



High dietary and habitat diversity indicate generalist behaviors of northern bog lemmings *Synaptomys borealis* in Alaska, USA

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ABSTRACT: The northern bog lemming *Synaptomys borealis* (NBL) is a rare small mammal that is undergoing a federal Species Status Assessment (SSA) under the US Endangered Species Act. Despite a wide North American distribution, very little is known about NBL dietary or habitat needs, both of which are germane to the resiliency of this species to climate change. To quantify diet composition of NBL in Alaska, we used DNA metabarcoding from 59 archived specimens to describe the taxonomic richness and relative abundance of foods in recent diets. DNA analyses revealed a broad diet composed of at least 110 families and 92 genera of bryophytes (mosses and liverworts), graminoids, fungi, forbs, and woody shrubs. Nine bryophyte genera and *Carex* sedges composed the largest portions of NBL diets. To quantify habitat preference, we intersected 467 georeferenced occurrence records of NBL in Alaska with remotely sensed land cover classes and used a compositional analysis framework that accounts for the relative abundance of land cover types. We did not detect significant habitat preferences for specific land cover types, although NBL frequently occurred in evergreen forest, woody wetlands, and adjacent to water. Our research highlights the importance of bryophytes, among a high diversity of dietary components, and describes NBL as boreal habitat generalists. Results will inform the current federal SSA by quantifying the extent to which ecological constraints are likely to affect NBL in a rapidly changing boreal environment.

KEY WORDS: Boreal forest · Compositional analysis · Diet · US Endangered Species Act · Habitat preference · DNA metabarcoding · Rodents

1. INTRODUCTION

The northern bog lemming *Synaptomys borealis* (NBL) is a small rodent in North America that is rarely encountered in small mammal biodiversity surveys (Christian 1999, MacDonald & Cook 2009, Gotthardt et al. 2013, DuBois 2016, Benson 2019). Currently, it is considered a Species of Greatest Conservation Need by the State of Alaska (Alaska Department of Fish & Game 2015a) and is listed as

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‘imperiled’ in several other US states (Jones & Melton 2014). In 2014, a petition was filed to list the NBL under the US Endangered Species Act (ESA; Jones & Melton 2014), leading to a Species Status Assessment (SSA) that is currently underway to determine its conservation status.

The 2014 petition justified ESA listing due to the relative rarity of detection of NBL (especially in the contiguous USA), the patchy nature of its habitat, and current and future threats to its habitat (Jones &

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Melton 2014, USFWS 2015). Potential threats include: climate change-induced shifts in available habitat and food sources, industrial deforestation, grazing, wildfire, peat mining, and competitive interactions with novel species, including southern bog lemmings *S. cooperi* (Williams & Jackson 2007, Jones & Melton 2014, Rose & Linzey 2021, Droghini et al. 2022). Climate change is predicted to push boreal species such as NBL northward and upward in elevation, as climate-related biome shifts are increasing the amount of boreal forest at the leading edge of their range while simultaneously constricting their range at the trailing edge in the contiguous USA (Soja et al. 2007, Hope et al. 2013, 2015, Baltensperger & Huettmann 2015a,b). Since the 2014 petition, small-mammal experts in Alaska have identified climate-induced vegetation change as the most important threat to NBL (Droghini et al. 2022), yet little is known about their populations and capacity to adapt in the face of habitat loss or changing diet availability.

Unfortunately, the relative rarity of individuals makes traditional field study of NBL population trends (e.g. through mark–recapture) or obtaining even basic ecological information (e.g. diet, habitat use) difficult to quantify (Coffin & Pfannmuller 1988). For example, extensive sampling of small mammals at 20 locations across mainland Alaska resulted in the detection of only 5 NBL in over 30 700 trap-nights using Sherman, pitfall, and Museum Special snap traps (Baltensperger & Huettmann 2015a). Low trapping success has led to persistent data gaps in the literature regarding basic life history information, population trends, and perceived threats to persistence that are important to fill in order to inform the SSA and prioritize conservation needs (Alaska Department of Fish & Game 2015b, D. Vincent-Lang [ADFG] pers. comm. to K. Ott [USFWS], May 2022).

Quantifying both dietary and habitat needs is an important first step toward understanding NBL resilience to a rapidly changing climate (Clavel et al. 2011, Hof et al. 2012, Moritz & Agudo 2013) that is altering available foods, competitors, and habitats (Chapin et al. 2010, Stralberg et al. 2020). Based on previous life-history accounts documenting the consumption of a range of food items (e.g. grasses, sedges, mosses, fungi, berries, invertebrates) and use of numerous habitat types (e.g. peatlands, mossy forests, subalpine meadows, alpine tundra) NBL appear to be both habitat and dietary generalists (Banfield 1974, West 1999, Jones & Melton 2014, Baltensperger et al. 2018). Species that act as ecological generalists typically have advantages over specialists because of the flexibility that generalist habits

allow, buffering individuals from negative outcomes and imparting greater flexibility as habitats change under rapid environmental and anthropogenic change (Blois et al. 2013, Moritz & Agudo 2013). To date, no research has used recent technology to quantify NBL habits to confirm generalist or specialist tendencies.

Although no formal quantification of NBL diet exists, isotope analysis of hair collected from a small sample of individuals revealed the possibility that NBL may occupy the broadest dietary niche of any small mammal in Alaska (Baltensperger et al. 2015), whereas other diet information is limited to descriptive observations only (Layser & Burke 1973, Godin 1977, Jones & Birney 1988, West 1999). Likewise, habitat use by NBL remains poorly understood, particularly at broad regional scales, such as within Alaska (Jones & Birney 1988, Alaska Department of Fish & Game 2015b, Baltensperger et al. 2018). Descriptions of habitat use at local scales suggest potential preference for cool, damp, moss-covered conifer forests and bogs (Layser & Burke 1973, Godin 1977, Jones & Birney 1988, West 1999), which are drying in a warmer climate regime (Dial et al. 2007, Ives et al. 2013)

Here we applied DNA metabarcoding and geospatial land cover analyses to quantify NBL dietary and habitat preferences, respectively. DNA metabarcoding provides the opportunity to quantify small mammal diets in detail, particularly for species that are difficult to capture, but small mammal studies have yet to employ this method widely (de Sousa et al. 2019). This technique uses DNA from fecal pellets to identify consumed taxa (Soininen et al. 2013a,b, 2014, 2015, Shively et al. 2018, Cloutier et al. 2019). Quantification via metabarcoding will help to determine the extent to which NBL are unique in having a broad diet, relative to other more common species in Alaska and the circumpolar boreal forest. A broad diet may enable individuals and populations to be more resilient to habitat shifts and interspecific competition associated with rapid environmental change (Morris 1996, Baltensperger et al. 2015, Kortsch et al. 2015). Likewise, a more comprehensive analysis of the types of habitat associated with occurrence records can aid assessments of how climate-driven change in habitat types may impact NBL (Droghini et al. 2022).

