

# The Beringian Coevolution Project: holistic collections of mammals and associated parasites reveal novel perspectives on evolutionary and environmental change in the North<sup>1</sup>

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**Abstract:** The Beringian Coevolution Project (BCP), a field program underway in the high northern latitudes since 1999, has focused on building key scientific infrastructure for integrated specimen-based studies on mammals and their associated parasites. BCP has contributed new insights across temporal and spatial scales into how ancient climate and environmental change have shaped faunas, emphasizing processes of assembly, persistence, and diversification across the vast Beringian region. BCP collections also represent baseline records of biotic diversity from across the northern high latitudes at a time of accelerated environmental change. These specimens and associated data form an unmatched resource for identifying hidden diversity, interpreting past responses to climate oscillations, documenting contemporary conditions, and anticipating outcomes for complex biological systems in a regime of ecological perturbation. Because of its dual focus on hosts and parasites, the BCP record also provides a foundation for comparative analyses that can document the effects of dynamic change on the geographic distribution, transmission dynamics, and emergence of pathogens. By using specific examples from carnivores, eulipotyphlans, lagomorphs, rodents, ungulates, and their associated parasites, we demonstrate how broad, integrated field collections provide permanent infrastructure that informs policy decisions regarding human impact and the effect of climate change on natural populations.

*Key words:* Arctic, Beringia, bioinformatics, climate change, ecological perturbation, geographic and host colonization, museum specimen archives.

**Résumé :** Le « Beringian Coevolution Project » (BCP), un programme sur le terrain en cours aux latitudes boréales polaires depuis 1999, se concentre sur le développement d'une infrastructure scientifique clé aux fins d'études intégrées sur les mammifères et les parasites qui leur sont associés, et ce, en se fondant sur des spécimens. Le projet BCP a contribué à de nouvelles perspectives à l'échelle temporelle et spatiale à savoir comment les changements climatiques et environnementaux anciens ont formé les faunes, et ce, en mettant en évidence les processus d'assemblage, de persistance et de diversification dans la vaste région béringienne. Les collections du BCP représentent aussi des relevés de base de diversité biotique à travers les latitudes boréales polaires à une période de changement environnemental accéléré. Ces spécimens et les données connexes forment une ressource inégalée afin d'identifier la diversité cachée, d'interpréter les réponses passées aux oscillations climatiques, de documenter les conditions contemporaines et de prévoir les conséquences sur les systèmes biologiques complexes se trouvant dans un régime de perturbation écologique. À cause de l'accent double du projet sur les hôtes et les parasites, le rapport du BCP apporte aussi le fondement pour des analyses comparatives pouvant documenter les effets de changement dynamique sur la répartition géographique, la dynamique de transmission et l'apparition de pathogènes. En utilisant des exemples précis de carnivores, d'eulipotyphlans, de lagomorphes, de rongeurs, d'ungulates et des parasites qui leur sont associés, nous démontrons comment de vastes collections de terrain intégrées fournissent l'infrastructure permanente qui informe des décisions stratégiques quant à l'impact humain et l'effet du changement climatique sur les populations naturelles.

*Mots-clés :* Arctique, Béringie, bio-informatique, changement climatique, perturbation écologique, colonisation géographique et d'hôte, archives de spécimens en musée.

## Introduction

The Arctic is experiencing pronounced environmental perturbation driven by accelerating climate warming and related anthropogenic forces (ACIA 2005; Hansen et al. 2010; IPCC 2013; Meltofte et al. 2013; Arctic Council 2016). Understanding historical patterns and anticipating the outcomes of contemporary processes of environmental change requires knowledge of communities, species, and populations, considered across expansive geographic and temporal scales. Such a knowledge base is fundamental for understanding the continuity of natural systems, the interface between people and the environment, and emergent pathogens and diseases, and for establishing efficient management and conservation practices for systems now undergoing dynamic change. Put simply, we cannot begin to recognize or understand the processes and impacts of environmental change in the Arctic without a refined picture of faunal and floral diversity across time and space. Until recently, this picture was blurred by a lack of a comprehensive historical sampling of environments and the organisms they support.

To begin to fill this void for mammals and associated parasites, the Beringian Coevolution Project (BCP) was initiated in 1999 with a National Science Foundation (NSF) award to Joseph Cook (then at the University of Alaska), Eric Hoberg (US Department of Agriculture (USDA), US National Parasite Collection), and Sam Telford (then at Harvard University), which supported field expeditions to collect and archive specimens from localities across Alaska and Far Eastern Russia. A second grant from NSF was awarded in 2004 to Cook (University of New Mexico) and Hoberg, supporting additional collections in Beringia, and finally, a third grant for fieldwork to Cook, Hoberg, Kurt Galbreath (Northern Michigan University), and Eric DeChaine (Western Washington University) was awarded in 2012, allowing mammal/parasite collections to be extended beyond the traditional boundaries of Beringia into central Asia (Mongolia) and interior Canada. A series of collaborative efforts with state (e.g., Alaska Department of Fish and Game) and federal agencies (e.g., US Forest Service, US Geological Survey, National Park Service) and international partners (e.g., Institute of Biological Problems of the North in Magadan, Siberia, Yukon Department of Environment, National University of Mongolia) augmented NSF-funded fieldwork and significantly expanded geographic and taxonomic sampling of mammal and parasite populations radiating from the Bering Strait (e.g., Hoberg et al. 2003, 2012a; Cook et al. 2005). These museum collections are site-intensive and taxonomically diverse and span the entire Holarctic nexus, providing unequaled research infrastructure to address pressing issues of global significance.

Our research group and many others have used these key Arctic snapshots to explore fundamental questions about the assembly, evolution, and ecology of northern biotas that have dominated Beringian biodiversity studies since the 1930s (e.g., Hultén 1937; Rausch 1994). Specifically, BCP questions targeted five themes: (1) the timing and direction of dispersal and subsequent contact of hosts and parasites across the Beringian nexus, (2) the role of Beringia as a refugium and driver of Arctic diversification, (3) the historical interactions of climate and landscape heterogeneity in structuring diversity across the high latitudes and adjoining regions, (4) impacts of accelerated warming in the Arctic on the dynamics of host–parasite associations and emerging disease, and (5) the pressing need to reframe conservation strategies and priorities.

