into terminal categories that minimize within-group variance. Machine-learning methods are non-parametric, and are especially adept at incorporating multi-variate interactions to analyze large, inconsistent datasets. As such, they are effective tools to describe and predict the

complexity of ecological systems (Craig and Huettmann 2009; Oppel et al. 2009, Wiersma et al. 2011). Predicted results are data-driven and not fit to an *a priori* model as in more commonly used frequentist methods (Breiman 2001a, b).

Data points were attributed with 24 environmental predictor variables including continuous raster (300-m accuracy) and categorical polygon layers, all of which have been shown to influence the biogeochemistry of the analyzed taxa either directly or indirectly (Table 4.1). Training datasets of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were then modeled in TreeNet for each taxa. We grew models to 500 trees with 10-fold cross-validation, and varied the maximum nodes per tree and minimum cases per node to determine the most accurate model. Aspatial performance was assessed using the root mean square error of the learning ($\text{RMSE}_{\text{learn}}$) and testing ($\text{RMSE}_{\text{test}}$) datasets, as well as the R^2 for each model. TreeNet was also used to rank the relative importance of environmental variables in models (based on the frequency each variable was used in tree splitting at each node). Partial-dependence plots were used to assess trends in predictions related to each variable in the models. We identified and removed variables that received importance scores of 0.0 from the models, resulting in model performance improvements in some cases.

TreeNet created a ‘grove’ file for each taxa containing the coded model, which was then ‘scored’ (applied) to each point in a regular lattice of points (also attributed with the environmental variables) spaced at 5-km intervals across Alaska. For better continuous spatial visualization, predicted isotope values were smoothed between neighboring points across Alaska using the *Inverse Distance Weighting* tool with 300-m resolution in ArcGIS 10.2.1 (ESRI, Inc., Redlands, CA) and clipped to the state coastline. This process yielded spatially continuous predictive isoscape raster maps of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for grasses, fungi, rodents, and shrews. All GIS models and predictor layers are archived and freely available on the online data repository, dSpace (www.dspace.org) at the University of Alaska.

4.3.5. Comparative Isoscape Analysis

In order to identify regions where diet-rodent shifts in $\delta^{15}\text{N}$ diverged from expected levels of trophic enrichment, we subtracted both the $\delta^{15}\text{N}_{\text{grass}}$ and $\delta^{15}\text{N}_{\text{fungi}}$ isoscapes from a trophically adjusted rodent $\delta^{15}\text{N}$ isoscape using the *Raster Calculator* in ArcGIS 10.2.1. The $\delta^{15}\text{N}_{\text{rodent}}$ isoscape was adjusted downward by uniformly subtracting 2.7 ‰ from each pixel value to account for trophic enrichment. We predicted that in areas where differences between adjusted

$\delta^{15}\text{N}_{\text{rodent}}$ and $\delta^{15}\text{N}_{\text{grass}}$ isoscapes were closest to 0 ‰, rodents would be consuming primarily grass. Similarly, rodents were predicted to consume fungi in areas where adjusted $\delta^{15}\text{N}_{\text{rodent}} - \delta^{15}\text{N}_{\text{fungi}} = 0$ ‰. Areas with grass-rodent shifts substantially greater than 0 ‰, but less than $\delta^{15}\text{N}_{\text{fungi}}$, would indicate areas where rodents were consuming a mix of grasses and fungi. Correspondingly, areas with fungi-rodent shifts greater than the 95 % upper confidence limit of fungi (1.2 ‰) would indicate areas beyond the range of expected trophic enrichment where rodents may be either omnivorous, incorporating some marine-derived nutrients, or foraging in disturbed or contaminated areas. We highlight these enrichment anomalies as areas worthy of additional investigation.

4.4. RESULTS

4.4.1. $\delta^{15}\text{N}$ Values

Mean $\delta^{15}\text{N}$ values of the training datasets showed a general increasing trend in the order of: grasses < fungi < rodents < shrews across Alaska (Table 2). However, when $\delta^{15}\text{N}_{\text{rodent}}$ values were corrected for trophic enrichment, values fell largely on a spectrum intermediate to grasses and fungi. $\delta^{15}\text{N}$ values for individual training data points were well segregated between taxa (Table 4.2). Values of grasses ranged widely between -8.9 ‰ and 17.1 ‰ and fungi from -4.6 ‰ to 16.1 ‰. Rodent $\delta^{15}\text{N}$ values were between -0.1 ‰ and 11.5 ‰ and fell within the ranges of grasses and fungi, but were lower than the $\delta^{15}\text{N}$ values of shrews, which ranged from 2.4 ‰ to 20.6 ‰.

The grass isoscape predicted $\delta^{15}\text{N}$ values that were consistent between -2.9 ‰ and 0.0 ‰ across the region (Fig. 4.2a, Supplemental File E). The isoscape predicted several ‘hot-spots’ with relatively high $\delta^{15}\text{N}$ values including many areas between -1.5 ‰ and 0.0 ‰ such as the Alaska Peninsula, Yukon-Tanana Uplands, Seward Peninsula, Lime Hills, and Ahklun Mountains. At the highest elevations $\delta^{15}\text{N}$ values were relatively low as well as in coastal south-central and south-east Alaska, the Chugach-St. Elias Mountains, Alaska Range, Yukon-Kuskokwim Delta, Yukon-Old Crow Basin, Nulato Hills, Eastern Brooks Range and the Brooks Range Foothills (< -2.3 ‰). The optimal model reached a $\text{RMSE}_{\text{learn}} = 3.4$, $\text{RMSE}_{\text{test}} = 4.0$, and $R^2 = 0.7$ after 37 trees. It used just 7 of the 24 variables and the top predictors (variable importance score > 50) were *Soils* and *Bedrock* (Table 3). In particular, poorly-drained gelsol

and andisol soil types and bedrock from Mesozoic and Paleozoic metamorphic rocks were important categories in identifying $\delta^{15}\text{N}$ hot-spots.

The fungus $\delta^{15}\text{N}$ isoscape ranged between -0.6‰ and 6.3‰ (Fig. 4.2b, Supplemental File E) and $\delta^{15}\text{N}$ values were higher than in the grass isoscape by between 0.7‰ and 7.7‰ . Hot-spots with relatively high $\delta^{15}\text{N}$ values (i.e. $> 4.0\text{‰}$) occurred in the Kuskokwim Mountains, Nulato Hills, Yukon-Tanana Uplands, Ray Mountains, and Brooks Range Foothills. In contrast, the lowest fungus $\delta^{15}\text{N}$ values ($< 2.5\text{‰}$) occurred throughout the Brooks Range, but also in low-elevation regions like the Yukon-Kuskokwim Delta, Yukon-Old Crow Basin, Cook Inlet Basin, and Tanana-Kuskokwim Lowlands (Fig. 4.2b). The best model reached error rates of $\text{RMSE}_{\text{learn}} = 2.5$, $\text{RMSE}_{\text{test}} = 3.9$, and $R^2 = 0.6$ after 241 trees. Of the 22 variables included in the model, *Bedrock* and *Soils* were the most important predictors (Table 4.3). Tertiary continental and Holocene bedrock deposits were important categories for predicting fungus $\delta^{15}\text{N}$ hot-spot and cold-spots respectively, and poorly-drained spodosol soils were important for identifying fungus $\delta^{15}\text{N}$ hot-spots.

The rodent $\delta^{15}\text{N}$ isoscape ranged between 1.3‰ and 7.5‰ (Fig. 4.2c, Supplemental File E) and $\delta^{15}\text{N}$ values were as much as 5.3‰ higher than the fungus isoscape. $\delta^{15}\text{N}$ values were lowest in some high-latitude/high-elevation regions and as much as 2.1‰ lower than the fungus isoscape. $\delta^{15}\text{N}_{\text{rodent}}$ hot-spots ($> 5.2\text{‰}$) occurred in the Yukon-Tanana Uplands (except at high elevations), the Brooks Range Foothills, the Kuskokwim Mountains, the Ray Mountains, the Yukon-Kuskowkim Delta, and the Copper River Basin. The lowest $\delta^{15}\text{N}_{\text{rodent}}$ values ($< 2.9\text{‰}$) occurred on Yukon-Tanana Uplands summits, across the Brooks Range, eastern Alaska Range, and eastern Beaufort Sea Coastal Plain. The model had error rates of $\text{RMSE}_{\text{learn}} = 1.0$, $\text{RMSE}_{\text{test}} = 1.5$, and $R^2 = 0.9$ after 210 trees. The best model utilized 22 of the 24 variables, the most important of which were *Soils*, *Bedrock*, and *Landcover* (Table 4.3). Soil categories predicting high rodent $\delta^{15}\text{N}$ values included poorly-drained gelisols and inceptisols, and bedrock categories from the Mesozoic and Paleozoic eras. $\delta^{15}\text{N}_{\text{rodent}}$ cold-spots were also related to landcover type especially in open/developed areas, while hot-spots were often found in mixed forests.

The shrew $\delta^{15}\text{N}$ isoscape ranged between 3.8‰ and 8.5‰ and showed sharp contrasts between regions of high and low $\delta^{15}\text{N}$ values (Fig. 4.2d, Supplemental File E). Predicted values exceeded those in the rodent isoscape by as much as 5.1‰ , but were also as much as 1.7‰ less than rodent values in the Copper River Basin and along the Upper Yukon River. Several $\delta^{15}\text{N}$

coldspots (< 3.8 ‰) occurred in the Brooks Range, the Yukon River Lowlands, the Copper River Basin, and the Yukon-Old Crow Basin. $\delta^{15}\text{N}$ hot-spots (> 7.0 ‰) included the Yukon-Kuskokwim Delta, the Nulato Hills, the Kotzebue Sound Lowlands, and the Yukon Tanana Uplands (except at high elevations). The best model had error rates of $\text{RMSE}_{\text{learn}} = 0.8$, $\text{RMSE}_{\text{test}} = 1.8$, and $R^2 = 0.5$ after 219 trees. Twenty-two of 24 variables were used in the model, the most important of which were *Soils*, *Ecoregion*, and *Landcover* (Table 3). Poorly-drained gelisol and inceptisol soils and low-intensity developed areas predicted the highest $\delta^{15}\text{N}$ values for shrews while the lowest values occurred in deciduous forests.

4.4.2. $\delta^{13}\text{C}$ values

Mean $\delta^{13}\text{C}$ values showed a general increasing trend in the order of: grasses $<$ fungi $<$ rodents $<$ shrews across Alaska (Table 4.2). Differences in $\delta^{13}\text{C}$ values were greatest between grasses and fungi, while $\delta^{13}\text{C}$ values were similar between fungi, voles, and shrews. $\delta^{13}\text{C}$ values of grass ranged between -33.8 ‰ and -24.6 ‰ and fungi $\delta^{13}\text{C}$ values were slightly higher, ranging between -28.3 ‰ to -19.9 ‰. Rodent and shrew $\delta^{13}\text{C}$ values were slightly lower relative to fungi and ranged between -31.5 ‰ and -24.0 ‰, and -27.8 ‰ to -21.5 ‰ respectively. $\delta^{13}\text{C}$ values overlapped substantially even between trophic levels, but consumers were higher relative to food sources (Table 4.2).

Predicted grass $\delta^{13}\text{C}$ isoscape values ranged between -29.7 ‰ and -26.6 ‰ (Fig. 4.3a, Supplemental File E) and varied minimally across the extent. $\delta^{13}\text{C}$ values were highest near Cook Inlet, in the Nulato Hills, the Kuskokwim Mountains, and the Upper Tanana River Valley, ranging from -27.3 ‰ to -26.6 ‰. The lowest $\delta^{13}\text{C}$ values (-28.9 ‰ to -29.7 ‰) occurred in the Yukon-Tanana Uplands, the Brooks Range Foothills, and the Ahklun Mountains. The best grass $\delta^{13}\text{C}$ model utilized 16 of the 24 predictors and had $\text{RMSE}_{\text{learn}} = 1.0$, $\text{RMSE}_{\text{test}} = 1.6$ and $R^2 = 0.8$ after 132 trees. The most important variables included *Soils* and *Bedrock* (Table 4.3). Grass $\delta^{13}\text{C}$ hot-spots occurred in poorly-drained gelisols, inceptisols and andisols derived from Tertiary bedrock.

Fungus $\delta^{13}\text{C}$ isoscape values varied between -26.4 ‰ and -22.8 ‰ (Fig. 4.3b, Supplemental File E) and were higher than grass $\delta^{13}\text{C}$ values by 1.1 to 5.7 ‰. The Yukon-Tanana Uplands, Ogilvie Mountains, Ray Mountains, and Davidson Mountains had the lowest $\delta^{13}\text{C}$ values (-25.2 ‰ to -26.4 ‰), while the highest values (-24.1 ‰ to -22.8 ‰) were found

in the Brooks Range, the Chugach Mountains, and the Yukon-Kuskowkim Delta. The best model yielded error rates of $RMSE_{learn} = 1.3$, $RMSE_{test} = 2.1$, and $R^2 = 0.4$ after 210 trees. The model used 15 of 24 predictors, the most important of which were *Bedrock*, *Soils*, and *Landcover* (Table 3). Spodosol soils predicted higher $\delta^{13}C$ values, as did bedrock categories from the Holocene epoch. Emergent herbaceous wetlands were most important for predicting $\delta^{13}C$ hot-spots.

Predicted values in the rodent $\delta^{13}C$ isoscape ranged between -26.6 ‰ and -23.7 ‰ (Fig. 4.3c, Supplemental File E). Compared to the fungus isoscape, $\delta^{13}C_{rodent}$ values were up to 2.4 ‰ higher, but as much as 3.5 ‰ lower in other areas. This is in contrast to the more uniform increase in rodent $\delta^{13}C$ values over grasses of 0.9 ‰ to 5.3 ‰. Ecoregions differed starkly in their $\delta^{13}C$ values, with upland areas like the Yukon-Tanana Uplands, the Ray Mountains, the Kuskokwim Mountains, the Davidson Mountains, and the Brooks Range demonstrating some of the highest values, ($\delta^{13}C = -24.6$ ‰ to -23.7 ‰), and similarly across low-lying regions like the Southeastern Islands, the Cook Inlet Basin, and the Bristol Bay Lowlands. The lowest values occurred in the Yukon-Kuskokwim Delta, Beaufort Sea Coastal Plain, and Kotzebue Sound Lowlands ($\delta^{13}C = -25.5$ ‰ to -26.5 ‰). The rodent $\delta^{13}C$ isoscape had error rates of $RMSE_{learn} = 0.8$, $RMSE_{test} = 1.1$ and $R^2 = 0.3$ after 459 trees. Of the 24 variables included in the model, 19 were deemed important, the top five of which included *Surficial Geology*, *Bedrock*, *Landcover*, and *Soils* (Table 3). Old, marine-alluvium geologic deposits and gelisol and inceptisol soils predicted the highest $\delta^{13}C$ values. Rodent $\delta^{13}C$ values were predicted to be lowest in open and barren lands and highest in evergreen forest and woody wetlands.

Shrew $\delta^{13}C$ isoscape values ranged between -24.6 ‰ and -23.0 ‰ (Fig. 4.3d, Supplemental File E) and were greater than those of voles by as much as 2.6 ‰. Shrew $\delta^{13}C$ values were highest in the Yukon-Tanana Uplands, the Ray Mountains, and the Davidson Mountains (-23.6 ‰ to -23.0 ‰), while lower-elevations areas such as the Beaufort Coastal Plain, the Brooks Range Foothills, the Yukon-River Lowlands, the Yukon-Old Crow Basin, the Cook Inlet Basin, and the Copper River Basin showed the lowest values ($\delta^{13}C = -24.6$ ‰ to -24.0 ‰). The best model utilized 17 of the 24 predictor variables and had error rates of $RMSE_{learn} = 0.6$, $RMSE_{test} = 0.9$ and $R^2 = 0.3$ after 274 trees. Top variables included *Soils* and *Distance to Coast* (Table 4.3). The highest $\delta^{13}C$ values occurred in gelisol and inceptisol soils

and values were directly related to distance from the coast, especially at distances greater than 128 km.

4.4.3. Trophic Position Model

The spatial model of continuous trophic position depicted regions where rodent $\delta^{15}\text{N}$ values diverged from the isotopic baseline (TP = 1.0; Fig. 4.4). Pixels with values between 1.0 and 2.0 indicated areas where rodents were greater by as much as one trophic level above the baseline, as would be expected for first-order, herbivorous consumers. This occurred on the Beaufort Coastal Plain and in the Yukon-Tanana Uplands (Fig. 4.4). Higher trophic positions were predicted across central Interior Alaska, especially along the Yukon and Koyukuk Rivers, where modeled trophic positions were as high as 3.82. The best model had error rates of $\text{RMSE}_{\text{learn}} = 0.5$, $\text{RMSE}_{\text{test}} = 0.6$ and $R^2 = 0.7$ after 498 trees. Of the 24 predictors, 19 contributed to the model, and of these *Soils*, *Bedrock*, and *Ecoregion* were the most important (Table 4.3). Trophic positions were predicted to be lowest in areas with poorly-drained gelisol soils from Pleistocene bedrock deposits.

4.4.4. Isoscape Comparison Analysis

Spatially-explicit differences between $\delta^{15}\text{N}$ isoscapes of rodents and their diets highlighted regions of trophic specialization and omnivory. Subtracting the grass $\delta^{15}\text{N}$ isoscape from the trophically-adjusted rodent $\delta^{15}\text{N}$ isoscape yielded levels of grass-to-rodent enrichment that ranged between 0.2 ‰ and 6.7 ‰ (Fig. 4.5a). Pixels closest to 0 ‰ occurred in regions such as the Beaufort Coastal Plain, Brooks Range, and Yukon-Tanana Uplands and indicated areas where $\delta^{15}\text{N}_{\text{rodent}}$ values were most similar to those of grasses (Fig. 4.5a). Greater differences, more similar to $\delta^{15}\text{N}$ values for fungi, were predicted for the remainder of the state.

Differences between the $\delta^{15}\text{N}$ isoscapes of trophically-adjusted rodents and fungi varied between a 4.8 ‰ increase to a 2.7 ‰ decrease (Fig. 4.5b). The map identified areas with pixel differences near 0 ‰, where fungi likely comprised large dietary proportions. These conditions were widely distributed throughout the southern and coastal regions of Alaska (Fig. 4.5b). Regions with pixels < 0 ‰ more closely approximated the $\delta^{15}\text{N}$ values of grasses or a mixture of both food sources. The map also highlighted several areas where $\delta^{15}\text{N}_{\text{rodent}}$ exceeded $\delta^{15}\text{N}_{\text{fungi}}$ by > 1.2 ‰, suggesting extraneous inputs of nitrogen with a higher $\delta^{15}\text{N}$ value relative to the diets

of rodents (Fig. 4.5b). These hot-spots included areas in the Yukon-Kuskokwim Delta, near the Yukon River Bridge, in two areas along the Kantishna River.