Our study had 2 objectives aimed at informing the SSA process for NBL: (1) quantify the diet composition and relative abundance of foods from individuals in Alaska, and (2) use NBL occurrence records to quantify habitat associations relative to the composition of land cover types available in boreal Alaska. Both objectives provide essential baseline informa-

tion relevant to evaluating the extent to which NBL exhibit generalist habits and their potential resilience to climate change and other stressors.

2. MATERIALS AND METHODS

2.1. Diet

We collected fecal samples from 59 NBL (31 female, 28 male) specimens, collected between 1996 and 2008, preserved in ethanol, and archived at the University of Alaska Museum of the North (arctos.database.museum; Table S4). Samples were balanced by sex and geography across Alaska to avoid multiple specimens from the same collection location (Fig. 1). We extracted 3–5 fecal pellets (composing 1 sample) from the intestines of each specimen, preserved the pellets in 95% ethanol, and sent them to a

commercial lab (Jonah Ventures, Boulder, Colorado, USA; jonahventures.com) for analysis. Pellet samples were not homogenized, but all individual pellet surfaces were swabbed to gather DNA for metabarcoding to detect the presence and frequency of vascular plant, non-vascular plant, and fungal DNA. High-throughput sequencing of the chloroplast *trnL* intron was used to determine the taxonomic composition of dietary items from pellets (Craine et al. 2015). Samples were read an average of 14 584 times, (range = 283–27 618) in a single PCR run. Sequences were assigned to dietary taxa by comparing public sequence databases that included 450 000 species (GenBank; ncbi.nlm.nih.gov/genbank). Sequences were clustered into operational taxonomic units (OTUs) with a standard $\geq 97\%$ base pair matching to an individual gene sequence (Craine et al. 2015, Schuette et al. 2022). We obtained family and genus names associated with each match from the National Center for Bio-

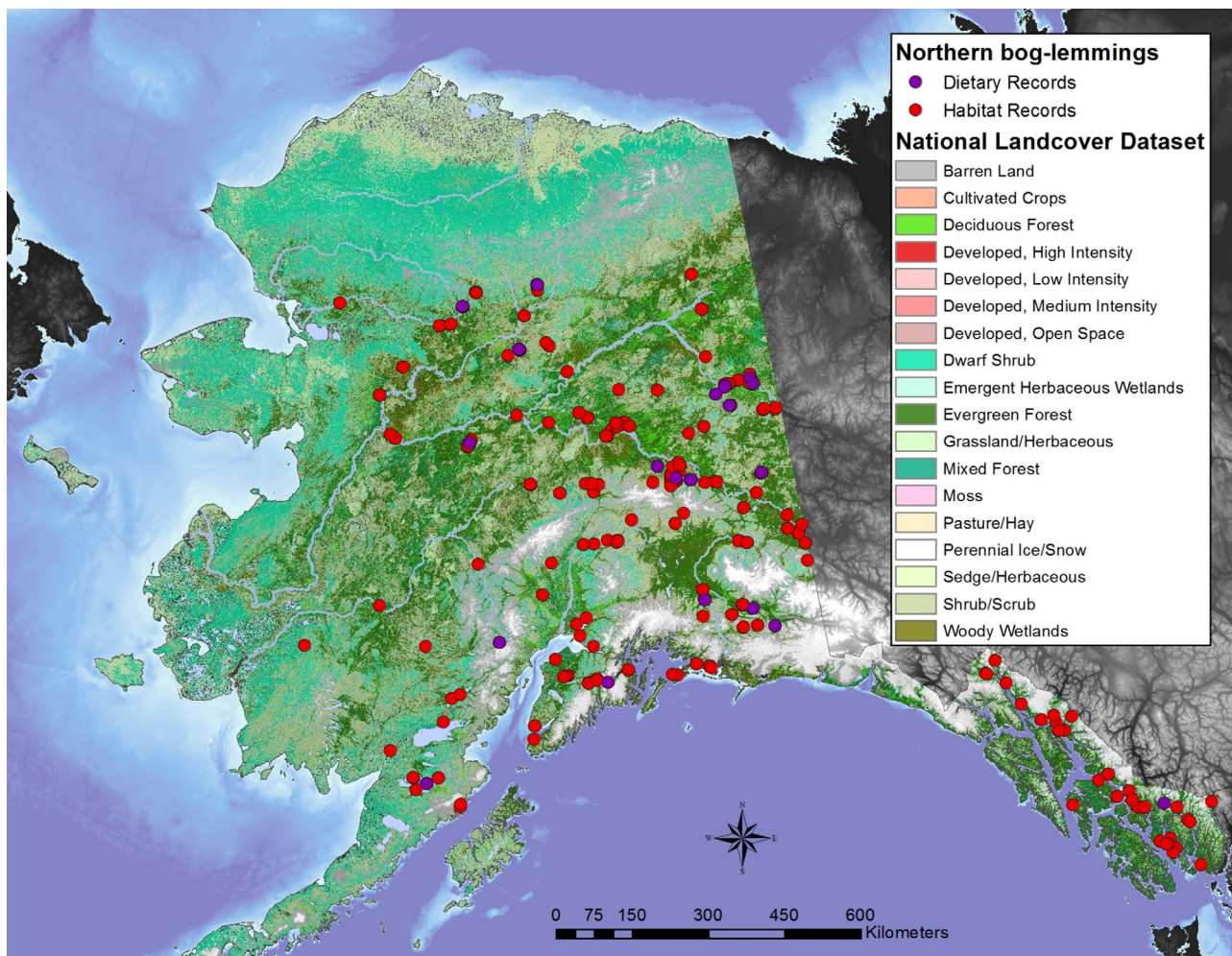


Fig. 1. Northern bog lemming *Synaptomys borealis* records used in dietary analyses ($n = 59$; purple) and in habitat preference analyses ($n = 467$; red and purple) in relation to the 2011 National Land Cover Database (Homer et al. 2015) in Alaska

technology Information (NCBI) to populate the OTU taxonomy assignment lists. Frequencies and proportional abundances were calculated for each vascular plant, non-vascular plant, and fungal OTU (Edgar 2013). Output received from the lab included both an occurrence list and abundance count of plant and fungi OTUs per fecal sample, which corresponded to individual bog lemming specimens collected in Alaska.

We used the 'vegan' (Oksanen et al. 2020) and 'BiodiversityR' (Kindt 2022) packages in R version 4.4.1 (R Core Team 2021) to calculate dietary richness and per-sample, proportional abundance of plants and fungi to taxonomic family and genus (Kindt & Coe 2005). We divided the frequency of detections for each family or genus by the total number of families or genera in each sample to yield proportional abundances. We defined 'dietary richness' as the number of unique families or genera detected per fecal sample, and 'proportional abundance' as the proportional representation of each family or genus in each sample.