New perspectives on high-latitude mammals and parasites have continually emerged from the BCP through historical ecology and biogeography, molecular phylogeography, phylogenetics, and predictive modeling. Using an integrated approach, our studies (and the work of others that incorporated BCP specimens) shed light on the pivotal roles of Beringian and other northern refugia in faunal diversification, colonization, coevolutionary processes, and community assembly. Although we restrict this paper to reviewing BCP studies of mammals and their associated parasites, we note that a number of parallel efforts have focused on other taxa (e.g., plants: Wen and Ickert-Bond 2009; Eidesen et al. 2013; Wen et al. 2016). Our combined insights up to this point form just a preamble to understanding the complex evolutionary and ecological forces that govern the dynamic Arctic region. Continued development of these archives will be necessary to anticipate how communities in the North are responding to contemporary climate change and other anthropogenic impacts. Therefore, we also focus on how the BCP approach facilitates core insights into biological patterns and processes across multiple scales and is thus a model for investigations in additional biomes.

### The setting

Quaternary glacial-interglacial oscillations (recurrent for the last 2.6 million years) formed a theater for the evolution of modern ecosystem structure at high northern latitudes. During glacial advances, the ranges of many high-latitude terrestrial species

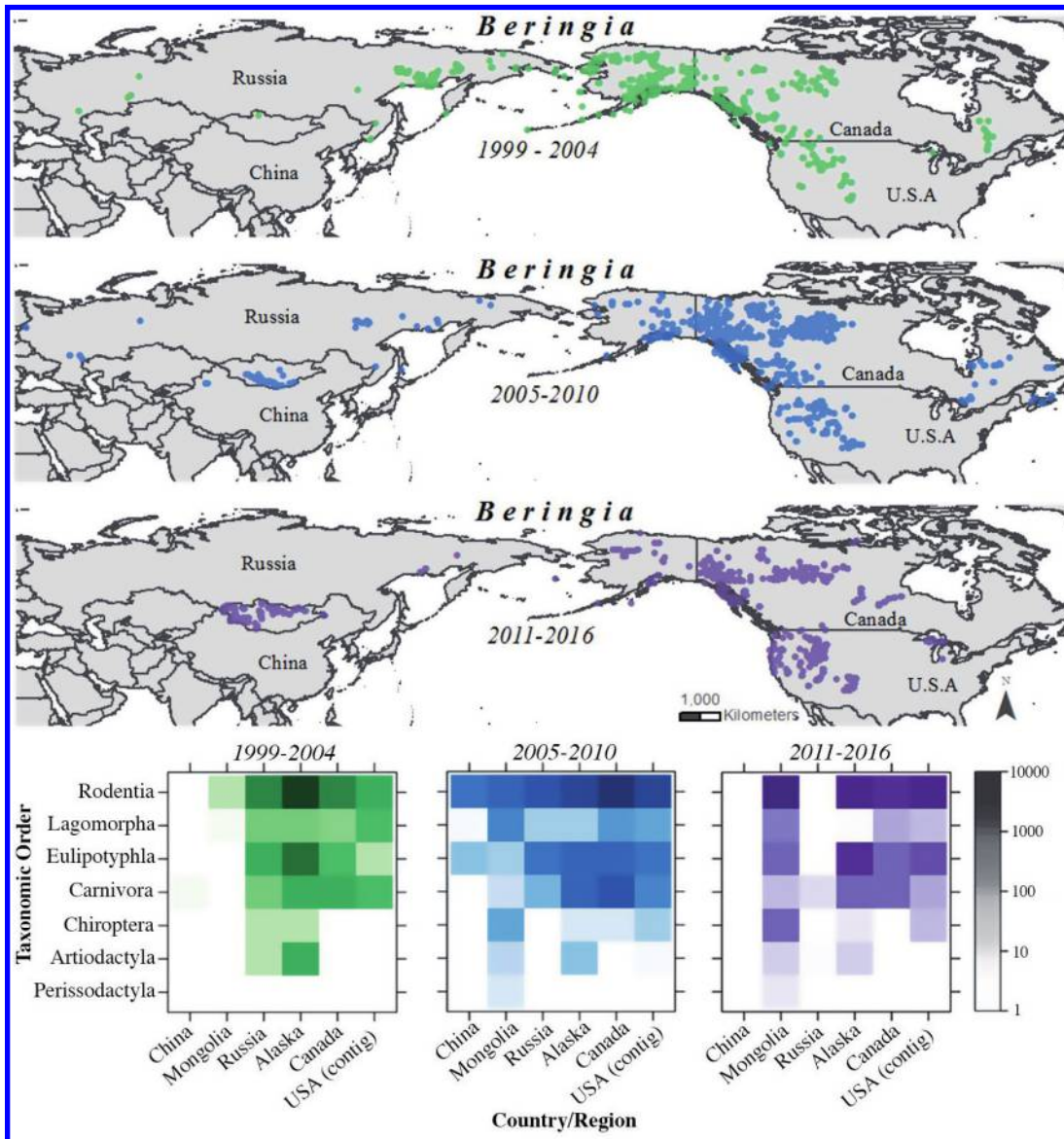
contracted or shifted to occupy refugial (ice-free) regions scattered across Europe, Asia, and North America (Pielou 1991). Persistence in these isolated refugial zones led to diversification over millennial time frames, while in other cases, extinction led to relaxation of fauna and flora (Hewitt 2000; Hoberg et al. 2012a). Paradoxically, even as glacial advances caused range retraction within continents for many species, they also exposed (via polar ice buildup and sea-level decrease) a vast plain connecting Asia and North America known as Beringia. What followed was a complex pattern of intercontinental expansion and exchange across Beringia.

Climate forcing of biological patterns and processes, however, was not restricted to long glacial periods. As glacial periods waned, intermittent warming periods drove many terrestrial species to expand from glacial refugia where they were isolated and had developed independent evolutionary trajectories. Recolonization by these source populations across the vast, previously ice-covered regions created zones of secondary contact both between divergent lineages of the same species and between distinct species (Hewitt 2004; Runck et al. 2009). It is this “replaying” of history, in terms of repeated episodic range expansion and contraction across the Quaternary, that produced the diverse faunal mosaic across temporal and spatial scales linking landscapes to regional ecosystems and communities in the North (e.g., Cook et al. 2006; Hoberg et al. 2012a; Hoberg and Brooks 2015).

In the Arctic, climatological forcing and environmental perturbation shape not only vertebrate community assembly and phylogeographic structure but also the distribution and assembly of associated parasite faunas. Parasites are elegant proxies for understanding contemporary and historical community ecology, biogeography, and the complexity of evolutionary diversification (e.g., Hoberg 1997; Hoberg and Klassen 2002; Nieberding and Olivieri 2007; Hoberg et al. 2012a, 2012b). For example, parasites often reveal “cryptic events” that are not apparent from host genetic signatures alone (Hoberg 1995; Wickström et al. 2003; Koehler et al. 2009a). Processes that unfolded across Beringia through the Quaternary contribute to a general model for exploring the impact of recurrent expansion, geographic colonization, faunal mixing, and host switching in the development and persistence of complex biotas (e.g., Hoberg and Brooks 2008, 2015; Araujo et al. 2015; Galbreath and Hoberg 2015). Understanding these assemblages has direct implications for recognizing and anticipating changes in pathogen distributions and potential for emergent disease among both wild mammals and humans (e.g., Kutz et al. 2004; Altizer et al. 2013; Hoberg et al. 2013; Jenkins et al. 2013; Brooks et al. 2014; Dudley et al. 2015).