4.5. DISCUSSION

The maps generated by this research represent some of the first regional $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isoscapes and the first trophic position map for terrestrial mammals that we are aware of. Rodent isoscapes, paired with those of their two primary over-winter and spring food sources (grasses and fungi; Chapter 2), provide detailed, spatially-explicit, isotopic baselines at 300-m resolution for the base of the terrestrial food web in Alaska (Figs. 4.2, 4.3). Geospatial patterns depicted in isoscapes and a consistent set of important environmental variables predicted the net results of a range of regional fractionation processes. Variables related to soil geology and vegetation were consistently among the most important for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isoscapes for all taxa. Isotopic hot- and cold-spots of $\delta^{15}\text{N}$ values occurred in similar patterns across trophic groups with notably lower $\delta^{15}\text{N}$ values occurring in high-elevation alpine habitats, and in low-lying wetland areas (Fig. 4.2). Inter-isoscape comparisons between trophic levels also highlighted tundra-dominated areas, where rodents likely maintained graminoid-based diets in a landscape that often has an abundance of dwarf shrubs such as *Vaccinium* spp., *Betula* spp., *Empetrum* spp., and *Dryas* spp., some of which are berry-producing (Fig. 4.5a). Other areas, especially across interior Alaska, were highlighted as trophic hot-spots, where fungi likely comprised larger diet proportions (Fig. 4.5b). Models also identified a handful of localized hot-spots along the Parks Highway where $\delta^{15}\text{N}_{\text{rodent}}$ levels were greater than what would be expected trophically, indicating supplemental inputs of nitrogen with elevated $\delta^{15}\text{N}$ values to the system (Fig. 4.4).

Complex interactions within the carbon (Welker et al. 2003; Sullivan and Welker 2007; Werner et al. 2012) and nitrogen cycles (Nadelhoffer et al. 1999; Craine et al. 2009) function to create highly variable spatial distributions of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across landscapes. The net isotopic $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values that manifest themselves in soils, vegetation and eventually wildlife are the end-results of numerous biogeochemical processes that include atmospheric deposition, soil biogeochemical processes, and photosynthetic efficiency (Kelly 2000; Wang et al. 2004; Craine et al. 2009; Werner et al. 2012). A multitude of interacting and opposing fractionation processes result in the patchy distribution of stable isotopes across landscapes that depend on spatially variable patterns in precipitation and temperature (Swap 2004; Männel et al.

2007). These climate variables are themselves dictated by geophysical characteristics like latitude, elevation, aspect, and proximity to the coast (Casey and Post 2011; Hobson et al. 2012). Our results indicate that the notion of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes predicted from trends in isolated variables, especially across regional landscapes, is a gross over-simplification. As such, here we do not attempt to untangle this complex web of environmental drivers to explain pixel-by-pixel predictions, but rather we provide a description of geospatial isotopic variation among trophic groups and review some of the interacting biogeochemical forces that produced the mapped patterns.

4.5.1. $\delta^{15}\text{N}$ Isoscapes

Patterns in all modeled isoscapes were related largely to diverse ranges of soil conditions and vegetation characteristics, and to a lesser extent, indirectly by precipitation, temperature, elevation, aspect, and latitude (Table 4.3). While the importance values of categorical variables were typically higher than those of continuous variables, machine-learning algorithms tend to inflate the importance of pre-categorized predictors. Accordingly, one should bare in mind the influence that continuous processes have in determining discrete geology, landcover, and ecoregion categories. Many different processes interact to produce the $\delta^{15}\text{N}$ values of soils, which are controlled by a balance of atmospheric fixation, mineralization, denitrification, and ammonia volatilization, which in turn are controlled by water availability (Shearer and Kohl 1986; Evans 2007; Casey and Post 2011). In addition to the latter two processes, soil $\delta^{15}\text{N}$ values can increase as a result of a variety of factors including nutrient availability and source (Swap et al. 2004), temperature (Ambrose 1991), soil maturity (Vitousek et al. 1989), soil depth (Ambrose 1991, Nadelhoffer et al. 1999), pH (Shearer and Kohl 1986), clay content (Vitousek et al. 1989), and land conversion (Verdade et al. 2014). Opposing these are several processes that can decrease $\delta^{15}\text{N}$ values including nitrogen fixation (Deniro and Hastorf 1985), precipitation (Mariotti et al. 1980) and elevation (Lajtha and Marshall 1994; Kelly 2000; Männel et al. 2007). Because these environmental drivers are not independent, and since determining the strength of each can be difficult, deciphering how they interact to determine the overall $\delta^{15}\text{N}$ values in soil is especially complicated (Casey and Post 2011).

Because grasses do not fix nitrogen, the range of $\delta^{15}\text{N}$ values in the grass isoscape is the result of the patchwork of soil morphology and chemistry across the region (Welker 2003;

Murphy and Bowman 2006; Männel et al. 2007). Graminoids tend to utilize inorganic sources of nitrogen throughout the soil profile and can have relatively high $\delta^{15}\text{N}$ values compared to many other forms of vegetation (Valentine et al. 2006; Table 4.2). This is in part due to their lack of mycorrhizal associations common to many woody plants that result in lower $\delta^{15}\text{N}$ values (Nadelhoffer et al. 1999; Michelson et al. 1996). For ectomycorrhizal (symbiotic) fungi, fractionation during nitrogen transfer to host plants results in an increase of $\delta^{15}\text{N}$ values in fungi by 3 ‰ over most vegetation (Hobbie et al. 2000; Table 4.3). Saprotrophic (free-living) fungi are similarly isotopically enriched over bulk soil, but because of a lack of host-plant interactions, this occurs as a result of internal fractionation between chitin and proteins (Hobbie et al. 2005, Taylor et al. 1997).

At the highest elevations (e.g., Alaska and Brooks Ranges or on summits of the Yukon-Tanana Uplands), $\delta^{15}\text{N}$ values were consistently low across all taxa in comparison to other regions in Alaska (Fig 4.2). Numerous studies have documented an overall decrease in $\delta^{15}\text{N}$ values with increasing elevation and precipitation (Kelly 2000; Murphy and Bowman 2006; Männel et al. 2007), although here the relationships were weak and non-linear. For grasses this may be the result of greater use of nitrate versus ammonium or differences in nitrogen mineralization in soils as grasses access inorganic nitrogen with lower $\delta^{15}\text{N}$ values in the upper soil profiles (Nadelhoffer et al. 1999; Michelson et al. 1996; Valentine et al. 2006). For fungi, decreases in soil organic material and profile depth at high elevations may result in decreased bulk soil $\delta^{15}\text{N}$ values and subsequently low fungi $\delta^{15}\text{N}$ values as well (Hobbie and Ouimette 2009). The low $\delta^{15}\text{N}$ values observed here for grasses and fungi at high elevations should ultimately result in the consumption of lower $\delta^{15}\text{N}$ sources by rodent herbivores (DeNiro and Epstein 1981). Accordingly, observed patterns of lower $\delta^{15}\text{N}$ values at high elevations remained consistent in both rodent and shrew isoscapes (Fig. 4.2).

Low-elevation basins also exhibited low $\delta^{15}\text{N}$ values for consumers, especially relative to nearby middle elevations (Fig. 4.2). This phenomenon cannot be explained by the elevation effect, but may be related to high levels of moisture available in these largely wetland-dominated regions (Aranibar 2004; Männel et al. 2007). The $\delta^{15}\text{N}$ values of herbivores have been shown to decrease with increased precipitation, but out of proportion with what would be expected from the depleting effects of precipitation on soils or grasses alone (Heaton et al. 1986; Sealy et al.

1987; Ambrose 1991). Such a difference in the influence of precipitation may account for some of the disparities observed between rodent and grass isoscapes (Ambrose 1991; Fig. 4.5a).

4.5.2. $\delta^{13}\text{C}$ Isoscapes

Isoscapes of $\delta^{13}\text{C}$ reflected variable patterns in soil geology, land cover, and ecoregion, as was observed for $\delta^{15}\text{N}$ values (Fig. 4.3). Within C_3 -dominated systems, such as Alaska, atmospheric CO_2 -uptake and water-use efficiency controlled by nutrient supply and loss, determines the $\delta^{13}\text{C}$ values of grasses (Welker et al. 1993, 2003). Factors that increase $\delta^{13}\text{C}$ values in plants include canopy height (Yoder et al. 1994), leaf size (Geber and Dawson 1990), leaf thickness (Vitousek et al. 1990), irradiance (Ehleringer et al. 1986), nitrogen availability (Guehl et al. 1995), and elevation (Knight et al. 1995, Männel et al. 2007). Other variables act to decrease $\delta^{13}\text{C}$ values including stomatal density (Hultine and Marshall 2000), salinity (Sandquist and Ehleringer 1995), soil moisture (Ehleringer and Cooper 1988; Welker et al. 2003), humidity (Dawson et al. 2002), precipitation (Stewart et al. 1995; Männel et al. 2007) and CO_2 concentration (Beerling et al. 1993).

Theoretical trends suggest that predicted $\delta^{13}\text{C}$ values should increase with higher elevation, and decrease with higher precipitation, temperature and latitude (Körner et al. 1988, Lajtha and Marshall 1994; Casey and Post 2011; Männel et al 2007). This effect is thought to be related to a lower ratio of internal to external partial pressure of CO_2 in plants at high elevations (Körner et al. 1988). However, observed trends for these variables in isoscapes were weak and non-linear, and relative importance values in models were only low to moderate (< 50 ; Table 4.3). Codron et al. (2013) also did not find strong relationships between temperature and precipitation for plant $\delta^{13}\text{C}$ values, which they attributed to a small range in available moisture over their study extent. Our models were influenced more by a suite of variables that included soil geology, landcover, and interactions with other environmental variables such as *NDVI*, *Slope*, *Distance to Village*, and *Aspect*. These variables combined to produce relatively consistent $\delta^{13}\text{C}$ values across Alaska for grasses across the study extent.

For the fungus $\delta^{13}\text{C}$ isoscape, in addition to soils and landcover, both *Mean annual precipitation* and *Mean January precipitation* were relatively important predictors (Table 4.3). Fungi derive their carbon from soil organic material, not directly from the atmosphere, so $\delta^{13}\text{C}$ values are likely to vary more based on underlying soil conditions (Hobbie et al. 2013). Because

litter decomposition accelerates in wet, warm conditions, soil moisture may be an important determinant for the $\delta^{13}\text{C}$ values of fungi (Schimel et al. 1999; Schimel and Chapin 2006). Saprophagic fungi tend to have higher $\delta^{13}\text{C}$ values than foliar plant tissues because of the high concentration of lignins that deplete overall foliage $\delta^{13}\text{C}$ values (Hobbie et al. 1999). In contrast, mycorrhizal fungi obtain more enriched photosynthate sugars from host plants (Finlay and Söderström 1992; Hobbie et al. 2013).

Rodent and shrew $\delta^{13}\text{C}$ isoscapes both showed lower than average values on the North Slope and Yukon-Kuskokwim Delta, but this pattern contradicts expected individual trends associated with precipitation and temperature. Low $\delta^{13}\text{C}$ values in these areas could be related to low elevations as well as high $\delta^{13}\text{C}$ values at high elevations in the Yukon-Tanana uplands, but the relative importance of elevation in both models was 0.0 (Table 4.3). Again, it appears that only the interaction of many variables together can adequately account for the observed patterns in these isoscapes. Models also showed little to no direct effect of climate variables in determining $\delta^{13}\text{C}$ values of rodents or shrews (Table 4.3), similar to Codron et al. (2013). The non-linear responses common to these variables and interactions among all of them suggest that $\delta^{13}\text{C}$ (especially of consumers) may not be correlated with individual environmental variables in a strong or even predictable manner (Comstock and Ehleringer 1992; Casey and Post 2011). In fact, interpreting many of these variables in isolation could lead to inappropriate oversimplifications and misleading predictions of isotopic values at large spatial scales (Casey and Post 2011).

4.5.3. Isoscape and Trophic Position Analyses

After trophically correcting the $\delta^{15}\text{N}_{\text{rodent}}$ isoscape, low $\delta^{15}\text{N}_{\text{rodent}}$ values in tundra-dominated regions were coincident with $\delta^{15}\text{N}_{\text{grass}}$ values there, indicating that rodents were consuming a high proportion of grasses in alpine habitats above treeline and in lowland wetlands and tundra (Fig. 4.5a). These were also identified by the trophic-position model as areas where rodents occupied trophic positions between 1.0 and 2.0, indicating areas where rodents should rely on purely herbivorous diets (Fig. 4.4). Such diets were also described in stomach content analyses (Rodgers and Lewis 1986; Bergmann and Krebs 1993) and isotopic mixing models of collared lemmings (*Dicrostonyx groenlandicus*) and root voles (*Microtus oeconomus*; Chapter 2).

Differences between trophically-corrected rodent and fungi $\delta^{15}\text{N}$ isoscapes were near 0 ‰ at intermediate elevations and lower latitudes, indicating regions where a larger proportion of the rodent diet was comprised of fungi (Fig. 4.5b). However, across the majority of Alaska, trophically-corrected $\delta^{15}\text{N}_{\text{rodent}}$ values were intermediate to $\delta^{15}\text{N}_{\text{grass}}$ and $\delta^{15}\text{N}_{\text{fungi}}$, identifying where rodents were consuming a mixture of grasses and fungi. This is a common dietary arrangement for many vole species in Alaska, especially red-backed voles (*Myodes rutilus*), singing voles (*Microtus miurus*), and yellow-cheeked voles (*M. xanthognathus*; Wolf and Lidicker 1980; Bangs 1984; Batzli and Henttonen 1993; Chapter 2). The trophic position map also indicated that for the majority of Alaska, rodent trophic positions exceeded 2.0 (Fig. 4.4), implying the inclusion of an isotopically enriched food source like fungi into their diets.

In some localized areas, especially in the Yukon River Basin where trophically-corrected $\delta^{15}\text{N}_{\text{rodent}}$ values exceeded $\delta^{15}\text{N}_{\text{fungi}}$ by 1.2 ‰ to 2.7 ‰, differences were too great to indicate grass/fungi mixtures or purely fungal-based diets (Fig. 4.5b). Instead, these locations represent isotopic anomalies that appear for the first time at the consumer level and cannot easily be explained by trophic or environmental processes alone. Rodents in interior Alaska were also predicted to have higher than expected trophic positions (Fig. 4.4), indicating where trophically-corrected $\delta^{15}\text{N}_{\text{rodent}}$ values were most disparate from the herbaceous plant $\delta^{15}\text{N}$ baseline. For this large area with elevated trophic positions, results point toward the addition of $\delta^{15}\text{N}$ sources with even more elevated $\delta^{15}\text{N}$ values compared to the rodent diet pool and could result from omnivory, food stress, marine-derived subsidies, pollution, or other anthropogenic inputs (Kelly et al. 2000; Williams et al. 2007; Craine et al. 2009).

A large area of anomalous isotopic enrichment occurred in the vicinity of the Yukon River Bridge in central Alaska (Fig. 4.5b). Sampling at this location documented the highest $\delta^{15}\text{N}_{\text{rodent}}$ values anywhere in the state, but corresponding $\delta^{15}\text{N}$ values of grass and fungi were not abnormally enriched. This anomaly could be related to a more omnivorous diet that may include invertebrates as well as fungi. However, the proximity to disturbances associated with the construction of the Dalton Highway, Yukon River bridge, trans-Alaskan pipeline, and associated facilities might also suggest that anthropogenic sources of elevated $\delta^{15}\text{N}$ values could be the cause for this $\delta^{15}\text{N}$ hot-spot.

The amount of trophic enrichment between consumers and diets depends, in part, on the proportion of dietary protein, with high-protein diets leading to higher levels of trophic

enrichment (Sponheimer et al. 2003; Sare et al. 2005). A difference in protein consumption is one proposed mechanism to explain intra-specific variation in $\delta^{15}\text{N}$ values (Sponheimer et al. 2003). One potential source of supplemental protein is from terrestrial invertebrates, which rodents (especially red-backed voles) have been shown to consume (Bangs 1984). Baseline-corrected mean $\delta^{15}\text{N}$ values of a variety of terrestrial invertebrates have been documented to range from 1.1 to 8.9 (Korobushkin et al. 2013, Zalewski et al. 2014). These values are higher than mean $\delta^{15}\text{N}_{\text{fungi}}$ values in this study (2.9 ‰) and could account for the additional enrichment of $\delta^{15}\text{N}_{\text{rodent}}$ and the elevated trophic positions not explained by fungi consumption (Symes et al. 2013). Invertebrate $\delta^{15}\text{N}$ values on this order are also consistent with what would be expected for $\delta^{15}\text{N}$ values predicted in the shrew isoscape, after correcting for trophic enrichment. Unfortunately, we did not sample invertebrate isotope diversity, but the creation of an invertebrate $\delta^{15}\text{N}$ isoscape would provide a valuable comparison to the shrew isoscape modeled here.

Other regions were highlighted by the trophic position model as trophic cold-spots including the northeastern Beaufort Sea coast, where the lowest positions (< 1.0) occurred (Fig. 4.4). Only collared lemmings were captured at this location in 2010 and their $\delta^{15}\text{N}_{\text{hair}}$ values were some of the lowest recorded for this study. Collared lemmings are considered obligate herbivores (Rodgers and Lewis 1986; Bergmann and Krebs 1993), but were also found, using a 2-way dietary mixing model, to consume mosses and lichens (Chapter 2). Because mosses and lichens have $\delta^{15}\text{N}$ values that are lower than the herbaceous plants used as the isotopic baseline (Table 4.2), this difference likely served to depress their calculated trophic position below 1.0.

4.5.4. Trophic Position Implications

The trophic position map created here highlighted regions where rodents with elevated trophic positions were maintaining a more omnivorous diet that included a combination of grasses, fungi, and potentially invertebrates. Northern red-backed voles comprised the majority of the rodent training dataset, and have been shown to be dietary generalists (Bangs 1984, Luoma et al. 2003). This is one reason why areas of elevated trophic position may have occurred across interior Alaska, within the central range of red-backed voles, but not north of the Brooks Range where this species is sparsely distributed (Baltensperger and Huettmann 2015). The widespread occurrence of red-backed voles may be due, in part, to their generalist, omnivorous

diet, which allows them to exploit a variety of protein-rich foods, thus releasing them from dependence on any single food source. Perhaps it is this type of generalist strategy that buffers against stochasticity and allows for the persistence of species and the resilience of food webs (Holyoak and Sambhav 1998, Verdade et al. 2014). In essence, documenting where species maintain elevated trophic positions could be a method for identifying where omnivory may be acting to stabilize food webs. Conserving such areas may go a long way towards promoting and maintaining intact and functional ecosystems.

4.5.5. Isoscape Applications

The broader purpose of the isoscape models created here was to provide spatially-explicit maps and assessments of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for four trophic groups: primary producers (grasses), primary consumers (rodents), secondary consumers (shrews), and decomposers (fungi). Stable isotopes vary based on a myriad of physical, chemical, and biological processes and also shift over time. As such it is necessary to have accurate isotopic baselines to standardize measurements against (Phillips and Gregg 2001, Post et al. 2007, Casey and Post 2011). Here we have incorporated many of the numerous environmental forces influencing isotopic variability to create continuous, baseline models, using easily applied methods and sampled data. Future isotopic research aimed at quantifying trophic position or niche overlap, making intersite comparisons, or for comparing temporal changes in isotopes may use these maps and methodologies for reference.