We cross-referenced families and genera identified via DNA metabarcoding against native occurrences of taxa in Alaska using Global Biodiversity Information Facility (GBIF; GBIF.org 7 March 2022) records and statewide taxa lists (Nawrocki et al. 2020). We followed recommended protocols from Jonah Ventures' laboratory and other investigators and removed the following data from analysis: (1) OTU sequences with <40 total reads, (2) taxonomic families and genera with only a single occurrence in the pooled sample set, and (3) families and genera that did not match taxa known to occur in Alaska (Craine et al. 2015, Kartzinel et al. 2015, Jorns et al. 2020, Schuette et al. 2022). These 3 criteria resulted in a more conservative array of items in the diet versus using all detections with ≥ 1 OTU reads and sufficient DNA matching.

We ranked functional groups, families, and genera by mean abundance per sample and by frequency of detection across samples. We used the 'vegan' package to scale the mean abundance for each functional group, by dividing its abundance by the sum across functional groups, yielding proportional consumption rates (0–100%) for each functional group relative to the full data set. This analysis was conducted for both the family- and genus-level data sets. We also calculated the Chao diversity index (a non-parametric estimation of Shannon's diversity index that accounts for unequal detection probability (Chao & Shen 2003) by collection location to quantify site-specific variation in diversity by genus, the most detailed taxonomic level in our analyses.

In ArcGIS 10.8 (ESRI), we paired each NBL occurrence record with a set of environmental parameters (uaf-snap.org), including the year of collection, latitude, elevation, mean maximum and minimum precipitation, mean maximum and minimum temperature, and distance to water at collection locations using the 'Extract Multi Values to Points' tool. We used general linear regression ('glm' package in R) to relate dietary richness to the above variables to identify statistically significant (at $\alpha = 0.05$) dietary trends in relation to environmental gradients hypothesized to influence the availability and diversity of food sources in Alaska. We did not analyze data at the species level because of the high proportion of missing taxonomic identifications in our data set.

2.2. Habitat

We assessed habitat preference of NBL in Alaska using a set of georeferenced records and the 2011 National Land Cover Database (NLCD; Homer et al. 2015; usgs.gov/programs/national-geospatial-program/land-cover) which provided the best land cover information for Alaska currently available at the statewide scale. To account for the relative availability of land cover types, we conducted a compositional analysis (Aebischer et al. 1993) for Alaska using 2011 NLCD data and 467 georeferenced NBL records from GBIF, collected in Alaska between 2000 and 2021. This approach compared habitat types associated with georeferenced NBL records relative to the available land cover composition as a means of detecting habitat preference (Aebischer et al. 1993, Boyce & McDonald 1999).

While resource-selection functions that compare both availability and individual use of land cover types within individual home ranges may provide better resolution on individual habitat preference, such analyses are not appropriate at the population level (Boyce & McDonald 1999). Instead, our analyses resolved the degree to which NBL in Alaska prefer multiple habitats (i.e. act as habitat generalists with flexible ecological needs), or prefer specific habitat types (i.e. act as habitat specialists with specific ecological requirements). To simplify land cover classes for the compositional analysis, we consolidated 20 NLCD land cover classes into 12 classes by combining 4 Developed intensity classes into a single 'Developed' class; Pasture/Hay and Cultivated into 'Cultivated'; Sedge/Herbaceous and Grassland/Herbaceous into 'Herbaceous Grassland'; and Barren Land, Perennial Ice/Snow, and Unclassified into 'Barren/Ice/Snow'. Consolidated classes represented

land cover types that contained <1% of NBL occurrences in Alaska.

For the compositional analysis, we used ArcGIS 10.8 to intersect NBL records with the modified NLCD land cover classes to quantify frequency of use, then calculated the area of each class within the minimum bounding geometry of all georeferenced NBL records in Alaska to quantify area availability. We calculated proportional use and proportional availability of each land cover class in ArcGIS and used the 'adehabitatHS' package (Calenge 2006) in R version 4.4.1 (R Core Team 2021) with the 'widesI' parameter for populations to calculate proportional use versus proportional availability by class to identify disproportionate preference of land cover classes by NBL in Alaska. We used 'adehabitatHS' to calculate W_i , the Manly selectivity measure (i.e. resource selection ratio = used/available), and $B_i = W_i/\sum(W_i)$, indicating relative selection by land cover class. Classes were ranked by importance using B_i , and we assessed statistical significance at $\alpha = 0.05$.

3. RESULTS

3.1. Diet

Of 91 273 OTUs with ≥ 1 detection, 82.0% exhibited $\geq 97\%$ base pair matching to an individual gene sequence at the family level, 71.9% to genus, and 50.4% to species, which resulted in a broad array of putative dietary items (7 phyla, 112 orders, 235 families, 405 genera, and 447 species). However, after applying the 3 minimum criteria we identified for inclusion in the data set (see Section 2.1), a more conservative list emerged. Specifically, we detected at least 110 families and 92 genera of vascular, non-vascular, and fungal taxa as consumed by NBL in Alaska (Fig. 2). Detected families included 78 fungi, 15 bryophytes, 9 forbs (flowering herbs), 5 woody shrubs, and 3 graminoids (sedges and grasses; Figs. 2 & 3).

Fecal samples were diverse and not typically dominated by any individual family (mean = 4.2%; SD = 10.4%; range: 0.1–80.7%; Fig. 2a), although bryophyte families were the single largest dietary component at 48% of NBL collection locations (1.3–91.6%; Fig. 3a). Among fecal samples, bryophyte families were most abundant (per-sample mean \pm SD = 13.4 \pm 19.3%, scaled proportion = 44.7%, $n = 207$) and 1.5 times more abundant than graminoids (per-sample mean = 8.8 \pm 12.7%, scaled proportion = 29.3%, $n =$

80). Bryophytes were also 4 times more abundant than both woody shrubs (per-sample mean = 3.5 \pm 4.6%, scaled proportion = 11.7%, $n = 35$) and forbs (per-sample mean = 3.1 \pm 0.7%, scaled proportion = 10.3%, $n = 50$), and 11 times more abundant than fungi families (per-sample mean = 1.2 \pm 2.1%, scaled proportion = 3.9%, $n = 743$).