The BCP has stimulated exploration of biodiversity across the Holarctic and beyond the boundaries of Beringia, but has also served as a powerful model for understanding global processes of environmental change. The BCP builds on a tradition of comprehensive (i.e., hosts and parasites collected together) specimen-based inventory established in Alaska and Siberia over the past 70 years (e.g., Rausch 1994). Early studies focused on discovery, documenting the complexity and structure of host–parasite systems in a poorly known and logistically challenging environment. A specimen-rich infrastructure for authoritative identification, delimitation, and description of new species and lineages, coupled with consideration of environmental connectivity through both evolutionary and ecological time, constitutes a cornerstone for systematic and historical biogeographic studies (e.g., summarized in Hoberg et al. 2003, 2012a; Cook et al. 2005). Critically, this foundation provides a trajectory for development and application of new methods for exploring genomic diversity, molecular systematics, ecology, phylogeography, conservation genetics, physiology, and epidemiology. Effective integration of these disciplines remains highly dependent on maintenance and growth of well-documented specimen archives (i.e., museum collections) from throughout the Arctic and globally (Cook et al. 2013).

**Fig. 1.** Collecting localities for Beringian Coevolution Project specimens are shown for three periods. Heat-maps showing the taxonomic density of specimens (number of specimens per mammalian order) preserved through the Beringian Coevolution Project since 1999.



### BCP: an integrated international approach

BCP field inventories of mammals and associated parasites were designed to address a range of specific hypotheses and to broadly sample habitats across latitudinal and longitudinal gradients. Fieldwork has emphasized the concurrent collection and holistic preparation of mammal and parasite specimens to ensure their potential for a range of interrelated studies. The BCP aimed to define and investigate diversity and evolutionary and ecological processes across regions, ecosystems, species, and populations using extended transect surveys (Fig. 1).

## Overview of fieldwork

Diverse mammal and associated parasite specimens were acquired using a range of methods (Fig. 1) (MacDonald and Cook 2009). Large-bodied animals (e.g., Carnivora and Artiodactyla) were collected through collaborative efforts with various natural resource agencies. In these cases, the status of populations and geographic ranges are fairly well known, but little genetic or parasite material exists. Smaller animals (chiefly Eulipotyphla, Rodentia, and Lagomorpha) were collected through site-intensive field surveys that were conducted as either longitudinal transects across the Arctic or latitudinal transects into the Arctic from the south. As a supplement to these efforts, and through NSF and other federal and state support, we developed an extensive collaborative network across wildlife agencies in the United States, Canada, and Russia that has also provided substantial series of mammal specimens, ranging from shrews to moose. Maintaining ties with long-term small mammal monitoring projects, subsistence and commercial hunting operations for ungulates (e.g., moose, caribou, muskoxen, and Dall's sheep), and commercial trappers of furbearers generated samples of high-latitude specimens that might otherwise be unavailable to science (e.g., Kutz et al. 2012).

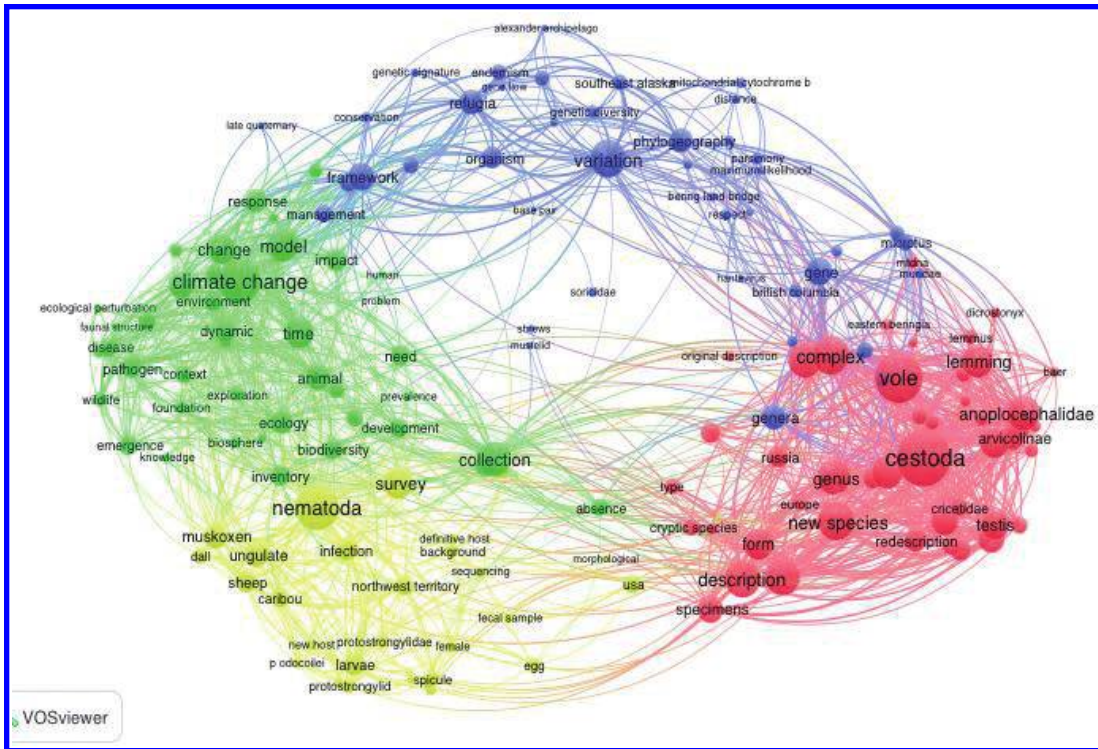
Parasitological specimens were acquired principally via immediate examination and necropsy of mammalian specimens in the field. Mammalian specimens collected directly by BCP field crews of mammalogists and parasitologists were screened for macroparasites (helminths and arthropods), which were preserved using methods appropriate to the taxon (e.g., heat-killing in saline for nematodes and hot water for cestodes and trematodes) and to maximize the utility of specimens for both morphological and molecular studies (e.g., frozen or preserved in 70% ethanol). Various tissues (e.g., lung, blood, tissue cysts, and gut contents) were also preserved (e.g., flash frozen or preserved in 95% ethanol) to enable future investigations of the occurrence, identity, and distribution of microparasites (e.g., viruses, bacteria, and protozoans). These protocols emphasize the necessity of preserving vouchers that document the structure of diversity in space and time (e.g., Hoberg et al. 2009; McLean et al. 2016a).