To obtain stable isotope baseline values, it is normally necessary to sample and analyze a range of potential dietary end-members, in addition to collecting samples from the target organism. Sampling all trophic levels simultaneously in such a manner can be both cost- and time prohibitive. Instead, these predictive isoscapes provide an efficient solution to this difficult obstacle. The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ grass isoscapes provide baseline vegetation values that allow for comparisons among herbivore diets throughout the state. Likewise, research examining the niche overlap or trophic position of meso-carnivores can use the rodent isoscapes to obtain baseline $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of prey end-members without coordinating separate small mammal sampling efforts. The fungus isoscape also provides a unique opportunity to include spatially-explicit values of a more isotopically enriched food source in the dietary mixing models of omnivores.

Similarly, the development of an isoscape for terrestrial invertebrates would be helpful for placing the shrew isoscape into a trophic framework relative to their prey.

Our maps also provide valuable temporal benchmarks against which environmental changes can be monitored. Because isotope diversity changes over time as climatic conditions act to shift soil and plant processes, paleoecological research can also utilize current isoscapes as a comparison for historical isotopic records of plant and animal fossils (Wooller et al. 2007, Casey and Post 2011). Such comparisons may provide inference to historic climatic conditions based on comparisons to current isotopic levels. Additionally, monitoring changes in isotopic baselines at regular intervals in the future may allow for the identification of regions where vegetation has changed over time. Future applications include (i) quantifying diet shifts in response to changing habitat conditions (Darling and Bayne 2010), (ii) documenting invasions of exotic species (Rascher et al. 2012), (iii) tracking the effects of climate change on nutrients (Schaffer et al. 2013), and (iv) identifying areas where anomalous isotope values may indicate the adverse effects of land conversion, pollution, or abnormal atmospheric deposition (Pataki et al. 2007, Williams et al. 2007).

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4.7. FIGURES

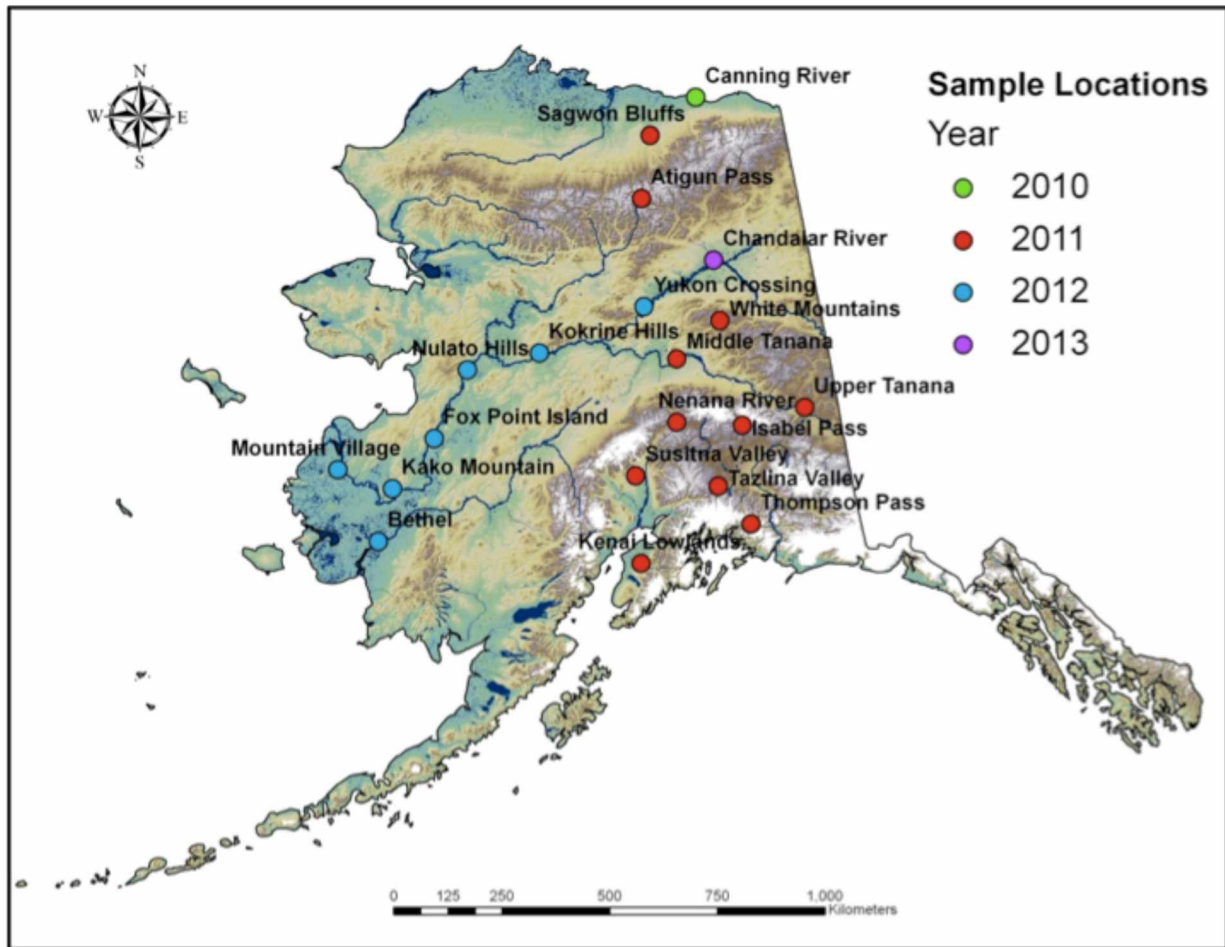


Fig. 4.1. Study area map.
Shaded relief map of Alaska depicting sampling locations by year

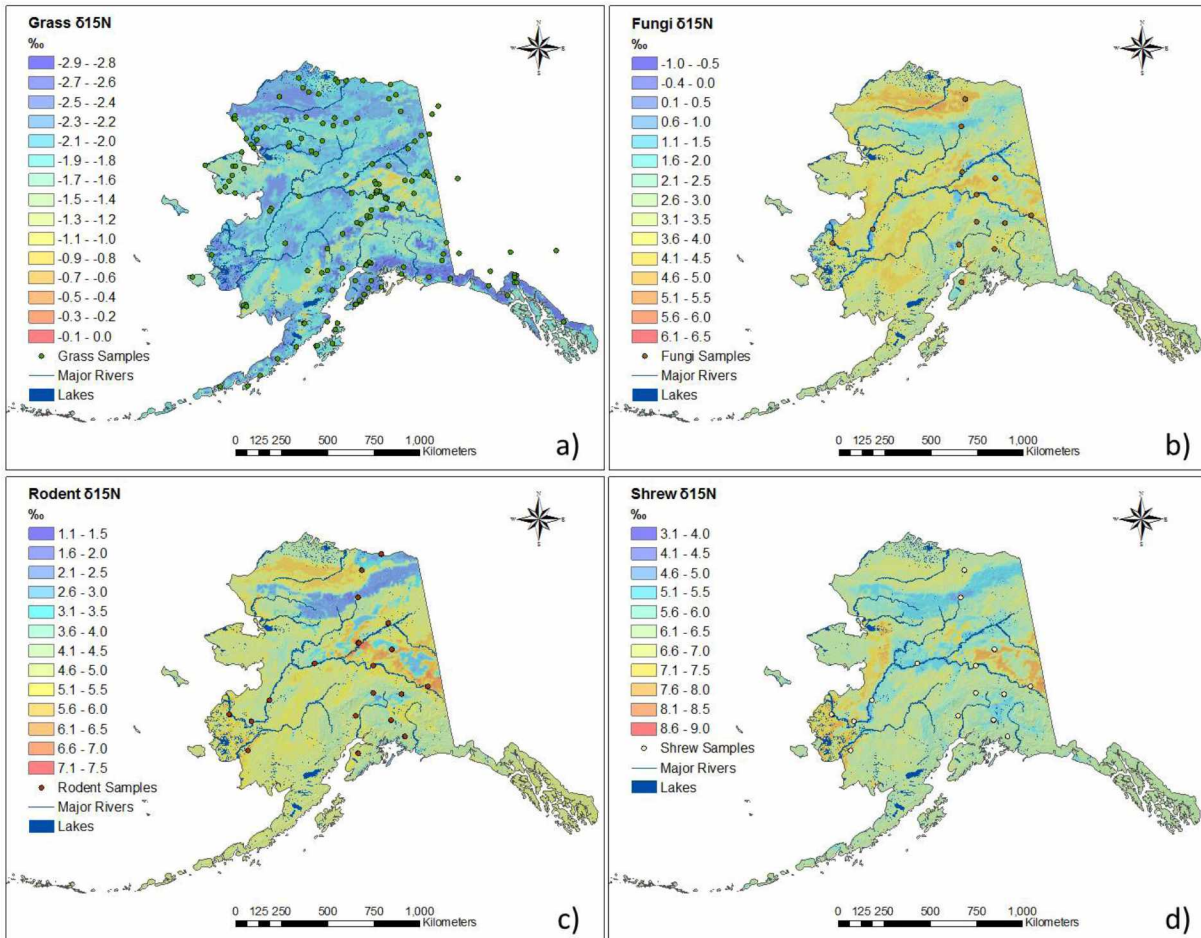


Fig. 4.2. Isoscape models of $\delta^{15}\text{N}$ values for Alaska
 Isoscape models for a) grasses, b) fungi, c) rodents, and d) shrews. Training points used as model input data are also shown for each isoscape.

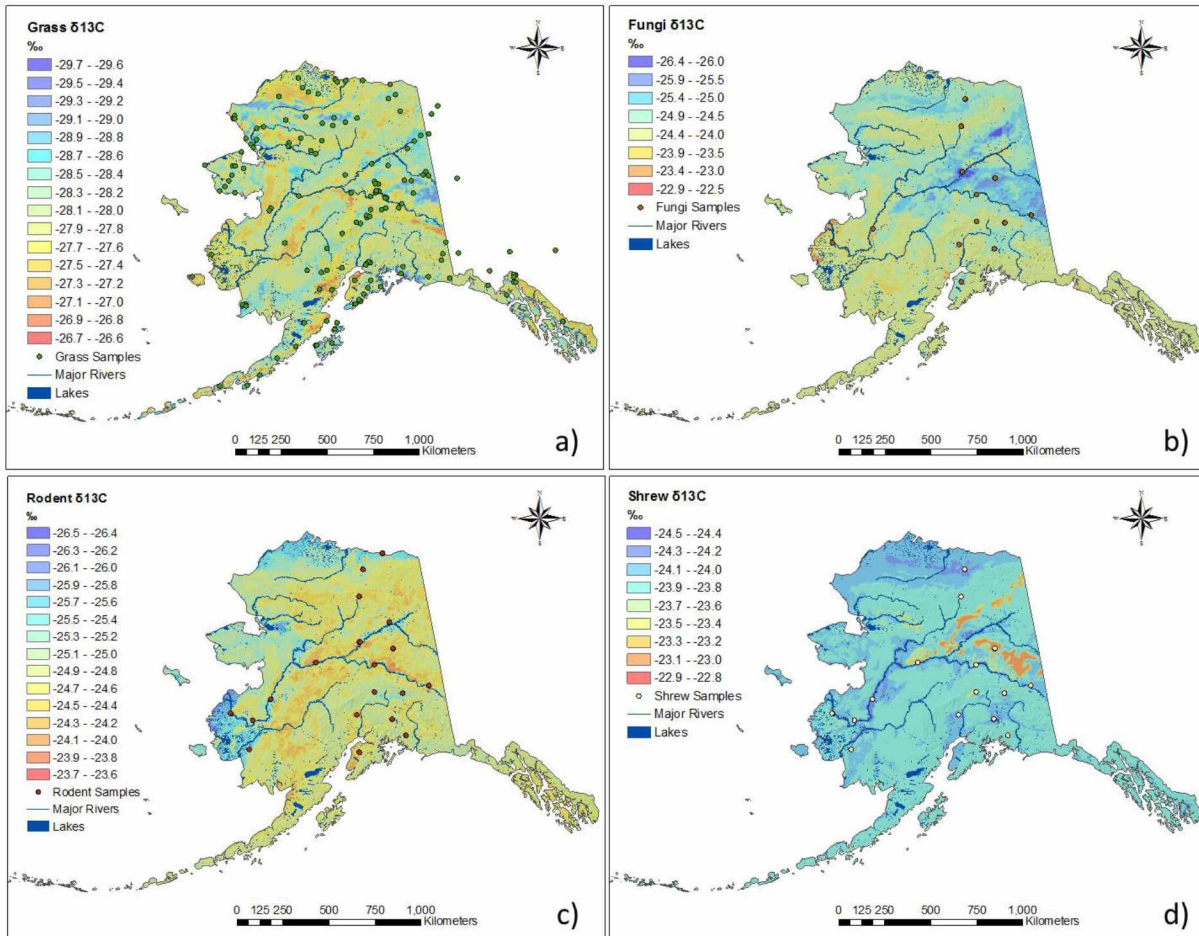


Fig. 4.3. Isoscape models of $\delta^{13}\text{C}$ values for Alaska
 Isoscape models for a) grasses, b) fungi, c) rodents, and d) shrews. Training points used as model input data are also shown for each isoscape.

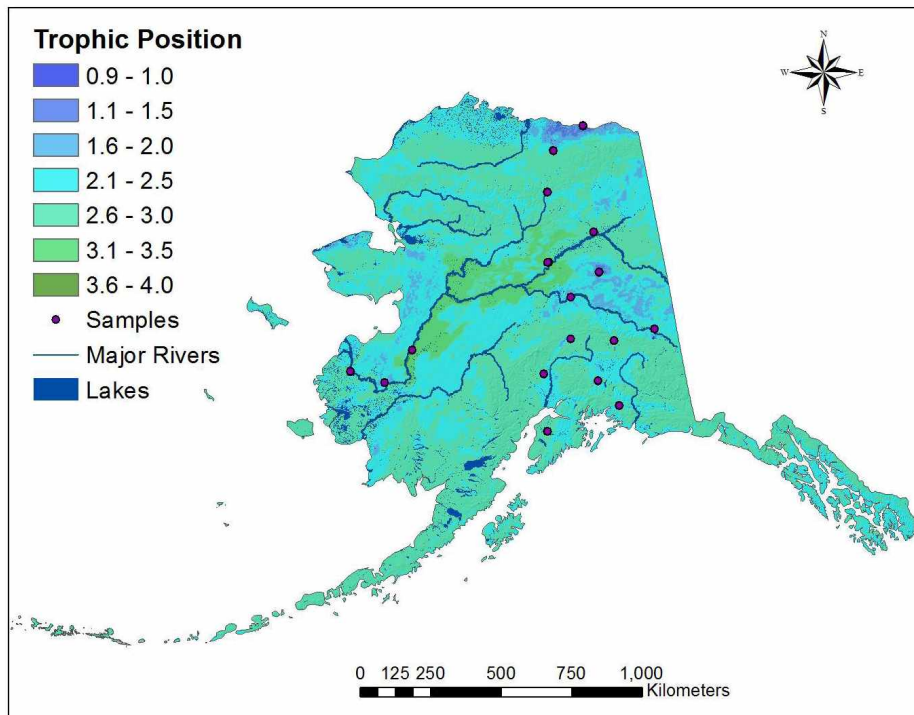


Fig. 4.4. Rodent trophic position map

Modeled trophic position of rodents based on trophic positions calculated for individual rodents using sampled herbaceous plants as an isotopic baseline. Training points are also shown.

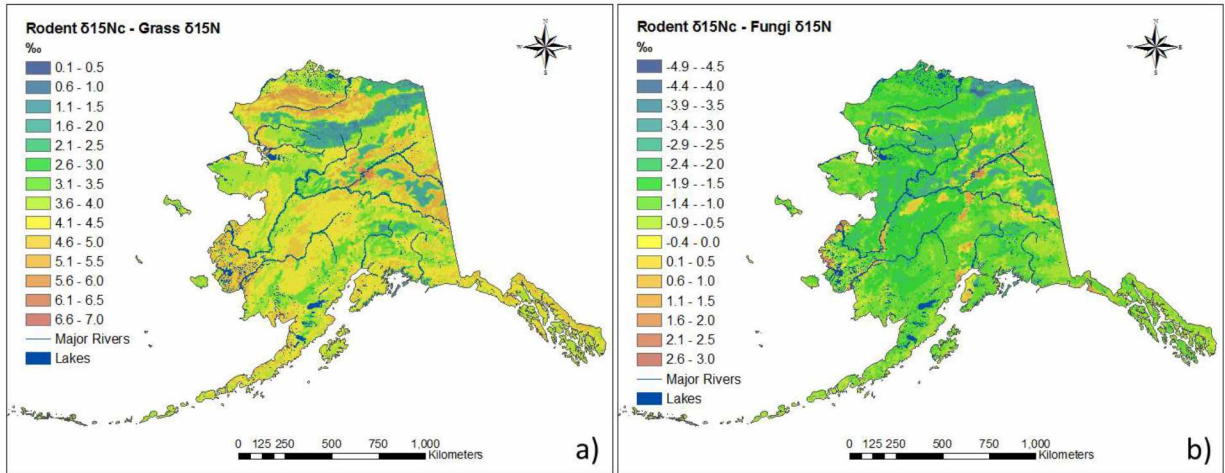


Fig. 4.5. Inter-trophic level difference isoscapes
Spatially calculated differences between $\delta^{15}\text{N}$ values of rodents and diets: a) grasses and b) fungi,
using the formula $\delta^{15}\text{N}_{\text{rodent}} - 2.7 - \delta^{15}\text{N}_{\text{diet}}$.

4.8. TABLES

Table 4.1. List of predictor variables used in isoscape models
 Predictor variables used in models, type of data (raster or polygon), and their online sources.
 Raster layers have a 300-m resolution.

Variable Name	Format	Source
Aspect	Raster	http://ned.usgs.gov/
Bedrock	Polygon	http://water.usgs.gov/maps.html
Distance to Coastline	Raster	http://dnr.alaska.gov/SpatialUtility/SUC?cmd=vmd&layerid=56
Distance to Glaciers	Raster	http://dnr.alaska.gov/SpatialUtility/SUC?cmd=extract&layerid=27
Distance to Infrastructure	Raster	http://www.snap.uaf.edu/data.php
Distance to Lakes	Raster	http://nhd.usgs.gov/
Distance to Permafrost	Raster	http://agdcwww.wr.usgs.gov/agdc/agdc.html
Distance to Village	Raster	http://www.adfg.alaska.gov/index.cfm?adfg=maps.data
Ecoregion	Polygon	http://agdc.usgs.gov/data/usgs/erosaf0/ecoreg/
Elevation	Raster	http://ned.usgs.gov/
Fire Year	Raster	http://forestry.alaska.gov
δ D Meteoric Water	Raster	http://wateriso.utah.edu/waterisotopes/pages/data_access/ArcGrids.html
Mean Annual Precipitation	Raster	http://www.prism.oregonstate.edu/
Mean Annual Temperature	Raster	http://www.snap.uaf.edu/data.php
Mean January Precipitation	Raster	http://www.prism.oregonstate.edu/
Mean January Temperature	Raster	http://www.prism.oregonstate.edu/
Mean July Precipitation	Raster	http://www.prism.oregonstate.edu/
Mean July Temperature	Raster	http://www.prism.oregonstate.edu/
Landcover	Polygon	http://www.mrlc.gov/nlcd2006.php
NDVI	Raster	https://lta.cr.usgs.gov/NDVI
δ^{18} O Meteoric Water	Raster	http://wateriso.utah.edu/waterisotopes/pages/data_access/ArcGrids.html
Slope	Raster	http://ned.usgs.gov/
Soil Type	Polygon	http://www.nrcs.usda.gov/wps/portal/nrcs/site/ak/home/
Surficial Geology	Polygon	http://agdc.usgs.gov/data/usgs/geology/metadata/beikman.html

Table 4.2. Stable isotope results for small mammals and dietary groups
Mean and 95% confidence intervals of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for small mammals, their potential dietary sources, and a predator. Asterisks denote taxa for which data were used as training points for isoscape models.