Eight families accounted for an average abundance >10% of detected dietary items per fecal sample (Fig. 2a), 6 of which were bryophyte families: Bartramiaceae, Rhabdoweisiaceae, Polytrichaceae, Aulacomniaceae, Hylocomiaceae, and Funariaceae. Cyperaceae sedges and Comandraceae (a parasitic family of forbs) also composed large proportions of diet samples at the family level (Fig. 2a). Among the most frequently detected taxa across samples were the fungal families Bulleribasidiaceae, Psathyrellaceae, Cortinariaceae, and Didymellaceae, although all occurred in low abundances (Fig. 2a). We also frequently detected the bryophyte families Aulacomniaceae, Rhabdoweisiaceae, and Polytrichaceae, and the graminoid families Cyperaceae and Poaceae (Fig. 2a). Only Aulacomniaceae and Cyperaceae were both frequently detected and composed large portions of average fecal samples (Fig. 2; Table S1 in the Supplement at www.int-res.com/articles/suppl/n049p145_supp.xlsx).

At the genus level, proportional abundance within individual samples was also generally low (mean = 4.0 \pm 9.9%; 0.1–80.7%), but in 17% of fecal samples, bryophytes and graminoids composed 50–81% of the taxonomic detections and were the main dietary components at 16 of 24 collection sites using the genus-level data set (0–98.8%; Fig. 3b). Three bryophyte genera composed, on average, >15% of detected dietary items within fecal samples (Fig. 2b; *Anacolia*, *Pleurozium*, and *Hylocomium*). Other abundant dietary components included the bryophyte genera *Polytrichum*, *Aulacomnium*, and *Funaria*, as well as *Carex* sedges. The most commonly detected genera within samples were the bryophytes *Aulacomnium* and *Polytrichum*. We also frequently detected *Carex* sedges, as well as *Cortinarius* fungi and *Vishniacozyma* yeasts, but the latter 2 occurred in low abundances (Fig. 2b; Table S1).

We did not detect any statistically significant relationships between dietary richness (response) at the family or genus level and temporal or environmental variables we analyzed (Table 1). Only one land cover class (shrub/scrub) showed a marginal level of statistical significance relative to diet (Table 1). Chao diversity indices showed a wide range of genus richness at 24 sample locations (2.3–221.5), with high

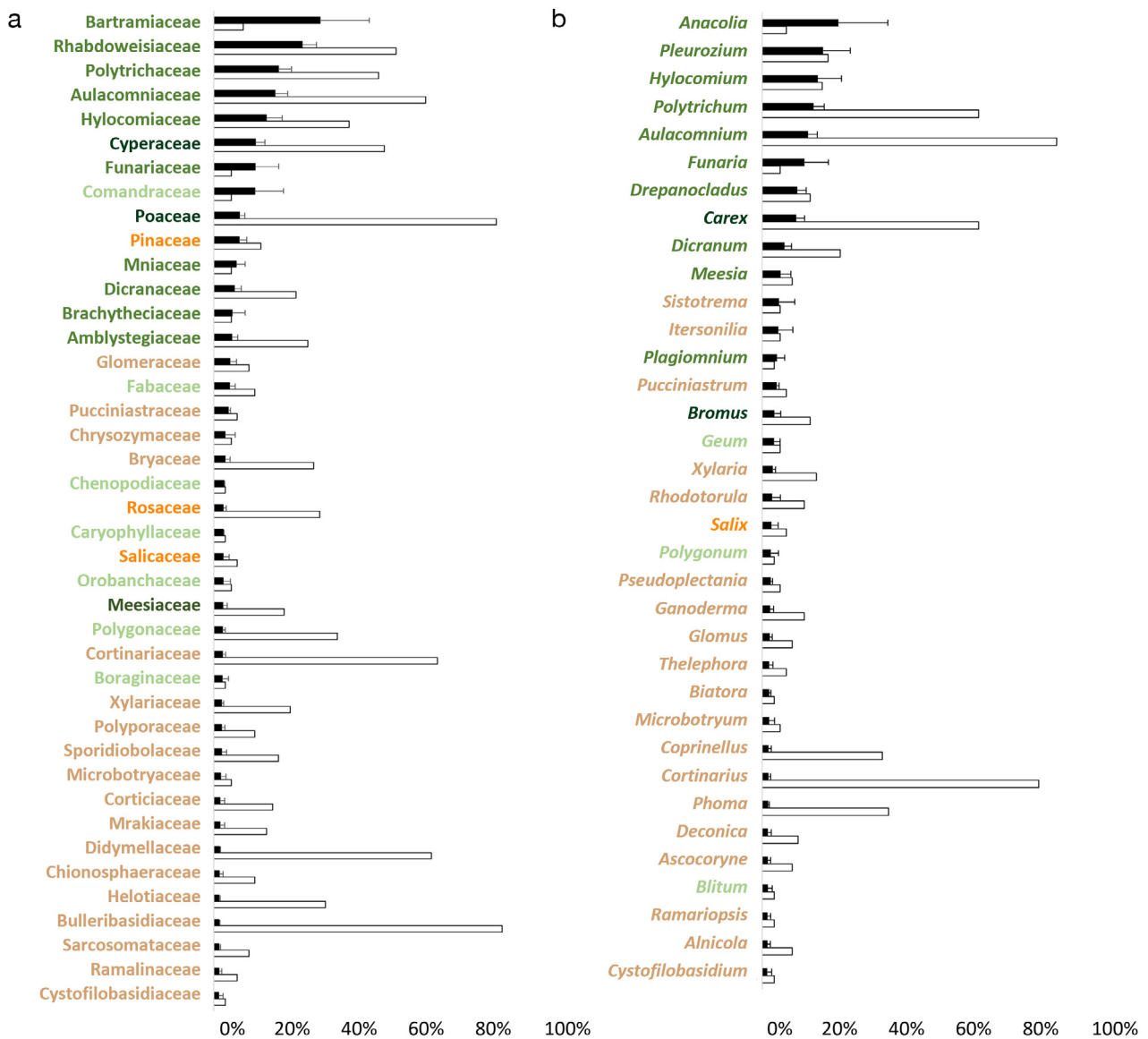


Fig. 2. Mean detected abundance per sample (>1.5%; black bars) and frequency of detections across samples (n ≥ 2; white bars) of bryophytes (green), graminoids (dark green), forbs (light green), woody plants (orange), and fungi (brown; order of colors is from top to bottom) by (a) family and (b) genus in fecal samples from 59 northern bog lemming *Synaptomys borealis* specimens collected in Alaska and analyzed using DNA metabarcoding. Error bars indicate SE

variability around those estimates and no discernible relationship with latitude ($0.9 \leq SE \leq 214.6$; Fig. 4).

3.2. Habitat

NBL records in Alaska occurred in a variety of land cover types, from low elevation (18 m) wetlands to upland evergreen forests to alpine shrub tundra (1418 m). Evergreen forest and shrub/scrub land cover classes accounted for a simple majority (57%) of occurrences. However, compositional analysis did

not detect any significant association between NBL occurrence and any of the major land cover types (Fig. 5). Nonetheless, several patterns were evident. First, Alaska records of NBL most frequently occurred in evergreen forest, followed by shrublands, woody wetlands, and adjacent to open water (Fig. 5). Second, open water and woody wetlands had the highest selection ratios of those habitats with >1% availability on the landscape, suggesting a tendency for greater use; a similar pattern was evident for evergreen forest, deciduous forest, and developed areas (Fig. 5). Third, the opposite pattern of

marginally less use relative to availability was evident for shrubs, herbaceous grassland, mixed forest, dwarf shrub, and barren ice/snow (Figs. 1 & 5). Finally, although developed and cultivated land cover classes had the highest relative selection ratios (B_i), together they composed <1% of total available area.