## Uses of collections

Specimens collected through the BCP provide a biodiversity reference for resource management, policy, and education (e.g., MacDonald and Cook 2009; Cook et al. 2014, 2016a) and a foundation for addressing diverse research questions (e.g., Weksler et al. 2010; Hoberg et al. 2013; Knowles et al. 2016). Consistent with their preservation as vouchers, they serve as the basis for authoritative identification of the existence of an individual organism (and the particular species it represents) at a specific time and location. Authoritatively identified specimens are the foundation for our understanding of diversity and the information that can be applied in understanding and defining the implications of host and parasite distributions. All mammal specimens were deposited at the University of Alaska Museum (before 2003) and Museum of Southwestern Biology (2003 to present).

BCP collecting methods ensure the preservation of high-quality samples that permit investigations spanning broad spatial and temporal scales, including topics such as deep phylogenetic relationships (Cook et al. 2004; Koehler et al. 2009b; Lanier and Olson 2009; Esteva et al. 2010; Haukialmi et al. 2010; Kohli et al. 2014), the mode and timing of speciation (Hope et al. 2011, 2013), community assembly and faunal mixing through time (Cook et al. 2006; Galbreath and Hoberg 2012, 2015; Hoberg et al. 2012a; Cook and MacDonald 2013; Hope et al. 2015), demographic responses to regional climate through interactions with major biotic and abiotic forces (e.g., Hope et al. 2014), conservation implications of population fragmentation and expansion (Small et al. 2003; Cook and MacDonald 2013;

**Fig. 2.** Specimen-based research integrates diverse approaches and stimulates new linkages across various themes in Arctic biology. The network is based on terms contained in the titles and abstracts of 174 publications resulting from the Beringian Coevolution Project that were accessed and downloaded from Web of Science. The network was constructed using Vosviewer v1.6.4 (van Eck and Waltman 2010) based on 169 unique terms with five or more occurrences across the publication records. Default clustering and attraction/repulsion settings were used. The sizes of both text and circles are scaled to reflect differences in term co-occurrences, with larger text/circles denoting more commonly occurring and co-occurring terms.



Malaney et al. 2013; Malaney and Cook 2013), recurrent gene flow (Runck et al. 2009; Lindqvist et al. 2010; Miller et al. 2012; McLean et al. 2016b), and isotopic investigations of dietary niche space (O'Brien et al. 2017). Museum specimens lend themselves to integrated approaches to science, especially sample-intensive fields of study that now are experiencing rapid technological and methodological advances (stable isotopes, disease ecology, and predictive modeling: Cook et al. 2013; McLean et al. 2016a; Dunnun et al. 2017).

## Results

Field collections completed under the BCP and related projects resulted in 53 043 mammal specimens and in excess of 14 000 lots of endoparasites and ectoparasites (ranging from single specimens to mixed species assemblages involving hundreds of specimens in a single host) collected from 8761 localities (unique georeferenced specimens) (Fig. 1). As evidence of the broad influence of integrated archives, the comprehensive specimen-based approach of the BCP has yielded over 200 publications and 20 graduate theses or dissertations with impacts in diverse fields (Fig. 2).

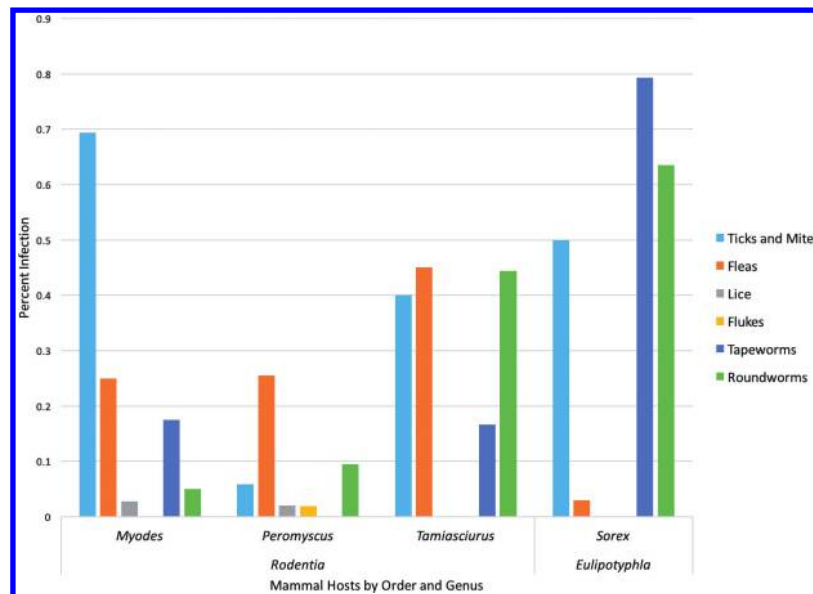
### Mammalian diversity

BCP and related collection efforts have resulted in specimens from seven mammalian orders and 27 families, with the majority of specimens being rodents. The sampled

**Table 1.** Ectoparasite and endoparasite diversity and prevalence in small mammals collected from Fairbanks, Alaska, to Terrace, British Columbia, along the Alaska and Cassiar Highways in 2013.

Mammal order	Mammal genus	No. of hosts examined for ectoparasites	No. of hosts infested with ectoparasites	Ectoparasite prevalence (%)	No. of hosts examined for endoparasites	No. of hosts infested with endoparasites	Endoparasite prevalence (%)
Rodentia	<i>Microtus</i>	1	1	100	1	0	0
Rodentia	<i>Myodes</i>	36	28	78	40	7	18
Rodentia	<i>Peromyscus</i>	51	16	31	53	6	11
Rodentia	<i>Tamiasciurus</i>	20	12	60	18	10	56
Eulipotyphla	<i>Sorex</i>	34	18	53	63	60	95
Carnivora	<i>Mustela</i>	1	0	0	2	0	0
Total/average		143	75	52	177	83	46

**Fig. 3.** Histogram showing the diversity and prevalence of parasites collected from the most common mammalian genera across the Alaska–Cassiar latitudinal transect conducted in 2013.