Taxa	<i>n</i>	$\delta^{15}\text{N}$		$\delta^{13}\text{C}$	
		Mean	95% CI	Mean	95% CI
Woody Plants	93	-13.1	-4.8 — -3.5	-28.7	-29.1 — -28.4
Lichens	58	-2.5	-3.2 — -1.7	-26.8	-27.7 — -26.0
Mosses	66	-2.3	-3.0 — -1.7	-28.7	-29.2 — -28.3
*Grasses	162	-1.3	-1.9 — -0.6	-28.1	-28.4 — -24.6
Herbaceous Plants	92	0.2	-0.5 — 0.9	-27.3	-27.6 — -26.9
*Fungi	52	2.9	1.7 — 4.2	-24.6	-25.2 — -24.1
*Rodents	233	4.1	3.8 — 4.4	-25.1	-25.2 — -24.9
*Shrews	93	6.2	5.7 — 6.6	-23.9	-24.1 — -23.7
Ermine	2	7.4	7.0 — 7.9	-23.5	-33.8 — -13.2

Table 4.3. Variable importance rankings for isoscape and trophic position models

Variable importance rankings are out of 100.0 with the maximum value assigned to the most important predictor in each model. A "-" indicates a variable whose importance was negligible and was not included in the model.

Variable Name	$\delta^{15}\text{N}$	$\delta^{15}\text{N}$	$\delta^{15}\text{N}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$	Trophic Position
	Grass	Fungus	Rodent	Shrew	Grass	Fungus	Rodent	Shrew	
Aspect	-	29.8	31.1	12.0	12.7	-	-	-	18.6
Bedrock	98.4	100.0	58.6	59.8	85.6	100.0	96.7	36.2	93.9
Distance to Coastline	-	7.2	29.0	20.2	2.3	-	-	36.5	18.0
Distance to Glaciers	-	17.3	32.2	28.5	-	9.8	14.3	-	4.6
Distance to Infrastructure	9.6	11.2	34.6	31.2	-	8.0	25.7	5.3	20.8
Distance to Lakes	-	8.0	31.3	36.4	6.3	-	-	14.2	10.8
Distance to Permafrost	-	2.7	25.9	19.7	-	-	9.3	19.3	8.3
Distance to Village	9.6	11.3	37.0	28.6	14.7	-	12.1	7.0	11.0
Ecoregion	13.6	-	39.6	62.3	41.1	12.7	82.6	36.1	67.8
Elevation	-	9.9	21.9	12.0	6.0	-	-	-	8.6
Fire Year	-	1.8	10.5	10.4	2.3	-	-	-	2.4
δD Meteoric Water	-	13.9	-	-	-	-	-	-	-
Mean Annual Precipitation	-	28.3	14.5	10.2	-	47.3	-	14.9	4.1
Mean Annual Temperature	-	6.6	14.6	10.7	11.0	-	-	-	-
Mean January Precipitation	-	15.6	10.0	8.1	-	40.5	-	9.1	-
Mean January Temperature	-	4.8	9.6	14.3	-	-	-	-	-
Mean July Precipitation	-	6.0	7.8	5.3	-	-	-	-	6.4
Mean July Temperature	-	6.6	30.7	11.4	6.4	-	-	-	4.4
Landcover	18.4	47.3	57.7	61.3	40.3	52.9	72.9	31.5	48.4
NDVI	-	25.0	15.6	11.8	17.1	29.2	50.7	7.9	11.1
$\delta^{18}\text{O}$ Meteoric Water	-	11.5	-	-	4.1	-	-	-	-
Slope	-	11.6	26.3	19.7	16.6	42.9	48.0	13.5	14.1
Soil Type	100.0	72.9	100.0	100.0	100.0	74.9	74.3	100.0	100.0
Surficial Geology	24.1	37.0	18.9	28.6	23.1	28.7	100.0	5.8	48.7

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CHAPTER 5. PREDICTED SHIFTS IN SMALL MAMMAL DISTRIBUTIONS AND BIODIVERSITY IN THE ALTERED FUTURE ENVIRONMENT OF ALASKA: AN OPEN ACCESS DATA AND MACHINE-LEARNING PERSPECTIVE⁴

5.1. ABSTRACT

Climate change is acting to reallocate biomes, shift the distribution of species, and alter community assemblages in Alaska. Predictions regarding how these changes will affect the biodiversity and interspecific relationships of small mammals are necessary to pro-actively inform conservation planning. We used a set of online occurrence records and machine-learning methods to create bioclimatic envelope models for 17 species of small mammals (Arvicoline rodents and shrews) across Alaska. Models formed the basis for sets of species-specific distribution maps for 2010 and were projected forward using the IPCC (Intergovernmental Panel on Climate Change) A2 scenario to predict distributions of the same species for 2100. We found that distributions of cold-climate, northern, and interior small mammal species experienced large decreases in area while shifting northward, upward in elevation, and inland across the state. In contrast, many southern and continental species expanded throughout Alaska, and also moved down-slope and toward the coast. Statewide community assemblages remained constant for 15 of the 17 species, but distributional shifts resulted in novel species assemblages in several regions. Overall biodiversity patterns were similar for both time frames, but followed general species distribution movement trends. Biodiversity losses occurred in the Yukon-Kuskokwim Delta and the Seward Peninsula while the Beaufort Coastal Plain and western Brooks Range experienced modest gains in species richness as species distributions shifted to form novel assemblages. Quantitative species distribution and biodiversity change projections should help land managers to develop adaptive strategies for conserving dispersal corridors, small mammal biodiversity, and ecosystem functionality into the future.

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5.2. INTRODUCTION

The world's biomes, specifically in the Arctic and boreal forest of the circumpolar North, are undergoing dramatic changes in climate, geographic distribution, ecosystem function, and food web structure [1-5]. The implications of these types of biome-level transitions for species persistence may be profound and without accurate spatial descriptions, predictions, and monitoring, the consequences of this change on ecological systems can scarcely be foreseen. As climate change shifts biome and ecosystem boundaries, and the expanding human footprint [6] encroaches further into wildlife habitat, species must either adapt to live within these new biological limits, disperse to regions with more favorable environmental conditions, or experience extirpation [4, 7-8]. As species respond to environmental change, we are likely to witness novel species interactions and community rearrangements that may have ecosystem-wide consequences [9-10].

Species ranges are already shifting at global decadal averages of 6.1 km towards the poles and 6.1 m upward in elevation as climate conditions release southern species from environmental constraints [8, 11]. In the Arctic, where climate effects will be especially pronounced, species turnover rates are expected to be 25–38% [3]. Biome-level transitions [12] are constricting species distributions, especially in arctic and alpine habitats where they are being confined to increasingly smaller areas [13-15]. As the tundra warms and dries, and permafrost melts, sedge-dominated vegetation is giving way to shrubs and trees that are expanding both their latitudinal and elevational extents, [14, 16-18]. Preliminary assessments show that tundra refugia are disappearing in southwestern Alaska and shrinking towards the Arctic coast north of the Brooks Range [12]. At the same time, alpine habitats are being pushed upward by rising treelines, their total area limited by the decreasing amount of land towards mountain summits [19-21]. Arctic- and alpine-adapted wildlife species are trapped in a waning biome with increasingly limited options for dispersal and persistence [4, 22-23]. Climate change is altering the habitat conditions that native arctic and boreal species are adapted to with reduced potential for species persistence and ecological functionality as the uncertain effects of species turnover cascade up the food chain [8, 20, 24-25].

In the context of these sweeping environmental changes, it is critical for the scientific conservation of species and ecosystem services to determine how the distribution and functionality of biotic systems will respond, especially in the North where changes are rapid and

extensive [16, 26-27]. Apart from decreasing carbon emissions, implementing a dynamic, adaptive strategy that focuses on maximizing species richness given future ecological conditions is mandatory if we are to keep pace with ecological changes [3, 28-29]. However, the consequences of climate-induced changes on Alaskan terrestrial food web systems, especially the bottom-up effects of prey composition, remain one of the least-studied and understood fields of global change biology [13, 26, 30]. To have an efficient system of global ecological management, it is essential to understand the details of these processes.

Despite general elevational and latitudinal trends in species movement, the exact nature of individual species responses to climate change remains complex and sometimes even counterintuitive as species react to new combinations of interacting environmental and ecological conditions [8, 23, 25, 31]. Often, these processes are discovered to be more complicated than initially predicted, as additional analyses reveal new drivers and interactions that change existing assumptions. Here we use a bioclimatic envelope modeling approach [32-36] to outline current environmental conditions conducive for the occurrence of small mammals (Arvicoline rodents and shrews) in Alaska. Based on the IPCC (International Panel on Climate Change; [2]) A2 emissions scenario, we project our models onto future bioclimatic conditions to outline regions likely to undergo major changes in biodiversity and community composition. These results will help to further pro-active ecological management based on the best available science.

While often not fully appreciated by land or wildlife managers and the public, small mammals comprise a diverse and populous set of primary and secondary consumers, and are themselves essential prey for a variety of carnivorans and raptors [15, 37-38]. Small mammals occupy a range of niches and maintain various combinations of herbivorous, frugivorous, granivorous, fungivorous, and faunivorous diets [39-41]. In Alaska, rodents provide numerous ecological services including seed dispersal [42], mycorrhizal fungal symbiosis [43], soil development [40], and herbivory [37-38, 44] whereas insectivorous shrews are known to be valuable for controlling invertebrate populations [45]. Currently, co-occurring species appear to be rather plastic in their realized dietary niche space, using resource partitioning to avoid competitors despite overlap in fundamental niche spaces that exist at the scale of Alaska [41]. Several core communities of sympatric small mammal species exist across the state [46], but it is

unknown whether these communities will withstand the disruptive pressures of anthropogenic climate change.

We used machine-learning techniques to develop bioclimatic models that describe the current fundamental niche spaces of 17 species of small mammals in mainland Alaska, and applied them to environmental conditions projected for 2100. Machine-learning uses a data-driven approach to describe patterns in datasets by categorizing points based on similarities to one-another. Traditional frequentist statistics apply a probabilistic framework that usually begins with testable hypotheses that are evaluated against an *a priori* model [47-48]. In contrast, machine-learning operates without assumed, underlying distribution models and instead uses a flexible, non-parsimonious, algorithm to describe generalizable patterns extracted from the input dataset [49]. Machine-learning algorithms (e.g., RandomForests, TreeNet, Mars, CART, MaxEnt, and others) are adept at predicting species distributions using sets of environmental conditions at detection locations to develop spatial models [50]. Because these methods allow the use of hundreds of ecological variables and their interactions to identify important patterns in the data [49, 51-52], they are capable of outlining many dimensions of the ecological niche. The resulting models can be applied across space and time [49, 53-54] while accounting for the complex, confounding, and non-linear relationships among variables that drive ecological processes [49, 55-58].

This bioclimatic envelope modeling approach assumes a stable and robust niche that is conserved over time, allowing for robust quantitative predictions into the future [36, 59-60]. This approach does not however, account for the effects that dispersal, interspecific interactions, and intrinsic or evolutionary adaptation could have in altering the predicted consequences of a changing climate on distributions [20, 61-63]. Following Murphy et al. [12], these models demonstrate a conservative but robust approach to providing minimum estimates of species distributional change. As such, bioclimatic envelope models can be valuable conservation tools, especially for species and regions around the world that lack known intrinsic parameters, as we seek to efficiently assess the risks of climate change on species persistence and ecosystem function [20, 27, 65].

5.3. METHODS

5.3.1. Data Collation

We compiled over 112,000 digital georeferenced records of small mammals collected from a diversity of arctic and boreal ecoregions across Alaska ([46], Fig. 5.1, Supplementary File A). A smaller, filtered, subset of this dataset was used as training data to create distribution models for 17 species of Arvicoline rodents and shrews across Alaska (Table 5.1). Data were collated from archived occurrence datasets, primarily from the Global Biodiversity Information Facility (GBIF; www.gbif.org), and from several natural history museum collections that do not yet serve their data to GBIF (Supplemental File B). The compiled set of presence-only records was filtered to remove spatial duplicates and records without geographic precision to at least five decimal places. Because of the presence-only nature of archived datasets that lack a geographically stratified design, we aimed to minimize the effects of sampling bias by using only one record per species within a 1-km radius of any given location. After manually removing imprecise and duplicate occurrence records, a total of 4,408 unique georeferenced small mammal records collected between 1900 and 2012 remained and comprised the current (2010) model-training dataset.

To create models with a binomial response (presence/absence) it was also necessary to generate a set of ‘pseudo-absences’ to represent areas where target species were unlikely to occur. We established that the presence of a non-target species, without the known coincidental occurrence of the target species within a 1-km radius, represented a pseudo-absence for the target species [66]. Despite potential differences in collection efforts between studies, this was the pseudo-absence option that resulted in the most accurate models and it performs as well as or better than other pseudo-absence scenarios [51, 66-67].

5.3.2. Model Development

We used RandomForests (Salford Systems, Inc., San Diego, CA, USA; www.salford-systems.com) to create spatial distribution models for each of the 17 species of mainland small mammals in Alaska. Presence points and pseudo-absence points for each species were attributed with 27 environmental predictor layers (Table 5.2) using the *Extract values to multi-point* tool in ArcGIS 10.2 (ESRI, Inc., Redlands, CA, USA). Environmental predictor variables included continuous raster (60-m accuracy) and categorical polygon layers, for which spatial GIS layers

were available for both the time periods of 2010–2020 and 2090–2100. Sets of ‘static’ predictor layers (those anticipated to undergo minimal change between 2010 and 2100) and ‘dynamic’ predictor layers (those undergoing substantial change as a result of climate effects) were selected based on their explanatory influence as documented in prior 2010 distribution models of small mammals [46]. The hypothesized and documented effects of these variables may occur directly at the ecosystem or landscape scales (e.g., habitat, proximity to resources, topography, etc), or indirectly at landscape or regional scales (e.g., climate, climate, etc.; Table 5.2).

The combined 2010 presence/pseudo-absence training datasets for each species were then modeled in RandomForests. Each model was grown to at least 500 trees and used all other software default settings to obtain the best-possible models. Aspatial performance was cross-validated internally in RandomForest using an ‘out-of-bag’ set of training points [55]. Predictive performance of each model was calculated using the area under the curve (AUC) [68] based on the receiver-operating characteristic (ROC) and average ‘% Correct’ both of which are quantifications of correctly-predicted presences and absences in each model [57, 69-70]. A symmetric threshold of 0.5 was used to differentiate between presences and absences for all models.

To create species distribution maps for 2010 and 2100, files containing the predictive algorithm (‘groves’), were applied to a regular lattice of points (5-km resolution) spanning Alaska. Points in the lattice were also previously attributed with the environmental variable sets for 2010 and 2100. Static variables were held constant across the 2010 and 2100 models, while dynamic variables were updated for the 2100 model using decadal mean projections for 2090 to 2100 based on the IPCC projections for using the A2 emissions scenario [2]. The A2 scenario describes a heterogeneous world with continuously increasing global population projected to reach 15 billion people by 2100 and rapid growth in carbon emissions related to land use in excess of 29 billion GtC/yr [71]. This is one of the most pessimistic emissions scenarios in the public discussion for which downscaled climate projections are available, and so models based on it represent a widely-accepted, ‘worst-case’ scenario for climate change [71]. Considering that current CO₂ emissions have exceeded those of the A2 scenario for the past decade with little reduction likely in the near future, this scenario seems a realistic choice [72].

Our model outputs generated relative indices of occurrence (RIO; a ranking of pixels from 0 to 1 representing the likelihood of belonging to the ‘presence’ class) for each point in the

regular lattice for 2010 and 2100. In ArcGIS 10.2, RIO values were smoothed for visualization between neighboring points across the study area extent using the *Inverse Distance Weighting (IDW)* tool with a 1-km resolution and clipped to the state coastline. This resulted in independent, spatially-continuous, predictive distribution maps for each species of small mammal in Alaska for the time periods of 2010 and 2100. RandomForests was also used to rank the relative importance of environmental variables in models.

5.3.3. Community Composition Analysis

To compare community composition between the two time periods (2010 and 2100) we created a set of 50,000 random points across Alaska and attributed each point with the RIO values from the 17 future species distribution models. This provided a means for determining co-occurring species at each point. We used the *chart.correlation* command from the *Hmisc* package (F. Harrell; <https://github.com/harrelfe/Hmisc>) in R 2.12.1 to provide a quantified assessment of the similarities among RIO values of all species at each point. Species-pairings with correlation coefficients ≥ 0.25 were considered to be positively correlated and likely to co-occur in space, whereas pairings with a coefficient < -0.25 were negatively correlated and unlikely to co-occur. Clusters of correlated species were visualized in tree form using the *varclus* command in *Hmisc*, so that we could easily identify main groups of sympatric species that occur together. These groups were named as the most frequent small mammal communities in Alaska. Comparisons between the tree structures of the two time periods identified how species-membership among these communities are likely to change between 2010 and 2100.

5.3.4. Spatio-temporal Change Analysis

To quantify biodiversity and biogeographic patterns across Alaska, we reclassified all species distribution models to binary rasters based on a threshold of 0.5. Pixels with $\text{RIO} \geq 0.5$ were classified as 1 (denoting species presence), and pixels with $\text{RIO} < 0.5$ were classified as 0 (denoting species absence). Binary rasters were summed across all species for each time period, yielding species richness maps for 2010 (Bio_{2010}) and 2100 (Bio_{2100}). Using the *Raster Calculator* in ArcGIS 10.2, we subtracted the species richness map for 2010 from that of 2100 to yield a map (ΔBio) depicting the projected net change in biodiversity across Alaska over the coming century. Similar calculations were used to compare continuous species RIO maps

between the two time periods. The resultant set of maps ($\Delta\text{RIO}_{\text{species}}$) depicted the projected change in relative occurrence for each species between 2010 and 2100. The mean RIO across all species was then calculated for each pixel resulting in a map (ΔRIO) that detailed the average net change in species relative occurrence for Alaska. For all species in each time period, we also calculated the median latitude, elevation and distance to the coast for pixels classified as presences. This allowed for the quantification of species distribution movement rates northward, coastward and upward in elevation.

To further analyze shifts in binary species distribution maps and to calculate the total difference in area and percent change for species distributions between 2010 and 2100, we used the Land Change Modeler (Clark Labs, Worcester, MA, USA) in ArcGIS 10.2. Resultant maps depicted areas of loss, gain and persistence for each species. The regular grid of 5-km spaced points across Alaska was also attributed with the pixel values of the four composite species models (Bio_{2010} , Bio_{2100} , ΔBio , and ΔRIO). The attributed lattice was then analyzed in TreeNet to determine the importance rankings of variables in each model.