4. DISCUSSION

4.1. Dietary diversity

Our DNA metabarcoding analyses fill important data gaps in NBL ecology (Alaska Department of Fish & Game 2015b) as germane to the current federal SSA under the ESA. Results indicated that NBL in Alaska consumed at least 110 families and 92 genera of non-vascular plants, vascular plants, and fungi, with bryophytes and graminoids consumed in the highest abundance (Figs. 2 & 3; Tables S1–S3). Family richness of NBL diets in Alaska was 2–7 times larger than in other northern rodent species (discussed below) also analyzed using DNA metabarcoding ($n = 7$, mean = 29.0, range: 15–74 families), and genus richness was larger than average results from the literature ($n = 5$, mean = 61.8, range: 23–126 genera; Soininen et al. 2013a,b, 2014, 2015, Iwanowicz et al. 2016, Goldberg et al. 2020, Schuette et al. 2022).

Our results therefore indicate that NBL diets are at least as diverse as other northern rodent species deemed as generalists using DNA metabarcoding. The only other known metabarcoding diet investigation of a rodent (arctic ground squirrel *Urocitellus parryi*) in Alaska showed that island populations consumed at least 40 plant families (Schuette et al. 2022). In Arctic Canada, diets of brown lemmings *Lemmus trimucronatus* and collared lemmings *Dicrostonyx groenlandicus* included 24 and 15 families, respectively (Soininen et al. 2015). It is important to note that the large number of families in NBL diets was partially attributable to fungi ($n = 78$ families), whereas most previous studies quantified plants only (but see Soininen et al. 2013a; $n = 9$ fungi families). When only plant families are consid-

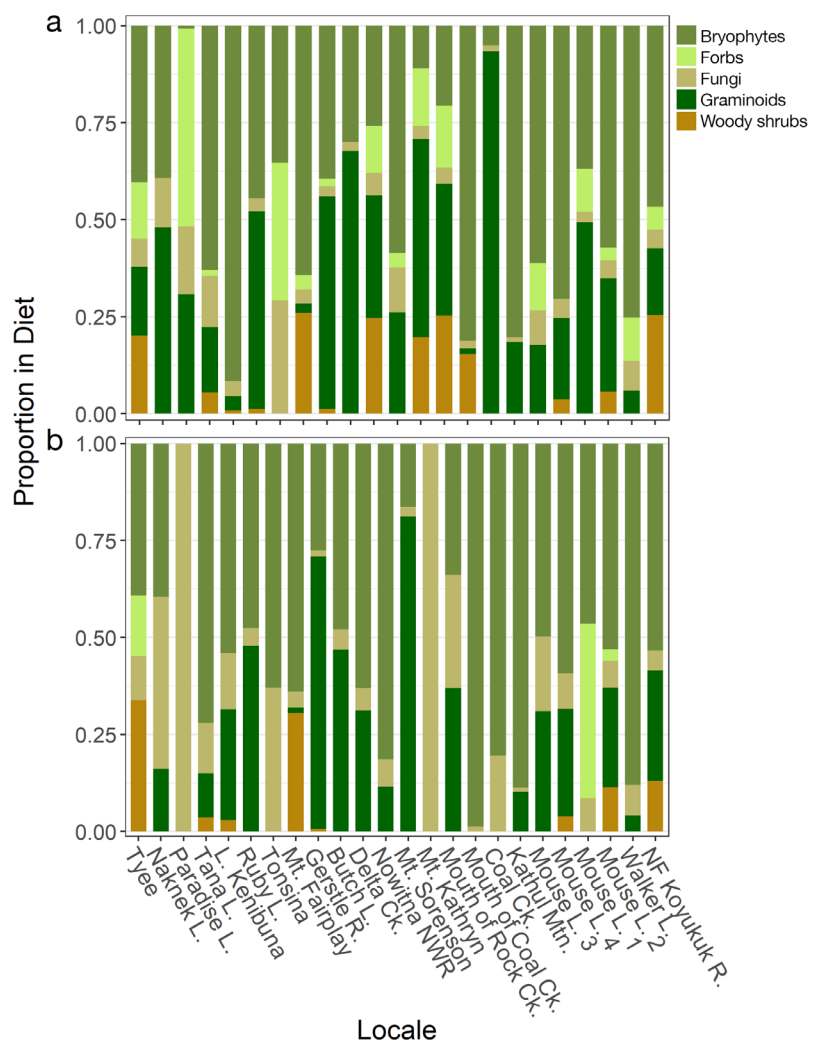


Fig. 3. Proportion of functional groups detected in fecal samples of 59 northern bog lemming *Synaptomys borealis* specimens collected in Alaska at (a) 23 locations to family and (b) at 24 locations to genus. Sites are arranged by increasing latitude. Data are limited to those identified to families and genera with ≥ 2 detections. R: River; Ck: Creek; L: Lake; Mt: Mount; Mtn: Mountain; NF: North Fork; NWR: National Wildlife Refuge

ered, NBL family richness ($n = 32$ families) is similar to the mean richness ($n = 29$ families) reported for other northern rodents (Soininen et al. 2013a,b, 2014, 2015, Goldberg et al. 2020, Schuette et al. 2022). Most fungi in our analysis were identified to family, but far fewer were identified to genus (while others have not yet been classified to family).