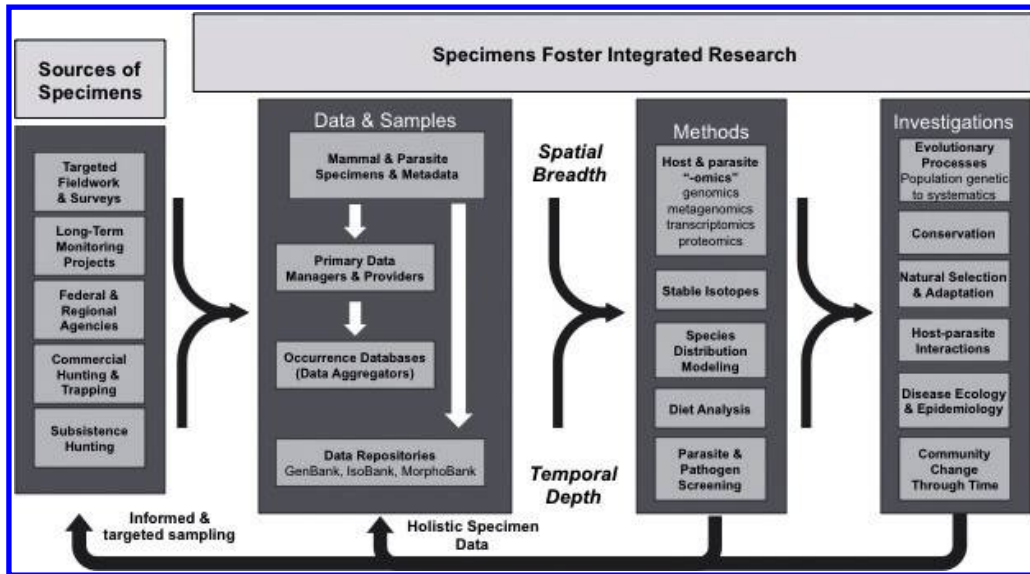
mammalian orders and families have varied through time (Fig. 1), depending on region being sampled and on particular collaborative projects with natural resource agencies and commercial trappers. Within most of the mammalian species examined using molecular genetic analyses, substantial phylogeographic structure and cryptic species have been identified (e.g., Cook et al. 2001; Dawson et al. 2014; Sawyer and Cook 2016).

### Parasite diversity

Sampling of mammalian host–parasite assemblages has revealed a diverse array of viruses, bacteria, protozoans, arthropods, and helminths (e.g., Table 1; Fig. 3). Given that parasite diversity substantially exceeds that of potential mammalian hosts, a synoptic treatment of micro- and macroparasites remains in development. However, substantial insights have been established for certain groups, including platyhelminths in rodents and mustelids and pulmonary and gastrointestinal nematodes among artiodactyls, by integrating



Fig. 4. Specimens help integrate across diverse research agendas and provide ready access to data and samples for scientists, managers, and policy makers.



morphology and molecular genetics to reveal history and phylogeographic structure (e.g., Cook et al. 2005; Hoberg et al. 2012a).

Initial field assessments of diversity demonstrate how species of parasites are partitioned across mammalian taxa and how characteristics of specific geographic sites along a transect may influence the structure of parasite faunas. For example, we have observed changing patterns of diversity for helminths in *Peromyscus* across a latitudinal transect between Yukon and British Columbia, with greater parasite diversity evident at lower latitudes. Such a pattern could reflect the dynamics of southern isolation and subsequent post-glacial expansion to the north. Further, this transect crossed the broad contact zone for *Myodes rutilus* and *M. gapperi* (Runck et al. 2009), a region already known to be associated with a substantial shift in tapeworm diversity (e.g., Makarikov et al. 2013). From this single temporal/spatial slice, we can begin to explore how endoparasite and ectoparasite faunas may be isolated or shared among cricetids, sciurids, and other mammals to better understand the ecological and historical processes associated with parasite circulation and faunal assembly.

The BCP has already substantially altered the existing view of northern systems as relatively simple and taxonomically depauperate in comparison to other regions of the world (e.g., Hoberg et al. 2013). Since the late 1990s, the BCP has been instrumental in establishing nine new higher-level taxa (genera of tapeworms) and recognition and (or) description of 63 previously unknown viral, protozoan, and helminth species while establishing a fundamentally new understanding of host and geographic distribution (e.g., Wickström et al. 2005; Makarikov et al. 2013; Haukisalmi et al. 2014, 2016). High levels of cryptic parasite diversity demonstrate how holistic surveys are necessary to comprehensively understand historical and contemporary patterns of faunal assembly and diversification (Fig. 4).

## Discussion

BCP field collections coupled with molecular methods and new theoretical and analytical approaches in population genetics, genomics, and systematics are yielding novel insights into biogeographic history, enabling tests of earlier concepts about this northern

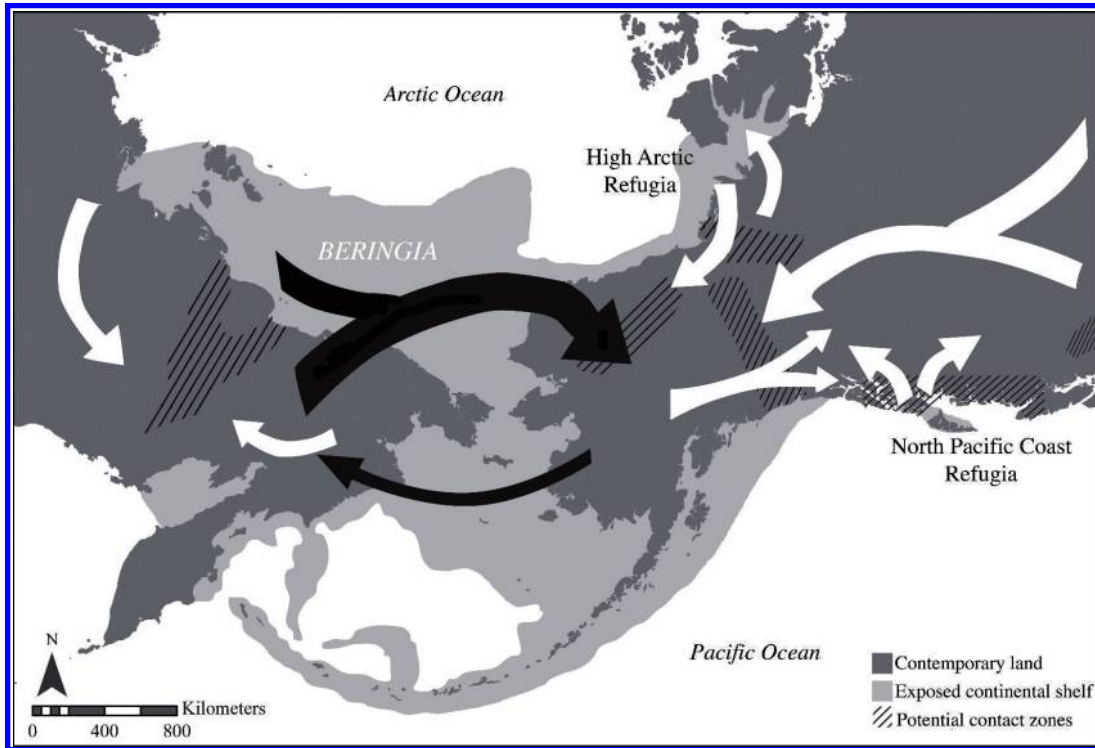
crossroads and generating new hypotheses of dispersal and diversification across the region. While coarse sampling was sufficient for early Beringian biogeographers to document general patterns (MacPherson 1965; Kontrimavichus 1976; Ryzhikov et al. 1978, 1979; Hoffmann 1981; Rausch 1994), BCP-based phylogeographic studies draw on more extensive sampling and are revealing considerable complexity belying the impacts of ancient, often-rapid climate change (e.g., Waltari et al. 2007; Hoberg et al. 2012b; Haukisalmi et al. 2016; McLean et al. 2016b). Here we outline longstanding concepts in Beringian science and discuss specific examples of BCP-enabled refinement of these ideas.