5.4. RESULTS

5.4.1. Future Distribution and Community Models

Models predicting the future distributions of 17 species of small mammals (Appendix 5A, Supplemental File F) were highly accurate, evaluated using withheld out-of-bag samples (Table 5.1). All models exceeded 80% accuracy except for the cinereus shrew (*Sorex cinereus*; 76.5%). When evaluated using the AUC ROC scores, all species exceeded 0.89 with the exception of the American water shrew (*S. palustris*; 0.83), which is notoriously difficult to detect.

Projected future distributions of small mammals were grouped into five distinct community groups across Alaska when using *varchus*. Community groups were remarkably similar in structure to those calculated for 2010 and included the same ‘continental’, ‘southern’, ‘interior’, ‘northern’, and ‘cold-climate’ aggregations (Baltensperger and Huettmann 2015). Species membership within groups remained the same between 2010 and 2100 with the exception that cinereus shrews moved from the southern community to the interior community and American water shrews moved from the continental community to the southern community (Fig. 5.2), reflecting a northward and interior contraction of the cinereus shrew distribution and a

broad predicted expansion of the water shrew distribution. The continental and southern communities were positively correlated with one another, but negatively correlated with all other groups. Likewise, the northern and cold-climate groups were also positively correlated, but were negatively correlated with all other groups.

5.4.2. Model Change Between 2010 and 2100

Comparisons between current and future species distribution models showed an average loss in area of 20.2% for all species in the cold-climate, northern, and interior community groups (Table 5.3). Among these groups, only the pygmy shrew (*S. hoyi*) experienced increases in total area (3.5%). In contrast, distributions of all species in the continental and southern communities increased by an average of 29.2%, with the only exception being that the area occupied by meadow voles (*Microtus pennsylvanicus*) decreased by 3.5%.

Distributions of all members of the cold-climate, northern, and interior communities also showed northward shifts in median latitude that averaged 111 km using the implemented modeling scenario. Only northern collared lemmings (*Dicrostonyx groenlandicus*) experienced a southerly shift of 25 km (2.8 km/decade) by 2100. Latitudinal changes for the continental and southern communities were mixed, with half of the species moving north and the other half moving south. Average upward shifts of 46.3 m in elevation (5.1 m/decade) were observed for species in the cold-climate, northern, interior and continental communities, whereas members of the southern community decreased by an average of 74.4 m (8.3 m/decade) in elevation. Only barren-ground shrews (*S. ugyunak*) and Alaska tiny shrews (*S. yukonicus*; but see [73] for taxonomy) moved downslope whereas meadow jumping mice (*Zapus hudsonius*) moved upslope, contradicting the elevational trends of their respective community groups.

Changes in median distance to the coast were more varied. The distributions of all interior community species moved further inland by an average of 14.7 km (1.6 km/decade), as did brown lemmings (*Lemmus trimucronatus*) and tundra shrews (*S. tundrensis*) from the northern community. Species distributions in the southern community (except meadow jumping mice) shifted closer to the coast, but responses among cold-climate and continental community species were equally divided in their movement relative to the coast (Table 5.3).

Land Change Modeler analyses highlighted core regions of persistence as well as areas of distribution loss and gain that were similar among each community's members (Fig. 5.3,

Supplemental File G). Among species of the cold-climate and northern communities, models showed major areas of distribution loss to occur in the Davidson Mountains, on the Seward Peninsula, and in the Yukon-Kuskokwim (Y-K) Delta. Similarly, interior community species distributions were reduced or eliminated from the southern extents of their ranges, especially on the Alaska Peninsula and in southeast Alaska. Northern red-backed vole (*Clethrionomys rutilus*; but see [74] for taxonomy) and yellow-cheeked vole (*M. xanthognathus*) distributions were also projected to shift inland across the western portions of their ranges. Most species in these communities were also predicted to experience distribution contractions at low to mid elevations in the Brooks Range and the mountain ranges of southcentral Alaska (Fig. 5.3). Minor distribution gains were predicted at the northern distribution extents of some species on the Beaufort Coastal Plain.

Distributions of species in the southern community were projected to gain an average of 40.3% in area between 2010 and 2100. Specifically, meadow jumping mice and American water shrews more than doubled the size of their distributions (Table 5.3). Species in this community expanded westward into the Y-K Delta, the Nulato Hills, and the Seward Peninsula and northward into the Alaska and Brooks Ranges. Continental community species distributions were also predicted to extend westward into mountainous regions of interior and south-central Alaska, and in the case of montane shrews (*S. monticolus*) as far as the Alaska Peninsula (Fig. 5.3). Projected distribution losses for these communities were minimal but included the disappearance of water shrews from southeast Alaska, meadow voles from the Kuskokwim Mountains and montane shrews from the Brooks Range.

5.4.3. Changes in Small Mammal Biodiversity

Geographic patterns of predicted small mammal biodiversity in 2100 were similar to those in 2010 (Fig. 5.4). Biodiversity ‘hot-spots’ with the highest species richness (14 species) in 2100 were predicted for 10 km² of the Brooks Range and the Ogilvie Mountains and 13 species were predicted to occur in 765 km² of mountainous boreal forest scattered throughout the upland regions of central Interior Alaska (Fig. 5.4). The lowest small mammal species richness (≤ 3 species) was predicted for southwest Alaska and the eastern Brooks Range (Fig. 5.4). Changes in species richness that were ± 1 or less occurred in 59% of the state, although some regions experienced changes in overall small mammal diversity as high as +9 and as low as -8 species

(Figs 5.4 and 5.5). A small decrease in overall biodiversity occurred between 2010 and 2100, yet areas containing 4 to 5 species underwent an increase of 1 to 2 species (Fig. 5.5). Areas of increased biodiversity were projected for mountainous regions as well as at lower elevations north of the Brooks Range. Top explanatory variables accounting for these patterns included *Soil Type*, *Surficial Geology*, *Distance to Sea Ice*, *Elevation*, *Distance to Coast*, and *Mean Active Layer Thickness*.

Analysis using mean RIO values highlighted potential movement into and out of regions, showing an overall increase in relative occurrence of species (Fig. 5.5). The largest increases (0.23) occurred on the Beaufort Coastal Plain, in south-central Alaska, and in the Y-K Delta (Fig. 5.4). The largest decreases in mean relative occurrence (-0.14) occurred in the Davidson Mountains, and on the Seward and Alaska Peninsulas. Additionally, the Yukon-Tanana Uplands, saw broad decreases in mean RIO despite high species richness there. Top explanatory variables in this composite model were similar to the other composite models with the inclusion of *Mean Number of Growing Days*. All GIS models and predictor layers were archived and are freely available on the online data repository dSpace (www.dspace.org) at the University of Alaska Fairbanks Elmer E. Rasmuson Library.

5.5. DISCUSSION

Extensive projected environmental changes across the state resulted in considerable directional shifts in the distributions of small mammals (Fig 5.3). Distributions of most members of the northern, cold-climate, and interior small mammal communities were projected to decrease in area and shift northward, upward in elevation, and away from the coast, whereas the opposite was true for many members of the southern and continental species (Table 5.3). While extreme rearrangements of communities were not predicted, novel patterns of species sympatry in some regions were apparent (Fig. 5.2). Principal species assemblages remained robust at a statewide scale and shifted mainly together as units, following the movement of bioclimatic envelopes and biomes. However, novel species interactions were predicted to occur at middle elevations in mountainous areas where a combination of varied topography and overlapping distributions provided for high species richness. Biodiversity losses occurred across southwestern Alaska and in central interior Alaska, as well as on the Seward Peninsula and in the eastern Brooks Range (Fig. 5.4). Areas with the largest species gains and the highest potential for

novel species interactions occurred in the mountain ranges of southcentral Alaska, in the western Brooks Range, and across the Beaufort Coastal Plain (Fig. 5.4).

5.5.1. Distribution Shifts

Shifts in the distributions of species as well as changes in species richness are occurring northward along a latitudinal gradient, upward in elevation, and away from the coast. The latitudinal and elevational trends are consistent with theory and other studies that have shown the global northward and upslope movement of species as they follow their bioclimatic envelopes [11, 22, 75-76]. Despite average northward shifts in the distributions of most species, high elevations at southern latitudes of Alaska are projected to preserve pockets of tundra as potential refugia for some cold-climate species such as singing voles (*M. miurus*) or collared lemmings [12]. As the lowland tundra biome transitions, cold-climate and northern species currently inhabiting such habitats could either move upslope through forested regions to alpine tundra refugia or they could remain at low elevations and follow the tundra biome northward. However, both of these alternatives depend on uncertain species-specific capacities for upslope and poleward dispersal that exceed the pace of climate change [23, 61]. Because of western tundra losses predicted for the Y-K Delta, distributions of tundra shrews, brown lemmings, and root voles (*M. oeconomus*) may be increasingly restricted to areas in the Brooks Range and northward where tundra ecosystems remain.

Indications that most species distributions will move inland (especially in southwestern Alaska) are somewhat counterintuitive to the general trends of northward and upward movements of bioclimatic envelopes. This shift in small mammal distributions corresponds to predictions that the western tundra biome will be converted into the warmer and drier 'boreal transition' and 'montane cordillera' biomes [12] as portions of this region may experience up to three-biome state changes over the coming century [12]. Although interior community species might seem to benefit from warmer, drier conditions, they are nevertheless projected to undergo contractions in the western and coastal portions of their ranges. Not only is the western tundra biome predicted to disappear from southwestern Alaska by 2100 (Murphy et al. 2010), so too is the boreal forest biome. Just as boreal species are encroaching on arctic species at mid-elevations and higher latitudes, southern and continental community species are predicted to replace interior boreal species in southwest Alaska. Warmer temperatures, increased precipitation, and the

interacting effects of sea ice loss will combine to dramatically alter the treeless sedge tundra of this region in favor of more wooded habitats [5, 12], providing the opportunity for southern and continental species expansions.

Projected distribution changes modeled here are similar to but less extreme than those predicted by other small mammal studies conducted for the Arctic [4, 22, 77-78]. Distribution models for 2010 corresponded closely with current distribution estimates for most species [22, 78]. Hope et al. [22] used MaxEnt combined with genetic analyses to project small mammal distributions as far as 2080. Their results outline analogous northward and upslope shifts in ranges that are somewhat more extreme (especially in the central Beaufort Coastal Plain) than predicted by our models. Nevertheless, patterns showing the loss of many species from the Y-K Delta and Seward Peninsula as well as increasingly overlapping distributions between boreal and arctic species are consistent between model sets [22]. Circumpolar distribution change models for collared lemmings predicted the loss of half of the current area of viable habitat by 2080 [4], while models for the Canadian Arctic projected losses of 60% given a 4° C rise in temperature by 2070 [77]. We predicted losses of just 6% in total collared lemming distribution by 2100, which sharply contradicts other results, but may in part be explained by the modest habitat gains predicted for the southern mountain ranges that are not apparent in results by Prost et al. [4].

5.5.2. Biodiversity Change

Patterns in species richness hot- and cold-spots in 2100 were similar to those predicted for 2010 that indicated the Yukon-Tanana Uplands to be an important biodiversity ecotone [46]. But biodiversity hot-spots in 2100 were also predicted to shift northward, inland, and upward in elevation achieving the largest gains in southern mountain ranges and on the Beaufort Coastal Plain. These are the areas most likely to experience new species interactions. As temperatures warm, areas at lower elevations will become suitable for new species (mostly from the expanding southern community) at a rate that exceeds the loss of cold-adapted species already living there [22].

Evidence from other studies has indicated that the highest small mammal species diversity often occurs at mid-elevations [79-81]. Here, the addition of new species to low-elevation habitats will likely push native species upslope resulting in overall increases in species richness in areas with diverse topography. Given the increasingly limited land area towards

mountain peaks, the concentration of species at mid to high elevations may be termed ‘alpine squeeze.’ This effect will inevitably lead to new species contacts between invading and resident species [10, 82].

The scenario is similar on the Beaufort Coastal Plain, but there an ‘arctic squeeze’ will confine an increasing number of species to a shrinking area [15, 77]. Models predict the addition of northern red-backed voles, cinereus shrews, singing voles, and Alaska tiny shrews to the Beaufort Coastal Plain, but only indicate range contraction, not extirpation, of native species there (e.g., collared and brown lemmings, tundra shrews, and barren ground shrews). This condensed arrangement is likely to result in at least a transitional confluence of species before resident arctic species are extirpated [77].

The largest losses in species richness were predicted for the western tundra ecosystems of the Y-K Delta and the Seward Peninsula. Importantly, these areas currently contain some of the last lowland tundra south of the Brooks Range [12, 22]. The disappearance of this habitat type from those regions would spell the eventual southern extirpation of cold-climate and northern species such as collared and brown lemmings, singing voles, root voles, tundra shrews, and barren-ground shrews from these areas.

5.5.3. Important Model Predictors

Average variable importance rankings indicated the categorical variable, *Soil Type*, to be the single most useful variable for determining small mammal distribution and biodiversity patterns. Coupled with *Surficial Geology*, static, categorical variables that interacted strongly with many other predictors, explained a large amount of variation in the models. This importance may be somewhat misleading however, as machine-learning algorithms tend to inflate the importance of predictors with many categories. Nevertheless, the fact that the models are largely driven by static variables, may have served to dampen the influence of climate on species distribution and biodiversity changes, resulting in more conservative distributional change predictions.

Secondarily important variables included many dynamic climate variables such as *Distance to September Sea Ice* and *Distance to March Sea Ice*, as well as *Mean Active Layer Thickness*, and *Growing Days*. Because the top variables were static across model years, differences between the 2010 and 2100 models were mainly the result of changes in dynamic

variables and their interactions with static variables. For example because of positive feedback between higher temperatures, melting sea ice and decreased albedo, *Distance to Sea Ice* plays important local roles in determining *Temperature*, *Precipitation*, and *Growing Days* [5]. Furthermore, those variables frequently interact with *Soil Type*, *Surficial Geology*, *Terrain*, *Distance to River*, and *Distance to the Coast*, and ultimately drive habitat conditions on the ground. As such, the consistently high variable importance rankings of both *Distance to Sea Ice* variables underscore the effect that large-scale losses in sea ice will have in driving distributions and community compositions for a variety of both terrestrial and marine species.

5.5.4. Community Structure

Community composition in 2100 remained akin to results from 2010, despite broad geographic and elevational shifts in the distributions of all modeled species. While theory predicts a rearrangement of community assemblages with changing environmental conditions [4, 7], our results indicated that community groups responded similarly to changing climatic envelopes at the statewide scale. In part, these similarities stem from our models not accounting for varied, species-specific adaptive capacity that would result in more diverse responses. But they also support the notion of niche conservatism. Some research suggests that niche dimensions are largely conserved at time scales shorter than those during which evolution operates [59, 83-84]. More recent research indicates that individual responses to climate change will vary based on the phenotypic and behavioral plasticity, dispersal ability, and adaptive capacity of each species over time [20, 63-64, 85].

Only two species (American water shrew and cinereus shrew) of 17 examined here altered their community membership and both exemplify broader trends in species turnover in Alaska. A very large predicted increase in the distribution of water shrews during the coming century was out of proportion with changes experienced by other species. Their large expansion of 64% in area appears to be an example of ecological release as environmental conditions align with the environmental niche of water shrews [7, 8, 86]. American water shrews are currently documented from a handful of locations in Alaska (the northern extent of their global range) but are more widespread throughout the Pacific Northwest and continental North America [87] (www.gbif.org). Their predicted expansion supports the notion that continental species from the south will continue to disperse into Alaska [77]. Because this analysis only considered resident

species currently in Alaska, it is also likely that the Alaskan fauna of 2100 will include an entirely new set of non-resident species from continental North America. Future field monitoring over the coming decades in southeast Alaska and the Yukon-Tanana Uplands can help document any such invasions.

Cinereus shrews, which previously belonged to the southern community, were classified in 2100 as members of the interior community and symbolize another front in Alaskan species invasion. Unlike water shrews, the distribution of cinereus shrews is predicted to decrease by 29% and constrict toward the interior of the state, similar to other members of the interior community. But despite losses in the southern portion of their range, they are also predicted to expand at the northern extent, similar to the other members of the interior community. The invasion of interior/boreal species into the Arctic will likely produce another zone of novel interaction and species turnover [22].

Comparisons of individual models also showed expansions of southern and continental species into areas where novel species interactions with persisting northern and cold-climate species will occur at the ecoregional scale [8, 82]. Most notably, these areas include the mountains of southcentral Alaska and the western Brooks Range, and on the Beaufort Coastal Plain. The strength of competition between new sets of species has not been quantified in most cases, although isotopic evidence suggests that realized foraging niche spaces of sympatric species are plastic enough to allow for their coexistence (Chapter 2). These results were consistent for interactions among 2 or 3 species, but it is uncertain whether higher numbers of interacting species from the increasingly crowded arctic and boreal communities would partition in the same manner. In regions with increasing species richness, if resources cannot be partitioned efficiently among new, increasingly saturated communities, poor competitors may suffer local extirpation [88]. Given current climate trajectories, the eventual replacement of native cold-climate and northern species by advancing interior, southern, or continental species would be the likely result [89].

5.5.5. Management Implications

Climate change is causing the transition of biomes, resulting in the decline of species that inhabit fading habitats, especially alpine and coastal tundra [12]. To conserve biodiversity and the ecosystem services associated with occupancy of a range of niches, it is vital to build

management strategies that are based not just on current biodiversity conditions, but to also incorporate projected future changes in biodiversity into such decisions [20, 90]. Potential management actions designed to conserve biodiversity and the persistence of sensitive species might include limiting road construction, extraction activities, development projects, as well as off-road recreation and disturbances in areas of high species richness.

Additionally, the conservation of genetic diversity is paramount for providing species with the capacity to adapt to changing environmental conditions [63]. Without a diverse gene pool from which adaptive genes may be drawn, species will be limited in their ability to evolve [63, 91]. Yet despite the value inherent in conserving biological and genetic diversity, few studies have included these as major components in reserve and corridor delineation [63, 92].

Given that distributions and biodiversity hot-spots are projected to move northward and into mountainous areas, efforts to conserve biodiversity should consider how best to facilitate the movement of dispersing species between current core biodiversity hotspots (e.g., Yukon-Tanana Uplands) and projected future hotspots (e.g., the Brooks Range and the Beaufort Coastal Plain). Reserve networks connected by corridors that span elevational, latitudinal and longitudinal gradients to allow for the upslope, northward, and inland dispersal of species respectively [20, 28, 50]. Although defining and implementing biodiversity reserves is difficult and time consuming, managing existing reserves and corridors with strategies that are cognizant of future trends in biodiversity movement is essential. In order to conserve biodiversity hotspots and important dispersal corridors, they should be managed so as to avoid disrupting important areas with roads, development, or other disturbances that may act as barriers to movement or persistence. Providing for core areas along these gradients may allow for the persistence of species long enough so that adaptive traits can have a chance to benefit populations [8, 63].

In Alaska where mountain ranges tend to run east/west, and where the expansive Yukon River system bisects the state, geographic-scale corridors that can aid in movement across these dispersal filters are already limited. Important corridors identified in our models include the Nulato Hills region, which provides connectivity between the rapidly changing Y-K Delta and Seward Peninsula ecosystems. Other latitudinal corridors with the potential to facilitate the dispersal of species to higher latitudes include the Kuskowkim and Ray Mountains, which also connect the southwestern coast to the Brooks Range. Additionally, the Yukon-Tanana Upland region, which has already been noted for its high species richness, provides rare high-elevation

refugia in Alaska's Interior between the Alaska and Brooks Ranges and is also a gateway from the continental interior. The DeLong Mountains within the Noatak National Preserve, and the Brooks Range foothills encompassed by the National Petroleum Reserve Alaska (NPR), should be recognized for their projected future biodiversity potential and these areas merit sound biodiversity-conscious conservation planning.