Southern bog lemmings, though not yet analyzed with metabarcoding, are also considered to have generalist diets (Linzey 1984, Rose & Ford 2012, Rose & Linzey 2021). Rose & Ford (2012) documented seasonal shifts in the proportions of low-nutrient foods including graminoids, herbaceous plants, woody stems, fungi, and berries, as well as small amounts of

Table 1. Statistical results for linear regressions of family and genus richness against year, elevation, latitude, maximum temperature, minimum temperature, precipitation, proximity to water, and 6 land cover types, where the estimate (β) is the effect size and t is the test statistic; results are considered significant at $p < 0.05$

Variable	Family richness				Genus richness			
	Estimate	SE	t	p	Estimate	SE	t	p
Year	-0.09	0.13	-0.68	0.50	-0.15	0.10	-1.45	0.15
Latitude	0.16	0.17	0.92	0.36	0.15	0.14	1.10	0.28
Elevation	<0.01	<0.01	0.66	0.51	>0.01	<0.01	0.02	0.98
Distance to water	<0.01	<0.01	0.59	0.56	<0.01	<0.01	0.56	0.58
Mean precipitation	<0.01	<0.01	-0.54	0.59	>-0.01	<0.01	-0.41	0.69
Min. temperature	>-0.01	<0.01	-0.53	0.59	>-0.01	<0.01	-0.80	0.42
Max. temperature	>-0.01	<0.01	-1.50	0.13	>-0.01	<0.01	-1.30	0.20
Deciduous forest	1.02	2.30	0.44	0.66	2.20	2.17	1.01	0.31
Dwarf shrub	0.27	3.75	0.07	0.94	-0.38	2.84	-0.13	0.90
Evergreen forest	2.06	1.65	1.25	0.21	2.30	1.57	1.47	0.14
Herbaceous grassland	2.43	3.34	0.73	0.47	4.29	2.84	1.51	0.13
Shrub/scrub	2.87	1.67	1.72	0.09	2.73	1.58	1.72	0.09
Woody wetlands	1.04	2.5	0.42	0.68	0.46	2.27	0.20	0.84

mosses, lichens, and sphagnum, especially in winter. Interestingly, following the experimental removal of meadow voles *Microtus pennsylvanicus*, a dominant competitor, southern bog lemmings expanded their diet to include greater proportions of more nutritious plants (Linzey 1984, Rose & Linzey 2021). If a similar effect applies to NBL, competitive exclusion may help to explain their generalist habits and low population densities across their range.

The diverse diet of NBL is also consistent with previous investigations that demonstrated a unique dietary composition and broad niche breadth for NBL, which overlapped little with other co-occurring species (Baltensperger et al. 2015). Although Alaska populations primarily consume a range of bryophyte

families and genera (discussed in Section 4.2), dietary diversity of NBL remains quite high due to ingestion of a variety of vascular plants and fungi in smaller amounts. Baltensperger et al. (2015) previously suggested that the isotopic position of NBL samples in $\delta^{15}\text{N}$ space highlighted a mixed consumption of herbaceous plants and fungi, whereas the broad ranges in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated that NBL also consumed mosses, lichens, and/or woody plants. Our metabarcoding results verify this broad dietary diversity, which we hypothesize confers resilience to rapid environmental change and interspecific competition by allowing wider flexibility in food and habitat choice (Hof et al. 2012, Lurgi et al. 2012, Moritz & Agudo 2013).

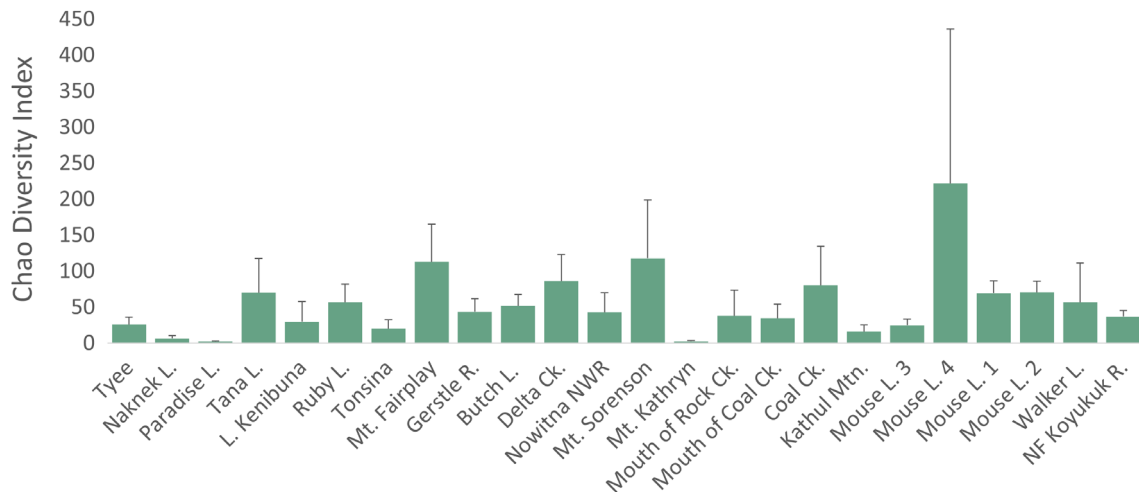


Fig. 4. Chao indices describing genus-level diversity of 59 northern bog lemming *Synaptomys borealis* diets at 24 collection locations in Alaska, arranged by increasing latitude. Error bars indicate SE

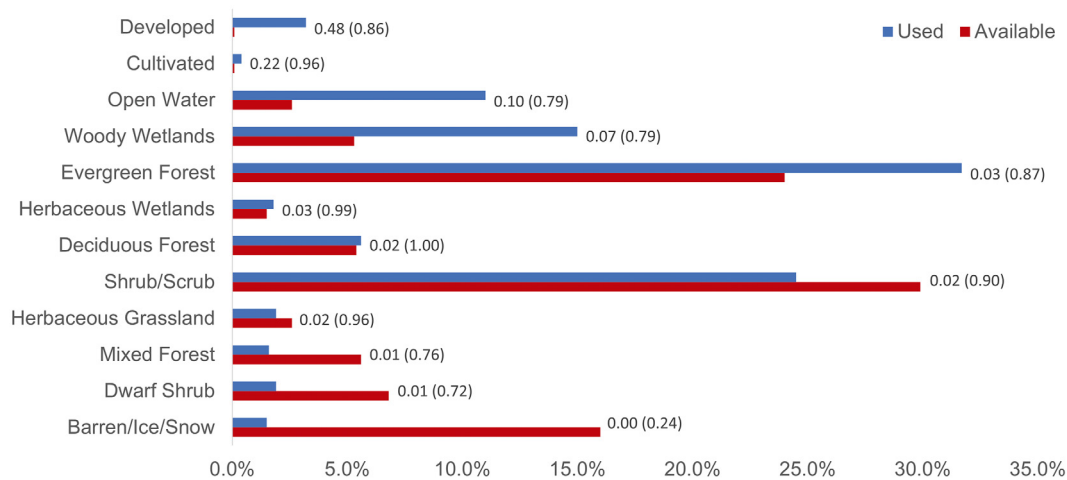


Fig. 5. Proportional use and proportional availability of 12 land cover classes in a compositional analysis of habitat preference for 467 georeferenced northern bog lemming *Synaptomys borealis* records in Alaska. Labels indicate the relative selection by land cover class (B_i), equal to $W_i/\sum(W_i)$, where W_i is the calculated Manly selectivity ratio; p-values are given in parentheses ($\alpha = 0.05$). Land cover classes were adapted from the 2011 National Land Cover Database (Homer et al. 2015) as described in Section 2

4.2. Bryophytes

Bryophytes (mainly mosses) composed the largest average portions of NBL diets (13.4%; Figs. 2 & 3), followed by graminoids (especially the sedge genus *Carex*). Bryophytes are also expected in habitats where NBL frequently occurred in Alaska, such as open-water areas and woody wetlands (see Section 4.5). Two bryophyte genera (*Aulacomnium* and *Polytrichum*) were among the most frequently detected foods in diets of the 59 individuals we sampled. These and other bryophytes (e.g. *Anacolia*, *Pleurozium*, and *Hylocomium*) consumed in the highest abundances are common in Alaska and across the boreal forest (Nawrocki et al. 2020; GBIF.org 11 February 2021, arctosdb.org). The high incidence and proportional abundance of mosses, both in fecal samples and at sampling locations, further highlights the outsized importance of bryophytes as a food for NBL.