### **Beringia: crossroads of northern continents — mammals and parasites address classic questions of intercontinental dispersal, contact, and exchange**

As a land bridge that repeatedly linked Eurasia to North America, Beringia mediated the flow of diversity between Arctic continents. During the Quaternary, the flow was predominantly west to east due to climatological gradients that developed in the late Pliocene and the relative size and timing of major dispersal barriers across the region (Hopkins et al. 1982; Waltari et al. 2007; Hoberg et al. 2012a). The general eastward trend (Rausch 1994), however, contrasts with some histories revealed by BCP analyses that reflect an important North American influence on Asian faunas (e.g., Demboski and Cook 2003; Hope et al. 2012). For example, data from cold-adapted species such as pikas (Galbreath and Hoberg 2012), arctic ground squirrels (Galbreath et al. 2011; McLean et al. 2016b), American marten now resident in interior Alaska (Small et al. 2003), jumping mice (Malaney and Cook 2013), and shrews (Hope et al. 2012) show evidence for distinct episodes of northward expansion from temperate North American latitudes into eastern Beringia or even farther into Asia. New evidence for multiple distinct transberingian colonization events by helminths associated with pikas as well as the presence of parasite lineages in Asia that may have North American ancestry (Toman and Galbreath, unpublished data), indicate a more important role for North American faunas (hosts and parasites) as a source for westward colonization than previously recognized. Further, phylodemographic studies are revealing complex episodes of geographic contraction and range expansion out of Asia (Fig. 5). For example, separate lineages of both northern red-backed voles (*Myodes rutilus*) and brown lemmings (*Lemmus trimucronatus/sibiricus*) appear to have undergone range retraction and subsequent recolonization across western Beringia (Fedorov et al. 1999; Kohli et al. 2015). Each of these snapshots of population history yields insight into the role and timing of processes shaping communities, such as the consequences of abiotic forces (e.g., climate change) for species range dynamics and population divergence (Hope et al. 2014). Still, issues such as the causes of the Late Pleistocene pause in eastward colonization of North America (Tamm et al. 2007; Meiri et al. 2014) or the influence of a possible mesic “buckle” in Beringia (Guthrie 2001) will be more clearly defined in the near future.

In addition to mediating intercontinental faunal exchange, climatic oscillations at northern high latitudes created new opportunities for population- and species-level contact. New specimen-derived genetic data from these areas have contributed to our general understanding of diversification and the permeability of species boundaries in the face of gene flow. In three species of *Urocitellus* ground squirrels, two sequential instances of ancient gene flow were identified, each resulting in mitochondrial capture (McLean et al. 2016b). Unlike many other examples of high-latitude hybridization, these taxa (*U. parryii*, *U. richardsonii*, and *U. elegans*) are now largely allopatric, demonstrating that historic genetic exchange among high-latitude mammals cannot be predicted based on current distributions alone. This and other instances of hidden gene flow within Beringian faunas are best understood when placed in the context of continental-scale analyses, an approach that BCP specimen archives are poised to contribute to significantly.

**Fig. 5.** Generalized model for the primary colonization pathways, contact zones, and hypothesized source refugia for the greater Beringian region (Table 2). Black arrows denote expected movement during cold periods of glacial maxima when sea levels were lower, while white arrows depict general pathways of colonization during warmer interglacials. These events likely played out repeatedly across a dynamic history of climate oscillation, environmental perturbation, and stability during the Quaternary.



Investigation of distinct lineages of ermine (*Mustela erminea*) utilizing BCP specimens led to novel insights about the origin of endemic, at-risk island populations (Colella et al., unpublished data) in the Alexander Archipelago. Additionally, next-generation DNA sequencing uncovered highly divergent brown bear (*Ursus arctos*) populations (Lindqvist et al. 2010; Miller et al. 2012) within the same archipelago. Admiralty Island, in particular, supports distinctive lineages of both ermine and brown bears. These discoveries highlight shared demographic histories across topographically complex regions of Beringia and the role of glaciation events in driving diversity.

### **Beringia: a northern refugium and engine of diversification — arvicolines, ground squirrels, and tapeworms challenge ideas of northern diversification**

As an expansive region that remained relatively ice-free during Pleistocene glacial periods, Beringia served as a refuge for populations of northern species through repeated climatic oscillations. It also provided a source for post-glacial recolonization of high latitudes. However, questions have persisted regarding the existence of additional smaller refugia in the North and their relative contributions to diversity and post-glacial colonization (Fedorov and Stenseth 2002; Fleming and Cook 2002; Shafer et al. 2010). For example, divergent genetic lineages endemic to Beringia were found (Fedorov et al. 1999; Fedorov and Stenseth 2002; Brunhoff et al. 2003; Fedorov et al. 2003) in the collared lemming (*Dicrostonyx*), brown lemming (*Lemmus*), and tundra vole (*Microtus oeconomus*), a finding that

**Table 2.** Summary of the taxa explored or discovered by BCP-based investigations to date and the tentative assessment of colonization history, potential contact zones between species or distinctive lineages, and refugial origin for mammals and helminth parasites.