Ultimately, treating just the symptoms of climate change (shrinking distributions, biodiversity loss, fragmented habitat connectivity, and genetic homogenization) by conserving only existing hot-spots and corridors will do little to curb the damage to ecological systems by the loss of species [29, 90]. Conservation science must continue to promote the minimization of climate change and habitat disturbance to address the root causes of issues affecting declining species persistence [20]. Reducing global greenhouse gas emissions and enhancing resource conservation must be prioritized to hold back the loss of species in the Arctic and around the world.

5.6. ACKNOWLEDGEMENTS

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5.7. FIGURES

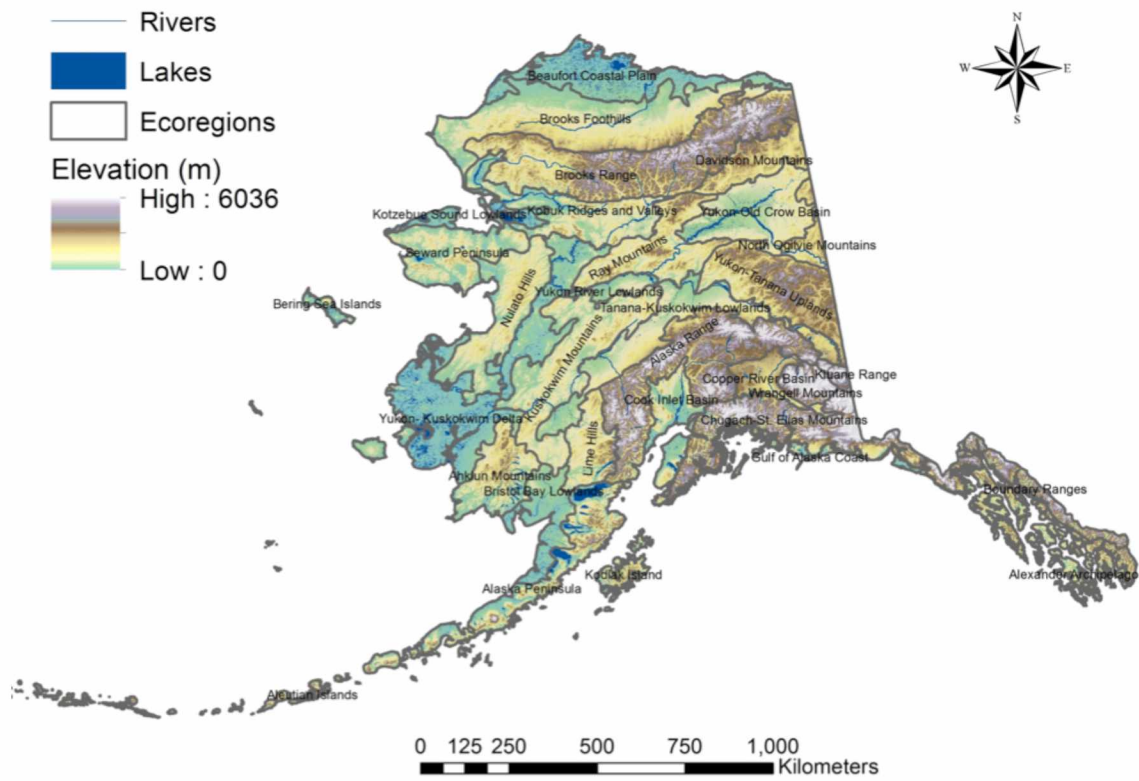


Fig. 5.1. Study area map
Depiction of the study area composed of the state of Alaska. Ecoregion boundaries are shown for reference.

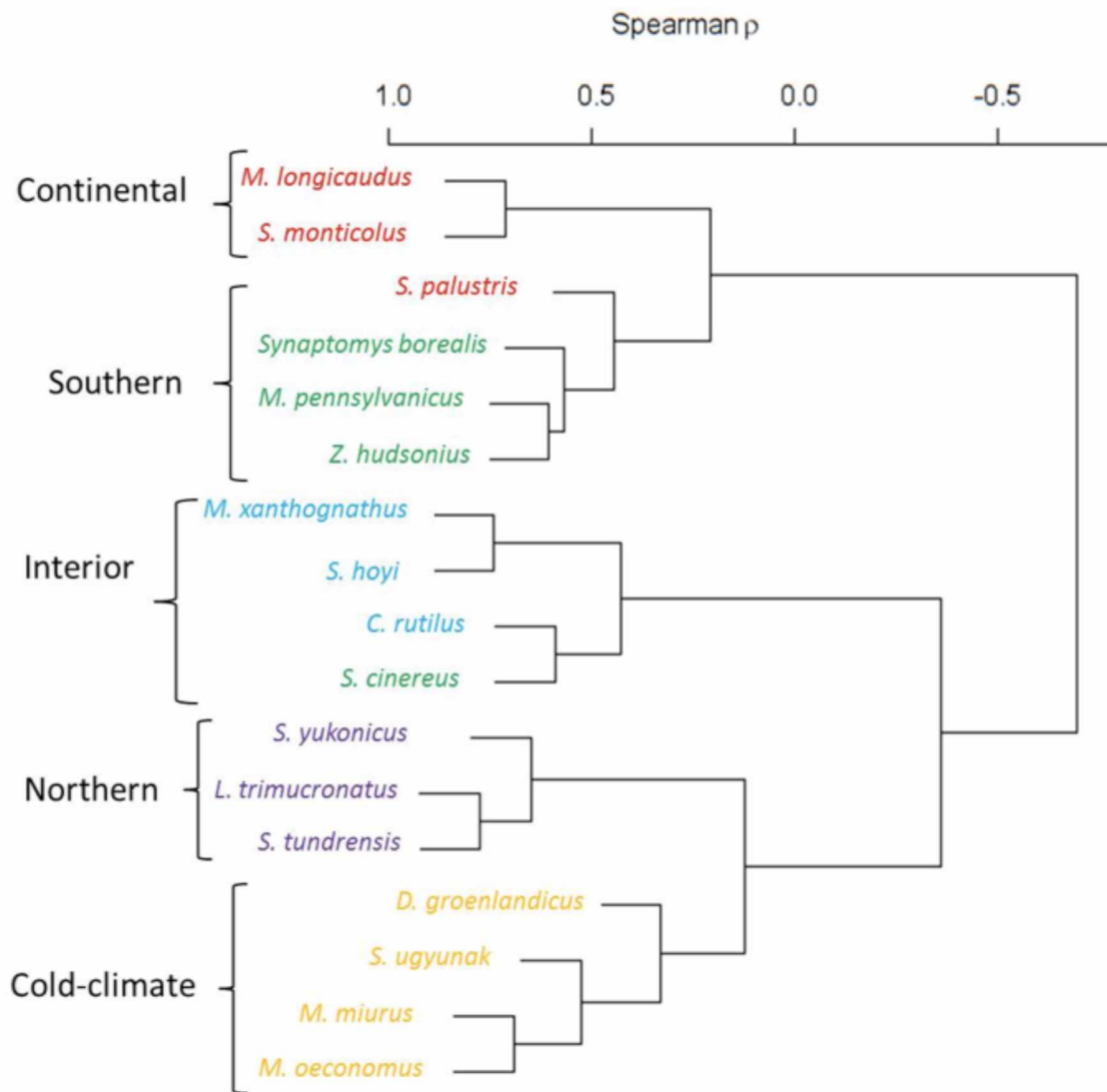
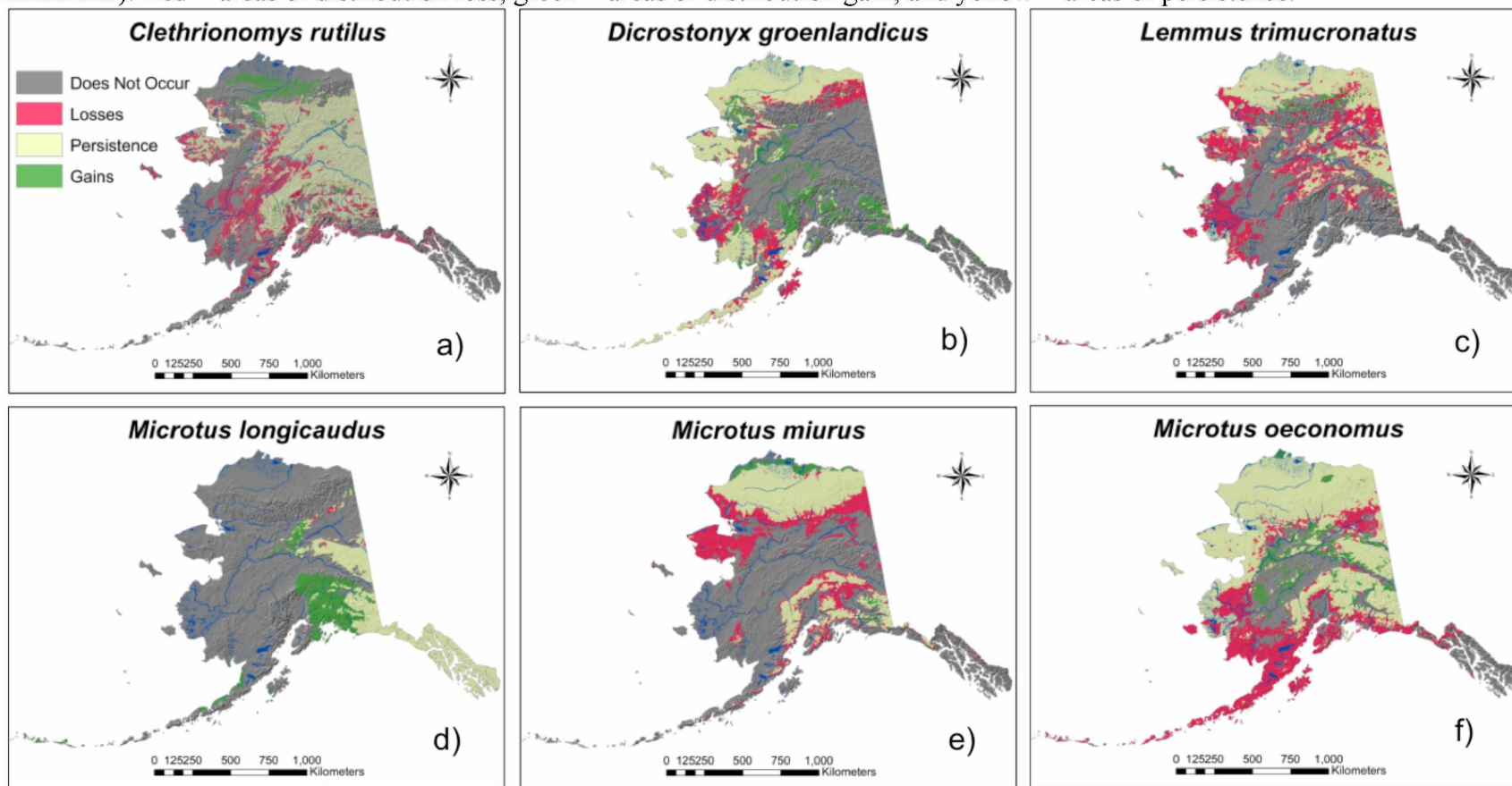


Fig. 5.2. *Varchus* correlation tree

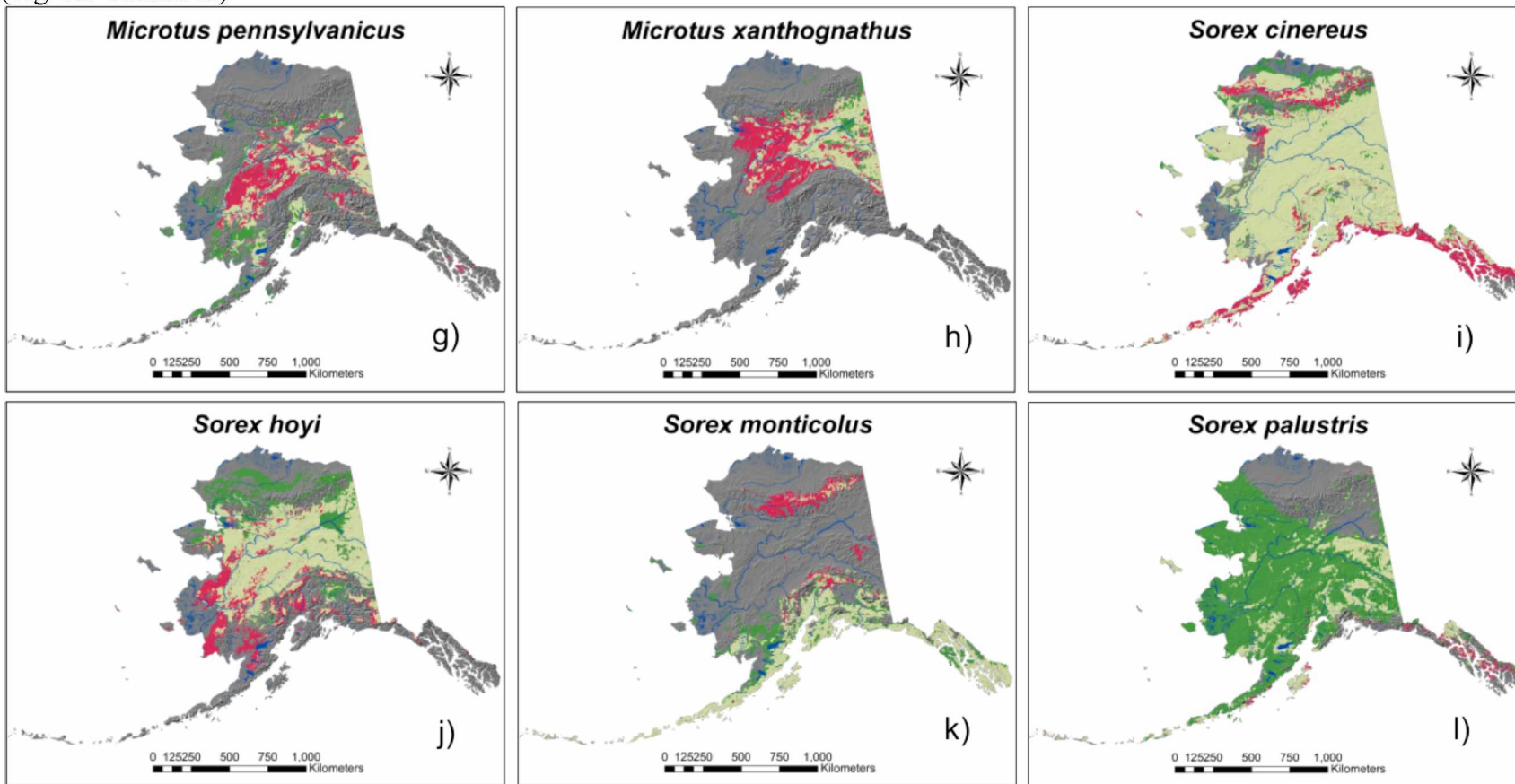
Projected 2100 community arrangements for 17 species of small mammals in Alaska based on a *varchus* correlation analysis in R. Brackets aggregate species into 2100 community groups, while colors indicate species membership in 2010 community groups.

Fig. 5.3. Distribution change maps

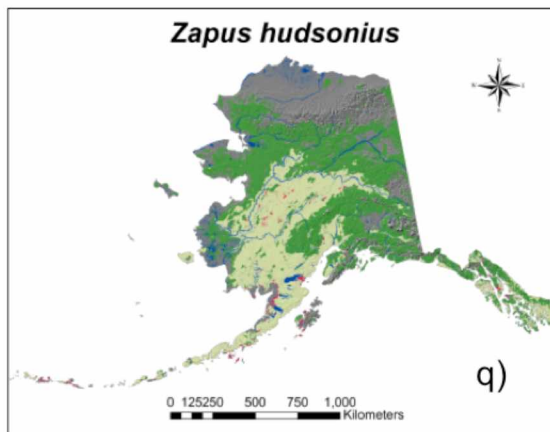
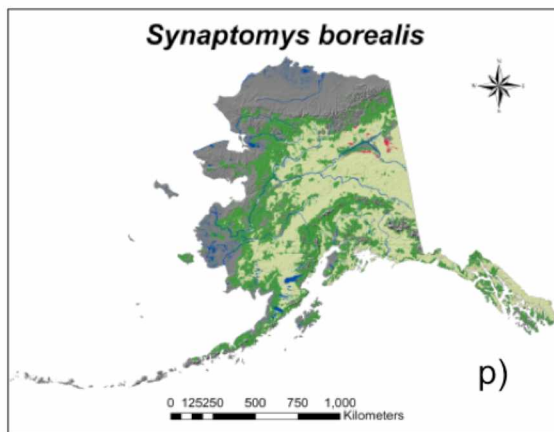
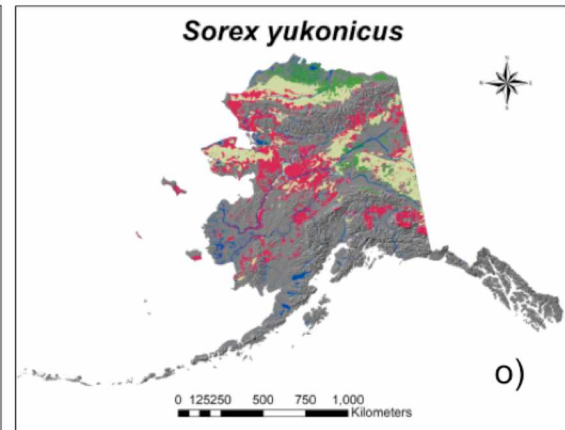
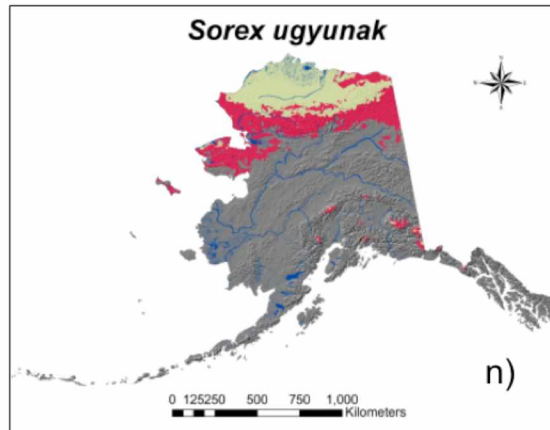
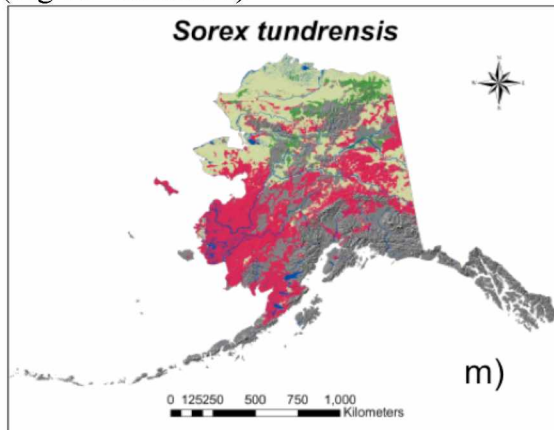
Predicted distribution change for each of the 17 modeled species of small mammal in Alaska: a) northern red-backed vole (*Clethrionomys rutilus*), b) northern collared lemming (*Dicrostonyx groenlandicus*), c) brown lemming (*Lemmus trimucronatus*), d) long-tailed vole (*Microtus longicaudus*), e) singing vole (*M. miurus*), f) root vole (*M. oeconomus*), g) meadow vole (*M. pennsylvanicus*), h) yellow-cheeked vole (*M. xanthognathus*), i) cinereus shrew (*Sorex cinereus*), j) pygmy shrew (*S. hoyi*), k) montane shrew (*S. monticolus*), l) American water shrew (*S. palustris*), m) tundra shrew (*S. tundrensis*), n) barren-ground shrew (*S. ugyunak*), o) Alaska tiny shrew (*S. yukonicus*), p) northern bog-lemming (*Synaptomys borealis*), q) meadow jumping mouse (*Zapus hudsonius*). Red = areas of distribution loss, green = areas of distribution gain, and yellow = areas of persistence.