The marked affinity of NBL for bryophytes appears to be unrivaled among rodents (Hansson 1970, 1971, Prins 1982, Soininen et al. 2013a,b, 2015). Our analysis showed that, on average, proportional consumption of bryophytes was 44.7%, relative to other functional groups (Fig. 3). Bryophytes are not considered especially nutritious, given their high lignin content, so they do not normally compose large dietary proportions, except in some species that inhabit cold environments (Prins 1982). Bryophytes composed 26% of the diet in overwintering brown lemmings in the Northwest Territories, Canada (Rodgers & Lewis 1986), the highest proportion for rodents reported in the lit-

erature, which was still 1.7 times less than what we quantified for NBL. Furthermore, bryophytes composed <1% of diets for other northern rodent species including collared lemmings in Nunavut, Canada (Soininen et al. 2015), and bank voles *Myodes glareolus*, wood mice *Apodemus sylvaticus*, and field voles *Microtis agrestis* in southern Sweden (Hansson 1970, 1971).

One possible reason for the consumption of bryophytes in cold environments is that mosses are high in arachidonic acid. This polyunsaturated fatty acid cannot be obtained in vascular plants, and it may afford boreal rodents protection against the cold (Prins 1982). While increased cold-tolerance could help explain the consumption of bryophytes in large amounts by some northern species, such as lemmings, this explanation fails to address the general lack of bryophytes as a significant dietary item in other species (Soininen et al. 2013a, 2015). Dietary niche segregation is an alternate mechanism that could account for high bryophyte consumption relative to other co-occurring species (Baltensperger et al. 2015). Physiological studies aimed at understanding the mechanisms and benefits of a bryophyte-heavy diet are needed.

4.3. Vascular plants and fungi

In addition to bryophytes, NBL in Alaska consumed high proportions of graminoids (particularly *Carex* sedges; mean \pm SE = 9.7 ± 2.3 % per sample; Figs. 2b & 3) from among the more than 50 *Carex* species found in a range of mesic and tundra habitats in

Alaska, including both open-water and woody wetland land cover classes that we examined (Tande & Lipkin 2003). *Carex* was by far the most common vascular plant genus detected and composed the largest portions of vascular plants in NBL samples. *Salix* (willows) were the only commonly consumed woody plants, but these were considerably less common than bryophytes, graminoids, and fungi (Figs. 2 & 3). For comparison, metabarcoding studies of brown lemmings and collared lemmings in Arctic Canada identified the primary consumption of willows (Salicaceae) and one family of graminoid (Poaceae; Soininen et al. 2015). We frequently detected Poaceae in our analysis and it was the second-most consumed family of vascular plants after another graminoid family, Cyperaceae. Finally, the only forbs detected in our analysis belonged to the family Comandraceae, but because identifications to genus did not match known Alaskan taxa, we cannot be certain of its taxonomic identification or importance beyond the family level.

Fungi represented a smaller proportion (1.2%) of NBL diets in Alaska. The genus *Cortinarius* produces fruiting bodies that NBL may consume, and it was the second-most commonly detected genus of fungus after *Vishniacozyma*. Many, but not all, species of *Cortinarius* contain the neurotoxin orellanine, which can be fatal to humans (Laurson & Seppelt 2010). NBL consumption of *Cortinarius* therefore suggests that individuals may be capable of avoiding toxic species or that they are perhaps physiologically tolerant to small amounts of orellanine. Other fungi identified in our analysis included yeasts, cankers, rusts, and parasitic or mycorrhizal fungi lacking macroscopic fruiting bodies (e.g. *Vishniacozyma*, *Rhodotorula*, *Phoma*). There are 3 plausible explanations for these groups: (1) they may have been consumed incidentally with other foods, (2) they occur naturally in the intestinal tracts of NBL, or (3) they entered samples as laboratory contaminants (de Sousa et al. 2019). The yeast *Vishniacozyma*, for example, is commonly associated with household dust (Izawa et al. 2020), and we cannot exclude it as a potential contaminant from the lab. Some *Vishniacozyma* yeasts (e.g. *V. ellesmerensis*) can survive sub-freezing temperatures and have been detected in Arctic Canada (Tsuji et al. 2019), but it is unknown whether this genus occurs in Alaska, outside of anthropogenic environments.

4.4. Caveats to DNA metabarcoding

While DNA metabarcoding offers new, high-resolution insight into the diets of species that are

difficult to study, it does have some limitations. First, accurate identification of taxa depends on the quality and completeness of the reference database used to match genetic sequences to taxa at increasingly detailed taxonomic levels. We used the GenBank database, which includes sequences for ~450 000 plant, fungi, and animal species to match diet sequences. The Checklist of Vascular Plants, Bryophytes, Lichens, and Lichenicolous Fungi of Alaska (Nawrocki et al. 2020), which we used to identify the presence of taxa in Alaska, contains 5505 accepted taxa, 17% of which currently do not have sequences in GenBank. If taxa do not occur in GenBank, sequences are still paired with the most similar sequenced taxon that exceeds the 97% base pair match threshold. However, since we lack sequences for all taxa in Alaska, it is difficult to determine whether taxonomic matches are accurate or whether they represent false positive matches to the closest available taxon (Harris 2003). False positives are especially problematic for understudied regions (e.g. high latitudes) or those with high diversity (e.g. tropics; de Sousa et al. 2019) and often occur more frequently in understudied taxa, such as fungi and bryophytes, where taxonomic information is incomplete (Osmundson et al. 2013). Furthermore, the proportions of some foods may be underrepresented in metabarcoding results because of differences in digestibility since the proportions of small mammal diets can show variable and sometimes weak correlations under laboratory conditions (Neby et al. 2021). Inter-specific field comparisons of dietary proportions derived from metabarcoding should therefore be interpreted with caution, due to a lack of experimental controls.