Focal group/host	Taxon	Origin	Colonization	Contact	Citation(s)
<b>Mammal</b> Higher-level origins	<i>Lepus</i>	NA/Eu/NA	W/E/N	Beringia, HA,	1
	<i>Ochotona</i>	Asia/NA	E/N	se Beringia	2, 3, 4
	<i>Dicrostonyx</i>	EuA	E, BE	Kolyma R, BStrait, e Beringia	5, 6, 7, 8, 9
	<i>Lemmus</i>	EuA	E, RE	Kolyma R, e Beringia	5, 9, 10,
	<i>Microtus</i>	EuA/NA	E/N	Omolon River, e Beringia	9, 11, 12
	<i>Myodes</i>	EuA	E	w Beringia	9, 13, 14, 15, 16
	<i>Myopus</i>	EuA	E	se Siberia	17
	<i>Tamiasciurus</i>	NA	N	se AK, s Beringia	18
	<i>Urocitellus</i>	NA	N/W	Central Beringia, e Asia	19, 20
	<i>Zapus</i>	NA	N	None	21
	<i>Sorex</i>	EuA/NA	E/W	BStrait, se AK	9, 22, 23, 24, 25
	<i>Camis</i>	EuA	E	?	26, 27
	<i>Martes</i>	EuA/NA	E/N	se AK	28, 29, 30, 31, 32
	<i>Mustela</i>	EuA/NA	E/N	se AK, e Beringia	33, 34
	Interspecific pairs	<i>Lepus timidus/L. oithus</i>	EuA	N/A	BStrait
<i>Dicrostonyx torquatus/D. groenlandicus</i>		Beringia	N/A	BStrait	5, 6, 7, 9
<i>Lemmus sibiricus/L. trimucronatus</i>		Beringia	N/A	Kolyma R, e Beringia	5, 9, 10
<i>Sorex camtschaticus/S. ugyunak</i>		NA	N/A	BStrait	25
<i>Sorex portenkoi/S. ugyunak</i>		NA	N/A	BStrait	25
<i>Sorex ugyunak/S. cinereus</i>		NA	N/A	n AK	25
<i>Martes caurina/M. americana</i>		NA	N/A	se AK, WY to BC	28, 29, 30, 31, 32
<i>Ochotona collaris/O. princeps</i>		NA	N/A	None	2, 3, 4
<i>Myodes rutilus/M. gapperi</i>		EuA/NA	N/A	se AK to Hudson Bay	9, 13, 14, 15, 16, 37
<i>Lemmus trimucronatus</i>		NA	BE, N	e Beringia	10
<i>Microtus oeconomus</i>		EuA	BE	Siberia, Omolon R	12, 38, 39
<i>Myodes rutilus</i>		EuA	BE	Kolyma R	13, 16, 37, 39
<i>Urocitellus parryi</i>		NA	BE/CHA	Central Beringia	19, 29, 40
<i>Sorex minutissimus</i>		EuA	E	Ural Mtns	9, 23
Holarctic species					

Table 2 (continued).

Focal group/host	Taxon	Origin	Colonization	Contact	Citation(s)
Palearctic endemic species	<i>Sorex tundrensis</i>	EuA	E	BStrait & Palearctic	9, 24
	<i>Canis lupus</i>	EuA	E	Coast Range	26, 27, 41, 42
	<i>Ursus arctos</i>	EuA	E	se AK, e Beringia	
	<i>Gulo gulo</i>	EuA	E	AK/Yukon?	
	<i>Mustela erminea</i>	EuA	se AK endemic/E	se AK, e Beringia	33, 34
	<i>Lepus timidus</i>	EuA	Widespread	None	35
	<i>Dicrostonyx torquatus</i>	EuA	RE	Kolyma R	5, 6, 7, 9
	<i>Lemmus sibiricus</i>	EuA	RE	Kolyma R	5, 9, 10
	<i>Myopus schisticolor</i>	EuA	E	se Siberia	17
	<i>Sorex camtschatica</i>	NA	BE	None	25
Nearctic endemic species	<i>Sorex portenkoi</i>	NA	BE	None	25
	<i>Lepus othus</i>	EuA	BE	None	35
	<i>Ochotona collaris</i>	NA	BE	None	3
	<i>Dicrostonyx groenlandicus</i>	NA	BE, High Arctic	e Beringia	5, 6, 7, 8, 9
	<i>Lemmus trimucronatus</i>	NA	BE, N	e Beringia	5, 9, 10
	<i>Microtus longicaudus</i>	NA	se AK, BE, N	se AK, se Beringia	44, 45
	<i>Microtus miurus</i>	?	BE	e Beringia	11
	<i>Microtus pennsylvanicus</i>	NA	N	None	46
	<i>Tamiasciurus hudsonicus</i>	NA	BE, N	se Beringia	47
	<i>Zapus hudsonius</i>	NA	N	None	48
Host	<i>Zapus princeps</i>	NA	N	None	49
	<i>Sorex cinereus</i>	NA	N	None	25
	<i>Sorex taylori</i>	NA	BE	None	25
	<i>Sorex monticola</i>	NA	N	se AK	50
	<i>Sorex palustris</i>	NA	N	None	51
	<i>Ursus americanus</i>	NA	N	?	52, 53
	<i>Martes caurina</i>	NA	se AK endemic	None	28, 29, 30, 31, 32, 54
	<i>Martes americana</i>	NA	N	None	28, 29, 30, 31, 32
	<b>Parasite</b>				
	Eucestoda-Hymenolepididae				
<i>Eulipotyphla</i>					
<i>Sorex monticolus</i>	NA	se AK endemic	??	55	
<i>Sorex cinereus</i>	NA	RE (Cal-AK-Rocky Mtns)	??	56	

Table 2 (continued).