(Fig. 5.3 continued)



(Fig 5.3 continued)



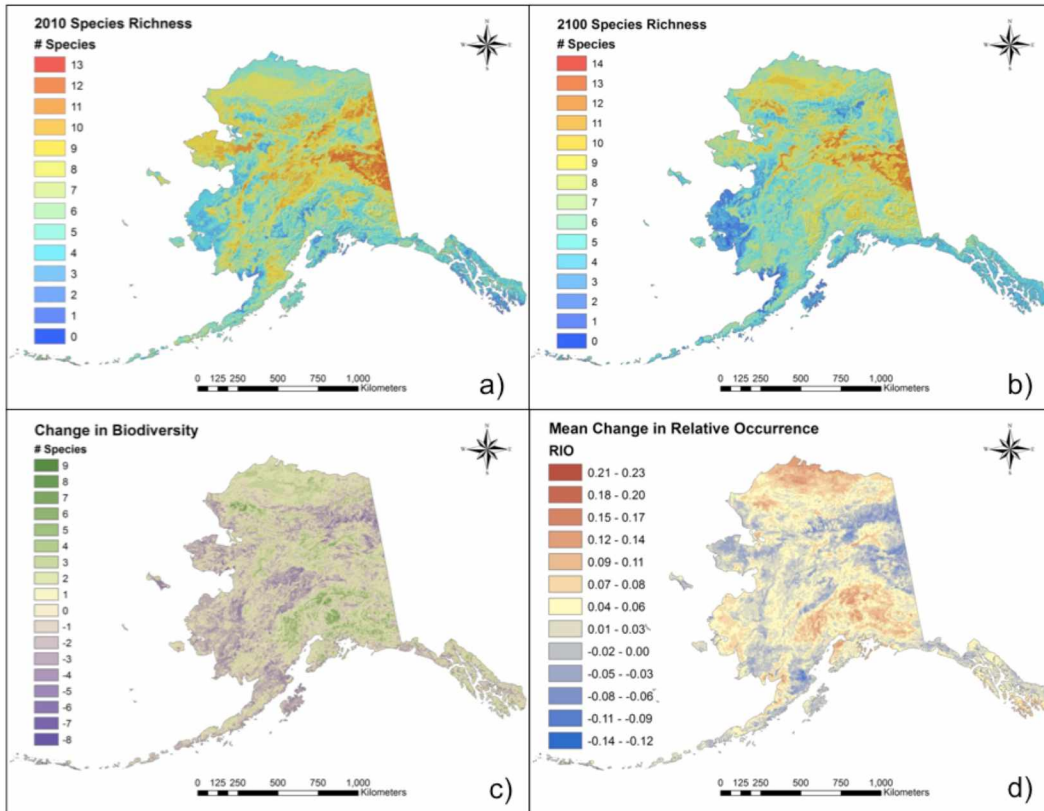


Fig. 5.4. Species richness change maps

Predictive species richness maps based on composites of binary (presence/absence) maps for 17 species of small mammals for the years a) 2010 (modified from Baltensperger and Huettmann 2015) and b) 2100. Maps also depict net change in c) species richness and d) relative indices of occurrence. Warm colors indicate net gains in RIO (relative index of occurrence) and species richness, whereas cool colors indicate net loss of RIO and species richness.

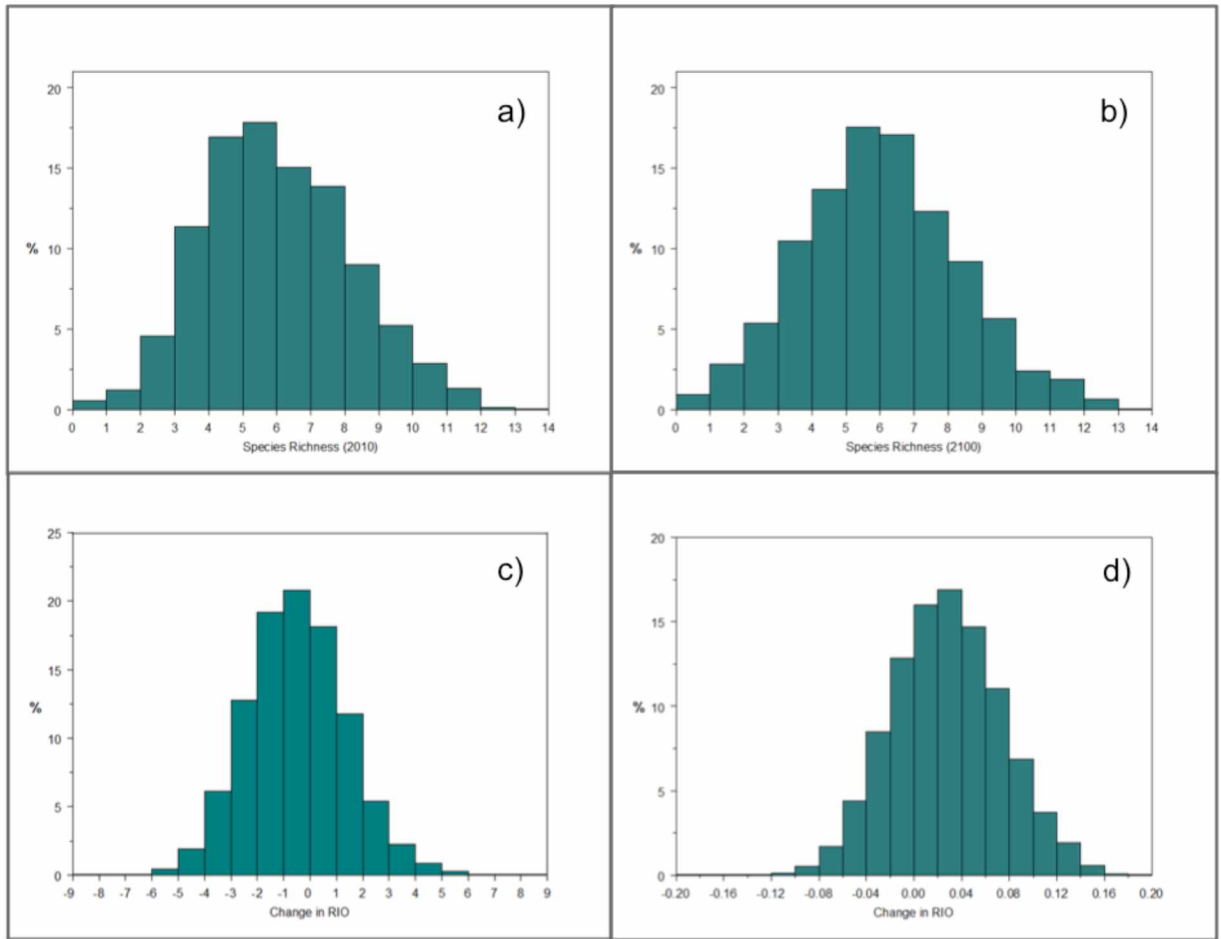


Fig. 5.5. Species richness graphs

Histograms depicting the frequency of pixels for the number of species in a) 2010, b) 2100, as well as the net change in c) species richness, and d) relative indices of occurrence.

5.8. TABLES

Table 5.1. Species list and model results

List of modeled small mammal species scientific and common names, their associated Taxonomic Serial Number (TSN), the number of presence and absence locations used to train models, the resultant area under the receiver operator characteristic (AUC ROC; 0 – 1), and % error averaged across the % of correctly identified presences and % of correctly identified absences.

Species	Common Name	TSN	<i>n</i> Presences	<i>n</i> Absences	AUC ROC	Accuracy (%)
<i>Clethrionomys/Myodes rutilus</i>	northern red-backed vole	180293	949	1157	0.94	86.3
<i>Dicrostonyx groenlandicus</i>	northern collared lemming	180328	35	2539	0.94	87.9
<i>Lemmus trimucronatus</i>	brown lemming	180320	142	2098	0.95	87.4
<i>Microtus longicaudus</i>	long-tailed vole	180299	191	2292	0.99	96.8
<i>Microtus miurus</i>	singing vole	180309	183	2153	0.98	92.2
<i>Microtus oeconomus</i>	root/tundra vole	180298	612	1029	0.94	85.8
<i>Microtus pennsylvanicus</i>	meadow vole	180297	244	1725	0.96	89.3
<i>Microtus xanthognathus</i>	yellow-cheeked/taiga vole	180301	88	2377	0.98	93.6
<i>Sorex cinereus</i>	cinereus/masked shrew	179929	818	267	0.89	76.5
<i>Sorex hoyi</i>	pygmy shrew	179946	97	1370	0.95	87.0
<i>Sorex monticolus</i>	montane/dusky shrew	179950	566	507	0.91	83.7
<i>Sorex palustris</i>	American water shrew	179933	13	1701	0.83	83.9
<i>Sorex tundrensis</i>	tundra shrew	179957	195	1071	0.95	86.9
<i>Sorex ugyunak</i>	barren-ground shrew	552509	37	1634	0.99	97.2
<i>Sorex yukonicus/minutissimus</i>	Alaska tiny shrew/Eurasian least shrew	555663	34	1610	0.95	92.6
<i>Synaptomys borealis</i>	northern bog-lemming	180323	142	1986	0.91	80.6
<i>Zapus hudsonius</i>	meadow jumping mouse	180386	72	2348	0.94	85.5

Table 5.2. Model variable list

Predictor variables used in models, type of data (categorical or continuous), whether variables were changing or constant across time. Online sources for layer downloads are also included. Continuous layers have a 60-m resolution.

Variable Name	Data Type	Temporal Stability	Source
Aspect	Continuous	Static	http://ned.usgs.gov/
Distance to Coastline	Continuous	Static	http://dnr.alaska.gov/SpatialUtility/SUC?cmd=vmd&layerid=56
Distance to Lakes	Continuous	Static	http://nhd.usgs.gov/
Distance to March Sea Ice	Continuous	Dynamic	Rogers et al. 2014
Distance to September Sea Ice	Continuous	Dynamic	Rogers et al. 2014
Distance to River	Continuous	Static	http://nhd.usgs.gov/
Distance to Village	Continuous	Static	http://www.adfg.alaska.gov/index.cfm?adfg=maps.data
Distance to Wetlands	Continuous	Static	http://www.fws.gov/wetlands/data/
Cliome	Categorical	Dynamic	https://www.snap.uaf.edu/projects/biome-shift
Elevation	Continuous	Static	http://ned.usgs.gov/
Mean Active Layer Thickness	Continuous	Dynamic	ftp://frosty.gi.alaska.edu/Out/Sergei/ALASKA_Model/GIPL1/
Mean Annual Precipitation	Continuous	Dynamic	https://www.snap.uaf.edu/tools/data-downloads
Mean Annual Soil Temperature	Continuous	Dynamic	ftp://frosty.gi.alaska.edu/Out/Sergei/ALASKA_Model/GIPL1/
Mean Annual Temperature	Continuous	Dynamic	https://www.snap.uaf.edu/tools/data-downloads
Mean January Precipitation	Continuous	Dynamic	https://www.snap.uaf.edu/tools/data-downloads
Mean January Temperature	Continuous	Dynamic	https://www.snap.uaf.edu/tools/data-downloads
Mean First Day of Freeze	Continuous	Dynamic	https://www.snap.uaf.edu/tools/data-downloads
Mean First Day of Thaw	Continuous	Dynamic	https://www.snap.uaf.edu/tools/data-downloads
Mean July Precipitation	Continuous	Dynamic	https://www.snap.uaf.edu/tools/data-downloads
Mean July Temperature	Continuous	Dynamic	https://www.snap.uaf.edu/tools/data-downloads
Mean Number of Grow Days	Continuous	Dynamic	https://www.snap.uaf.edu/tools/data-downloads
Mean January Snow Day Fraction	Continuous	Dynamic	https://www.snap.uaf.edu/tools/data-downloads
Mean July Snow Day Fraction	Continuous	Dynamic	https://www.snap.uaf.edu/tools/data-downloads
Slope	Continuous	Static	http://ned.usgs.gov/
Soil Type	Categorical	Static	http://www.nrcs.usda.gov/wps/portal/nrcs/site/ak/home/
Surficial Geology	Categorical	Static	http://agdc.usgs.gov/data/usgs/geology/metadata/beikman.html
Terrain	Continuous	Static	http://ned.usgs.gov/

Table 5.3. Species model-change metrics

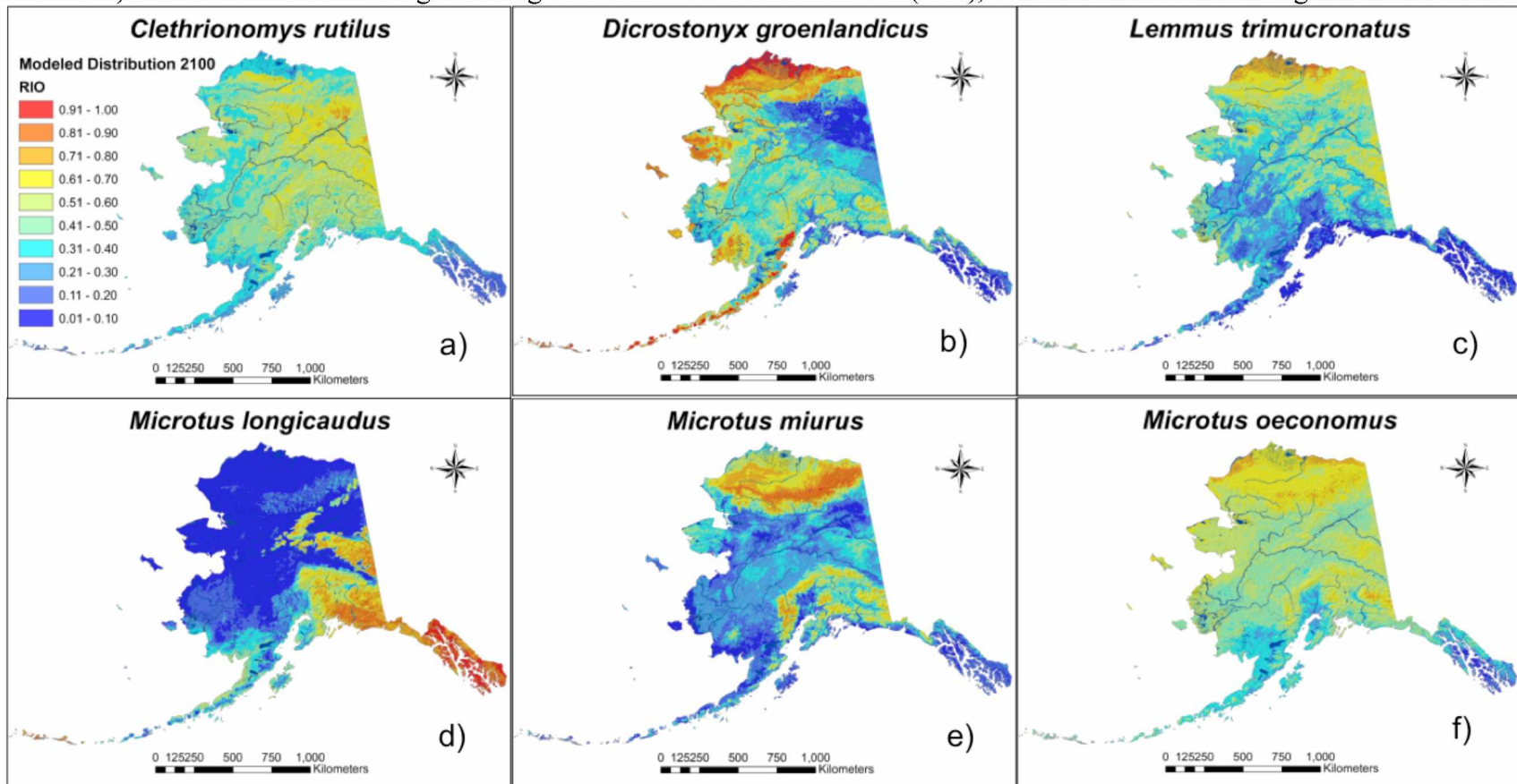
Total predicted areas of presence for each of 17 species of Alaskan small mammals in 2010 and 2100. Net change is the 2010 area subtracted from that of 2100. % change is the number of pixels changed in the presence class divided by the area of the presence class for 2100. Changes in latitude, distance to coast, and elevation were calculated by subtracting the median value in 2100 from that of 2010. Negative values for latitude, coast distance, and elevation indicate southerly, coastward, and downslope shifts, respectively.