Although most field investigations lack laboratory data, it is essential to control for the many ways in which uncertainty can be introduced into results. An important first step is to validate all taxa identified in diets using local herbarium records and to work closely with regional botanical experts capable of recognizing spurious matches at all taxonomic levels. For example, we eliminated 84 family and 239 genus identifications because taxa did not occur in or were improbable for Alaska (e.g. Cactaceae, Cucurbitaceae, *Musa*, *Eriogonum*, *Comandra*). We believe false positives or taxa not classified to species may explain the relatively low percentages of matched OTUs in our data set (see Section 3), but without a complete checklist of Alaska taxa in GenBank, it is currently impossible to distinguish between taxa that result from false positives and those resulting from accidental DNA contamination (e.g. during sample

collection or processing). It would be especially useful to increase focus on genomic sequencing of regionally available taxa in Alaska and elsewhere, especially fungi and bryophytes, to bolster reference libraries and thereby reduce uncertainty by increasing the proportion of identifiable and correctly matched sequences.

4.5. Habitat preference

NBL occurred across Alaska in proportion with all land cover classes, according to the compositional analysis (Fig. 5). This suggests that this species is a generalist at the landscape scale, capable of existing in a variety of land cover types at low densities, similar to the habitat preference of southern bog lemmings (Stephens & Anderson 2014, Rose & Linzey 2021). Marginally disproportionate use of open water and woody wetlands, as well as frequent detections in upland forest and alpine shrub classes, corresponds well with previously documented habitat affinities (Banfield 1974, Pearson 1991, West 1999). Our results were also consistent with a broader analysis (Baltensperger et al. 2018) that classified NBL occurrences by habitat type at the continental scale using the land cover data set that we employed here (2011 NLCD), as well as 2 others, the North American Land Change Monitoring System (Homer et al. 2015), and the Alaska Vegetation and Wetland Composite (accscatalog.uaa.alaska.edu/dataset/alaska-vegetation-and-wetland-composite). Baltensperger et al. (2018) showed a higher frequency of NBL in evergreen forest, shrub/scrub, woody wetlands, and adjacent to open water, relative to other land cover types. Despite large relative selection ratios (B_i) for developed and cultivated areas, a combination of high variability, comparatively low use, and availability of these anthropogenic classes in Alaska suggest that their relative importance in our analysis may be overestimated (Fig. 5). Finally, we acknowledge the limitations of the 2011 NLCD data set with regards to accuracy (83%; Wickham et al. 2017). While the 2011 NLCD data set provides the only land cover resource for all of Alaska, NBL habitat outcomes may differ if future studies employ higher-resolution maps. Additionally, the extent of some land cover types may have changed since the development of the 2011 NLCD data set, particularly given the accelerated impact of climate change in the boreal biome (e.g. Loarie et al. 2009).

As rapid climate change pushes the leading edge of the boreal forest northward, NBL may benefit in

Alaska and boreal Canada if their unusually broad diet and generalist habitat affinities confer competitive advantages over other species with narrower dietary requirements (Blois et al. 2013, Moritz & Agudo 2013). Many boreal land cover classes likely provide cool microhabitats that buffer against the physiological stresses of warm temperatures in summer, while insulating snow and abundant bryophyte cover (and high dietary concentrations of arachidonic acid) offer thermal protection from cold ambient temperatures in winter (Frey 1992). Testing the physiological limits and thermal plasticity (Valladares et al. 2014) of NBL may offer avenues of future research aimed at clarifying their physiological requirements or survival limits in different habitat types.

While cool, mossy, and mesic (cryomesic) habitats are widespread in boreal Alaska (Flagstad et al. 2018), these habitats are also subject to long-term drying as temperatures rise (Ives et al. 2013). The impacts of drying are most apparent along the southeastern edge of the NBL range in the contiguous USA, where contraction and fragmentation of once widespread suitable habitat may now be confining NBL to isolated, cryomesic relict areas in Maine, Minnesota, and Idaho (Jones & Melton 2014, Baltensperger et al. 2018, A. P. Baltensperger unpubl. data). Compared to the southeastern extent of the range, our results provide a degree of optimism for both the persistence and possible expansion of NBL in Alaska. Environmental conditions suitable for NBL are predicted to expand in Alaska by 47% by 2070 (Hope et al. 2015) and 84% by 2100 (Baltensperger & Huettmann 2015b). Increased environmental suitability, combined with a uniquely diverse diet and flexible habitat preferences, may therefore allow NBL populations at the northern extent of their range to keep pace with climate-induced shifts in food and habitat resources expected over the coming decades (Lurgi et al. 2012, Moritz & Agudo 2013).

5. CONCLUSIONS

This research represents the first comprehensive, high-resolution quantification of NBL diet and habitat preference and contributes new scientific knowledge to the ESA review process. NBL in Alaska consumed a broad diet composed of a high diversity of functional groups, taxonomic families, and genera, including unusually high quantities of bryophytes, which appears to be unique among small mammals. A lack of significant preference for different boreal land cover types also points to the gener-

alist nature of NBL habitat use at the landscape scale in Alaska.

Our analyses suggest that NBL in Alaska do not appear to be limited by the availability of obligate dietary taxa or specific land cover types, as long as resources fall within broad conditions common to the boreal biome (e.g. cool, moist habitats with abundant bryophytes and cover (Frey 1992, West 1999). The generalist habits of NBL may therefore confer greater resilience in the context of a warmer, drier climate than if they required a narrower set of specialized foods or habitats (Kortsch et al. 2015). In Alaska, at the northern extent of the boreal forest, conditions conducive to NBL persistence are predicted to expand with climate change (Baltensperger & Huettmann 2015b, Hope et al. 2015), providing additional reassurance for the future of this species. However, the situation in Alaska is in striking contrast to the southern edge of the species' range in the contiguous USA, where climate drying appears to have fragmented habitats, resulting in restricted and relict patches of suitable habitat. Research aimed at predicting distribution changes of NBL across North America using ecological niche models is ongoing and will provide sets of testable spatial predictions for species presence and persistence from 1900 to 2100 (A. P. Baltensperger et al. unpubl. data).

To confidently determine how NBL populations are responding to ongoing environmental changes, we offer some recommendations for future research. Due to the difficulty in capturing NBL with standard trapping methods, new approaches for field detection are necessary. Some researchers have had success capturing southern bog lemmings in pitfall traps (e.g. Rose 2006), which could be more frequently used to target NBL as well. Alternative approaches include the use of remote cameras, 'scat boards,' or opportunistic collection of their distinctive green fecal pellets from natural runways. Fecal collection paired with DNA metabarcoding has shown promise for identifying NBL in Montana and offers the most efficient means of identification and should be expanded to systematically survey other areas (DuBois 2016). Once NBL can be reliably detected, monitoring population dynamics should become the priority. We recommend monitoring at both the leading and trailing edges of their range, which currently represent the extremes of environmental suitability. These locations would facilitate quantification of population responses to climatic and anthropogenic pressures and provide prognoses for appropriate listings in a conservation assessment context (Droghini et al. 2022).

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