Species	Presence Area 2010	Presence Area 2100	Net Change (km ²)	% Change	Latitude Change (km)	Coast Distance Change (km)	Elevation Change (m)
<i>Clethrionomys/Myodes rutilus</i>	803,289	609,189	-194,100	-31.9	135	9.3	105.2
<i>Dicrostonyx groenlandicus</i>	603,960	550,725	-53,235	-6.0	-25	8.3	66.8
<i>Lemmus trimucronatus</i>	702,596	395,636	-306,960	-38.6	210	19.7	40.5
<i>Microtus longicaudus</i>	206,803	336,130	129,327	10.0	35	6.7	32.9
<i>Microtus miurus</i>	589,108	377,223	-211,885	-4.3	130	-3.0	167.0
<i>Microtus oeconomus</i>	1,083,164	823,741	-259,423	-4.8	105	44.9	88.5
<i>Microtus pennsylvanicus</i>	335,399	294,218	-41,181	-3.5	-90	-71.3	-0.9
<i>Microtus xanthognathus</i>	355,644	219,628	-136,016	-11.9	45	31.7	75.9
<i>Sorex cinereus</i>	1,192,694	1,105,717	-86,977	-28.5	50	11.7	3.7
<i>Sorex hoyi</i>	607,161	637,943	30,782	3.5	130	5.9	20.7
<i>Sorex monticolus</i>	335,761	382,230	46,469	4.0	-595	-147.9	108.2
<i>Sorex palustris</i>	237,571	1,049,427	811,856	64.4	85	-0.9	-202.4
<i>Sorex tundrensis</i>	867,006	455,138	-411,868	-65.3	280	2.0	5.8
<i>Sorex ugyunak</i>	412,527	198,763	-213,764	-19.7	85	-6.0	-65.8
<i>Sorex yukonicus/minutissimus</i>	418,908	259,669	-159,239	-14.8	75	-11.6	-47.2
<i>Synaptomys borealis</i>	532,151	979,025	446,874	46.3	-50	-62.9	-19.8
<i>Zapus hudsonius</i>	438,181	1,010,635	572,454	54.0	155	12.1	115.2

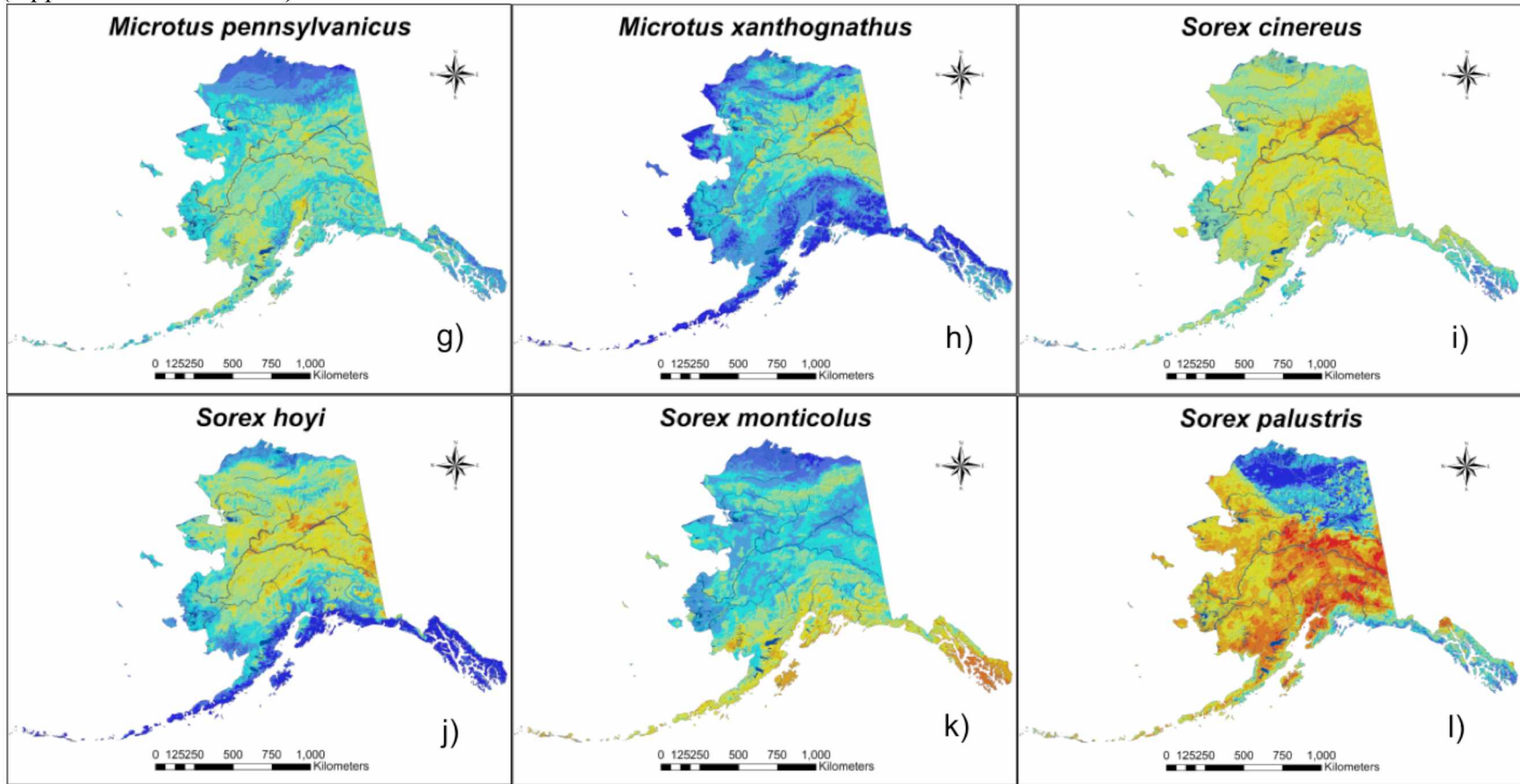
5.9. APPENDIX 5

Appendix 5A. Predicted 2100 distributions of 17 small mammal species

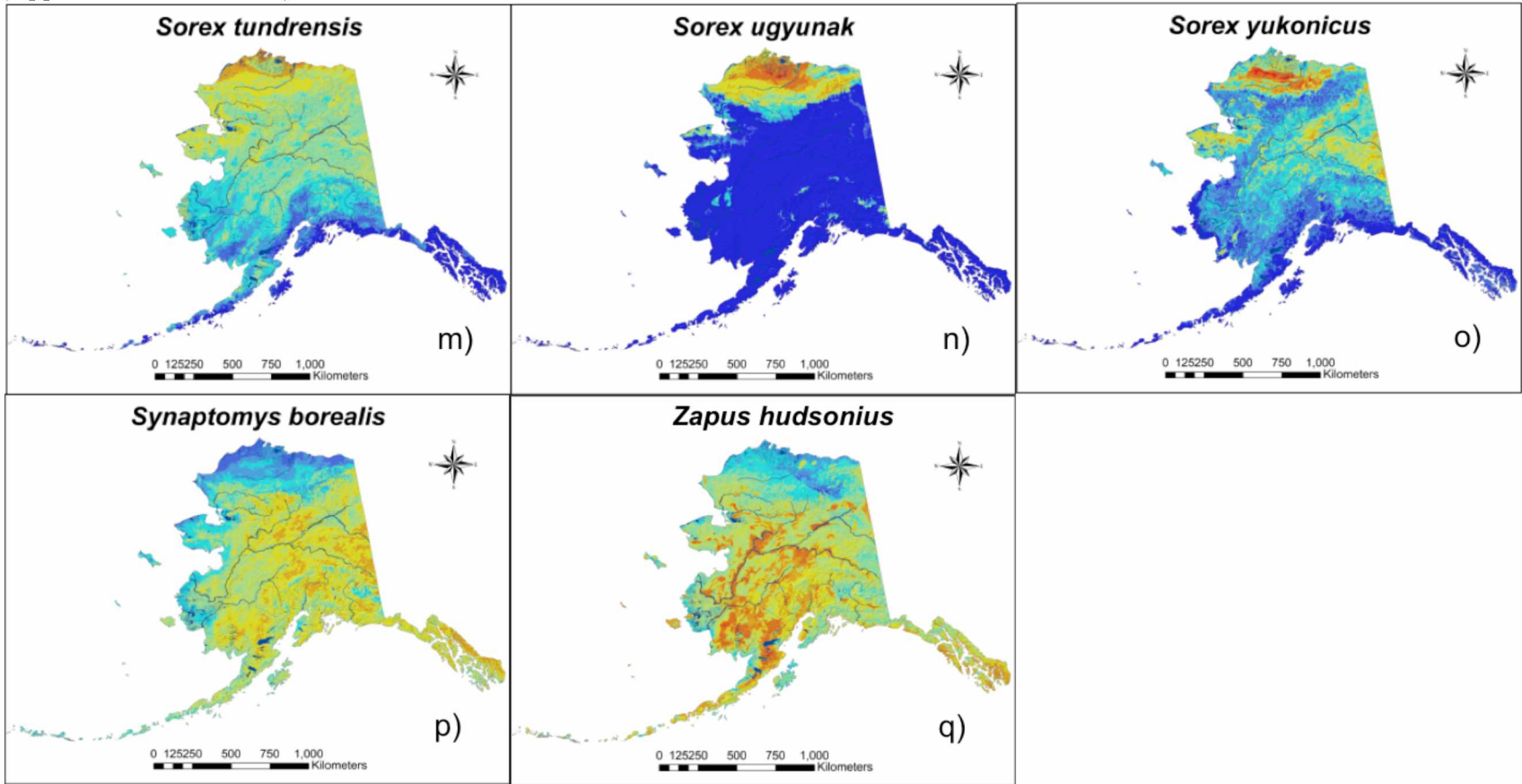
Predicted distributions of species and their training points modeled across Alaska for 2100: a) northern red-backed vole (*Clethrionomys rutilus*), b) northern collared lemming (*Dicrostonyx groenlandicus*), c) brown lemming (*Lemmus trimucronatus*), d) long-tailed vole (*Microtus longicaudus*), e) singing vole (*M. miurus*), f) root vole (*M. oeconomus*), g) meadow vole (*M. pennsylvanicus*), h) yellow-cheeked vole (*M. pennsylvanicus*), i) cinereus shrew (*Sorex cinereus*), j) pygmy shrew (*S. hoyi*), k) montane shrew (*S. monticolus*), l) American water shrew (*S. palustris*), m) tundra shrew (*S. tundrensis*), n) barren-ground shrew (*S. ugyunak*), o) Alaska tiny shrew (*S. yukonicus*), p) northern bog-lemming (*Synaptomys borealis*), q) meadow jumping mouse (*Zapus hudsonius*). Warm colors indicate region of high relative indices of occurrence (RIO), and cool colors indicate regions of low RIO.



(Appendix 5A continued)



(Appendix 5A continued)



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CHAPTER 6. CONCLUSIONS

The research presented here demonstrates the utility of machine-learning methods and open-access data to describe and predict changes to the trophic and geographic niche spaces of the small mammal fauna of Alaska. The resulting dietary niche quantifications, community assemblage patterns, isoscapes and spatial distribution models provide some of the first comprehensive baseline descriptions of small mammal niche spaces in Alaska using Geographic Information Systems (GIS). Projected future distribution models also depict predicted changes to the geographic patterns of species over the coming century. Results can be used to anticipate climate-induced changes to species occurrence and community assemblages in order to inform wildlife management and conserve biodiversity and ecosystem health in the North.

6.1. SMALL MAMMAL STABLE ISOTOPE ANALYSES

When small mammal diets were compared among species, considerable overlap occurred between the fundamental niche spaces of many Alaskan small mammals. Most species incorporated a variety of foods into their diets, but in different proportions (Chapter 2). Niche breadths of red-backed voles and root voles (*Microtus oeconomus*) were similar, but did not overlap entirely. The average fundamental dietary niche of red-backed voles consisted of a much larger proportion of fungi compared to root voles. Additionally, both of these species consumed more herbaceous material than other rodents with more varied diets (Chapter 2). CART analyses of continuous trophic positions indicated that red-backed voles, root voles, singing voles, meadow voles (*M. pennsylvanicus*), and yellow-cheeked voles (*M. xanthognathus*) had the most similar overall diets (Chapter 2). Stable isotope mixing models largely supported small mammal dietary patterns as determined through prior stomach content analyses (Lensink 1983; Bangs 1984; Batzli and Henttonen 1990, 1993; Bergman and Krebs 1993).

At the local scale, co-occurring small mammal species were more segregated in their use of available food resources with minimal amounts of overlap between the realized dietary niche spaces of co-occurring species (Chapter 2). Species appeared to be plastic in their use of resources, shifting away from foods that were also utilized by competitors, resulting in substantial niche partitioning (Holt 1993; Stewart et al. 2003; Amarasekare 2008; Soininen et al. 2013). This polarizing effect in dietary composition was best exemplified by red-backed voles

favoring more fungi and less herbaceous material, while sympatric root voles and singing voles (*Microtus miurus*) consumed more herbaceous plants and less fungi. This flexibility to adjust dietary proportions to minimize interspecific competition may provide a means for the coexistence of many species of small mammals in the same area (Churchfield et al. 1999; Morris 1996; Amarasekare 2008). This may also allow for the integration of new, invading species into communities as climate change and transitioning habitats result in novel species assemblages in the future.

6.2. SMALL MAMMAL DISTRIBUTIONS

Small mammal trapping efforts at 20 locations documented a wide diversity of species ($n = 17$, $\bar{x} = 3.3$ species/site) and highlighted northern red-backed voles as the most-commonly occurring species across Alaska. Root voles and singing voles were most frequently encountered as secondary or tertiary species, whereas cinereus shrews (*Sorex cinereus*) and tundra shrews (*S. tundrensis*) were the most common shrew species. An average species richness accumulation curve showed that even after 1,500 trap-nights, no asymptote in species richness had been reached. This means that efforts aimed at documenting the full complement of small mammal diversity in an area should exceed even the intense level of trapping employed here (McCain 2005; Thompson et al. 2007).

Geographic distribution models for 17 species of small mammal across Alaska were, on average, 75% accurate in predicting the number of species detected in the field (Chapter 3). These models represent some of the first, high-resolution (1 km²), statewide distribution assessments for the Alaskan small mammal fauna, and provide useful baselines for documenting landscape ecological change. Top model predictors at the geographic scale included a multivariate combination of *Soil Type*, *Ecoregion*, *Landfire Land-cover*, *December Sea Ice*, and *July Temperature*, indicating the importance of many interacting habitat and climatic conditions for predicting wildlife distributions.

Community *varclus* analysis parsed overlapping small mammal distributions into five community groups (cold-climate, northern, southern, interior, and continental) sharing similar regional distributions (Chapter 3). Some amount of overlap between community groups was common, however this classification provided an objective means for identifying dominant patterns in community membership and will be useful for tracking assemblage changes over

time. Summing all species distributions across the extent of Alaska, species richness was highest (11–13 species) throughout the Yukon-Tanana Uplands, an area previously not well recognized for its biodiversity value (Chapter 3). Other biodiversity hotspots occurred near the headwaters of the Kobuk and Noatak Rivers, and in Denali National Park. Statewide, the majority of lands with the highest small mammal diversity fell under the management of the State of Alaska, as well as the Bureau of Land Management (BLM), and regional Native corporations, especially Doyon Ltd. Spatial models presented here that detail species distributions, community arrangements, and biodiversity patterns provide an initial framework for monitoring and conserving wildlife distributions across Alaska over time.

6.3. ISOSCAPE MODELS

Using machine-learning to analyze stable isotope values from small mammals and their dominant food sources I created the first $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isoscape models explicit in space and time for rodents, shrews, grass, and fungi (Chapter 4). For all taxa, $\delta^{15}\text{N}$ isoscapes highlighted mid-elevations in the Yukon-Tanana Uplands, Brooks Range foothills, and the Yukon-Kuskokwim Delta as ‘hot-spots’ indicating where isotopic values were considerably higher than trophic baselines. Within these hotspots, fungi likely comprised a larger proportion of rodent diets than herbaceous plants. Models also identified a handful of localized hot-spots where $\delta^{15}\text{N}$ rodent levels were outside the range of what would be expected via trophic enrichment alone, indicating supplemental inputs of nitrogen with elevated $\delta^{15}\text{N}$ values to the system (Symes et al. 2013).

High elevation alpine areas in the Brooks Range and Yukon-Tanana Uplands as well as some lowland tundra regions were predicted as ‘cold-spots’ for all taxa (Chapter 4). Inter-isoscape comparisons between rodents and their main food sources also highlighted tundra-dominated habitats as areas where rodents likely maintained more graminoid-based diets instead of consuming fungi. Carbon isoscapes were less variable without consistent spatial patterns among taxa and by themselves were not as useful for identifying dietary inputs to consumers. A multivariate set of predictors including *Soil Geology*, *Landcover*, and *Ecoregion* were consistently among the most important contributors to the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isoscapes for all taxa, affirming the importance of the environment in determining isotopic values of both food sources and consumers (West et al. 2010).

I also produced the first map of modeled continuous trophic positions for rodents across Alaska (Chapter 4). Predicted trophic positions were highest in the Middle Yukon valley and lowest on the Beaufort Sea Coast, demonstrating the increased omnivory of rodents (Post 2002) and the complexity of trophic systems in the Alaskan interior versus coastal, terrestrial systems (Gilg et al. 2009). All of these new isoscapes can serve as isotopic baselines for future studies examining trophic position, food web complexity, niche overlap, and paleo-ecological conditions, and for identifying and monitoring regions undergoing environmental change (Bowen et al. 2010; Pardo and Nadelhoffer 2010; Pataki et al. 2010).

6.4. FUTURE DISTRIBUTION MODELS

Applying projected environmental changes (A2 scenario of downscaled regional IPCC climate projections) to the geographic niche spaces of small mammals yielded considerable directional and some compositional shifts in the distributions of species over the coming century (Chapter 5). Distributions of most members of the northern, cold-climate, and interior small mammal communities were predicted to decrease in area, shift northward, upward in elevation, and away from the coast, whereas the opposite was true for many species in the southern and continental communities. Many members of the southern and continental communities expanded their distributions, and also moved down in elevation and toward the coast, as they followed warmer, drier conditions more conducive for their persistence (Murphy et al. 2010).

Under the environmental scenarios of 2100, broad rearrangements of communities were not predicted to occur. Instead the composition of community assemblages remained robust for 15 of 17 species which moved together largely as community units, corresponding to underlying shifts in bioclimatic envelopes (Chapter 5). But individual species distributional shifts resulted in novel species assemblages in some regions including in the western Brooks Range and throughout the Alaska Range. Novel species interactions were predicted to occur at middle elevations in mountainous areas where a combination of varied topography and overlapping distributions provided for high species richness (Heaney 2001; McCain 2004; Novillo and Ojeda 2012). Presumably, new species invasions can also be expected along the southern and eastern borders of the state as continental species move towards Alaska.

Overall biodiversity patterns were similar in both the 2010 and 2100 models, but followed the general upward, northward, and inland movement trends of most species

distributions (Chapter 5). Biodiversity losses were most pronounced in the Yukon-Kuskokwim Delta, in central interior Alaska, as well as on the Seward Peninsula and in the eastern Brooks Range due to the projected extinction of many cold-climate and northern species like tundra shrews (*Sorex tundrensis*), barren-ground shrews (*Sorex ugyunak*), northern collared lemmings (*Dicrostonyx groenlandicus*), brown lemmings (*Lemmus trimucronatus*), and root voles. In contrast, the Beaufort Coastal Plain and western Brooks Range were projected to experience modest gains in species richness as the distributions of southern and continental species like meadow jumping mice (*Zapus hudsonius*), northern bog-lemmings (*Synaptomys borealis*), and American water shrews (*S. palustris*) move northward (Chapter 5).

Quantitative species distribution and biodiversity change projections should help land managers to develop adaptive strategies for conserving dispersal corridors and refugia that help to promote small mammal biodiversity and ecosystem functionality in the face of a changing climate (Lawler et al. 2003; Glick et al. 2011; Monzon et al. 2011). However, addressing only the symptoms of climate change by conserving existing hot-spots and corridors in the hopes that species will adapt will ultimately do little to stem biodiversity loss and ecological damage (Glick et al. 2011; Stein et al. 2013). In addition to promoting adaptive contingencies, conservation science must address the root causes of declining species persistence by reducing carbon emissions that are driving climate change and by conserving wildlife habitats (Bellard et al. 2012).

In order to observe changes in small mammal niche space over time and to validate the accuracy of predictions made here, it will be important to establish and maintain an integrated network of small mammal monitoring sites across the region. Documenting trends in biodiversity and stable isotope patterns of small mammals will ultimately provide a means for evaluating community and ecosystem health conducive for the continued persistence of small mammal species, ecosystem function, and human well-being as we move toward the 22nd century.

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