Focal group/host	Taxon	Origin	Colonization	Contact	Citation(s)
<i>S. cinereus</i> , <i>S. tundrensis</i> , <i>S. ugyunak</i>	<i>Staphylocystoides serrula</i> ●	NA	Widespread (AK-TN)	??	56
<i>S. araneus</i> , <i>S. caecutiens</i> , <i>S. tundrensis</i> , <i>S. gracillimus</i> , <i>S. urguiculatus</i>	<i>Staphylocystoides spasskii</i> ●	EuA	E Siberia (Baikal-w Beringia)	??	56
<i>S. minutissimus</i>	<i>Staphylocystoides</i> sp. ●	NA	E Beringia (AK-YK)	??	57
<i>S. cinereus</i>	<i>Spasskylepis rauschi</i> ★	NA	BE	??	58
<i>S. minutissimus</i>	<i>Lineolepis parva</i> ●	NA	Widespread (AK-IA)	??	57
<i>S. tundrensis</i>	<i>Neoskrjabimolepis fertilis</i> ★	Beringia?	BE (Chukotka-Seward Peninsula)	??	59
<i>S. tundrensis</i>	<i>Neoskrjabimolepis hobergi</i> ★	NA	BE	??	59
	Eucestoda-Dilepididae				
<i>S. caecutiens</i> , <i>S. daphaenodon</i>	<i>Monorcus dokuchaevi</i> ★	EuA	BE	??	60
	Nematoda-Dioctophymatoidea				
<i>S. cinereus</i> , <i>S. urguiculatus</i> , <i>S. tundrensis</i>	<i>Soboliphyme baturini</i> ●	Asia?	Holarctic	??	32, 61, 62, 63
	Eucestoda-Hymenolepididae				
<b>Rodentia, Arvicolinae</b> (+Neotominae/Geomyidae/ Heteromyidae)	<i>Arostrilepis</i>	EuA	Multiple E expansions	Stikine R & Liard-MacKenzie R	64, 65, 66
Cricetidae/Neotominae/ Scuridae	<i>Hymenolepis</i>	EuA	E expansion	??	67, 68
<i>Myodes gapperi</i>	<i>Arostrilepis cooki</i> ★	w NA	N	??	65
<i>Myodes rufocanus</i> , <i>Microtus oeconomus</i>	<i>Arostrilepis gulyaevi</i> ★	Asia	Widespread Siberia	??	65
<i>Microtus oeconomus</i> , <i>M. longicaudus</i> , <i>M. miurus</i> , <i>M. pennsylvanicus</i> , <i>M. xanthognathus</i>	<i>Arostrilepis rauschorum</i> ★	w NA	??	??	65
<i>Myodes californicus</i>	<i>Arostrilepis kontrimavichusi</i> ◆	w NA	Pacific Coast endemic	??	69
<i>Microtus oeconomus</i>	<i>Arostrilepis</i> c.f. <i>janickii</i> ●	e Ber	w AK endemic	??	65
<i>Lemmus trimucronatus</i> , <i>Synaptomys borealis</i>	<i>Arostrilepis beringiensis</i> ●	Asia	Holarctic	??	65, 90
<i>Myodes rutilus</i> , <i>Microtus xanthognathus</i> , <i>Tamiasciurus hudsonicus</i>	<i>Arostrilepis macrotrrosa</i> ●	Asia	E into NA	Kolyma R	65, 90
<i>Myodes rufocanus</i> , <i>M. rex</i> , <i>M. rutilus</i> , <i>M. glareolus</i>	<i>Arostrilepis tenuicirrosa</i> ●	Asia	W across Asia	??	116
<i>Microtus pennsylvanicus</i>	<i>Hymenolepis evagnata</i> ●	e NA	LE (Manitoba)	??	90

Table 2 (continued).

Focal group/host	Taxon	Origin	Colonization	Contact	Citation(s)
	Eucestoda-Anoplocephalidae				
Arvicolinae	Anoplocephaloides	EuA	W and E expansion	??	70, 71
Arvicolinae	Microcephaloides	EuA?	E?	??	72
Arvicolinae	Paranoplocephala complex	EuA	Multiple expansions	??	73, 74, 75, 76
Arvicolinae	Gulyaevia	EuA	??	??	74, 75,
Arvicolinae	Mitotocola	EuA?	E	??	76, 77
Arvicolinae	Beringtaenia	NA?	??	??	76
Arvicolinae	Arctocestus	EuA?	E?	??	76, 78
Arvicolinae	Rauschoitides	EuA?	Multiple expansions	??	8, 76
Arvicolinae	Douthittia	EuA	Multiple expansions	??	70, 79, 80
Arvicolinae	Rodentocestus	EuA?	E?	??	74, 76
Microtus oeconomus, M. miurus, M. pennsylvanicus	Anoplocephaloides c.f. dentata III ★●	Asia	E into NA	??	70, 71
Microtus xanthognathus	Anoplocephaloides c.f. dentata IV ★●	NA	e BE	??	71
Synaptomys borealis	Anoplocephaloides kontrimavichusi 1 ★●	NA	RE (BC-AK)	??	70, 71, 81
Synaptomys borealis	Anoplocephaloides kontrimavichusi 2 ★●	NA	RE (BC-AK)	??	70, 71, 81
Lemmus trimucronatus, L. sibiricus	Anoplocephaloides lemni 1 ★●	Beringia	Holarctic	Kolyma R	70, 71, 81
Lemmus sibiricus	Anoplocephaloides lemni 2 ★●	Asia	n Siberia endemic	??	70, 71, 81
Microtus xanthognathus	Microcephaloides n. sp. 2 ★●	NA	e BE	??	82
Microtus longicaudus	Microcephaloides n. sp. 3 ★●	NA	e BE	??	82
Microtus miurus	Microcephaloides n. sp. 5 ★●	NA	e BE	??	82
Microtus pennsylvanicus, M. longicaudus	Microcephaloides n. sp. 6 ★●	NA	RE (Cal-Ak)	??	82
Microtus miurus, Myodes rutilus	Paranoplocephala batzlii ★●	NA	e BE	??	74, 75, 76
Microtus oeconomus	Paranoplocephala jarrelli ★	EuA	E into NA	??	74, 76
Microtus sp.	Paranoplocephala c.f. omphalodes n. sp. I ★●	Eur	Widespread Europe	N/A	70, 76, 80, 83
Microtus oeconomus	Paranoplocephala c.f. omphalodes n. sp. II ★●	EuA?	Holarctic	??	70, 76, 80, 83
Microtus oeconomus, M. miurus	Paranoplocephala c.f. omphalodes n. sp. III ★●	NA	e BE	??	70, 76, 80, 83

Table 2 (continued).

Focal group/host	Taxon	Origin	Colonization	Contact	Citation(s)
<i>Microtus oregoni</i> , <i>M. pennsylvanicus</i> , <i>M. townsendi</i>	<i>Paranoplocephala macrocephala</i> complex ★●	NA	Widespread NA	??	73
<i>Myodes rufocanus</i>	<i>Gulyaevia buryatiensis</i> ★★	Asia	Central Siberia endemic	??	70, 75, 76
<i>Myodes rutilus</i>	<i>Gulyaevia longivaginata</i> ★●	Asia	Central Siberia endemic	??	74, 75, 76
<i>Microtus pennsylvanicus</i> , <i>M.</i> <i>longicaudus</i>	<i>Microticola etholeni</i> ★●	NA	N	N/A	76, 77
<i>Microtus miurus</i>	<i>Beringtaenia nanushukensis</i> ★●	NA	e BE	??	76
<i>Dicrostonyx torquatus</i> , <i>D.</i> <i>groenlandicus</i>	<i>Arctoceustus serratus</i> ★	??	Holarctic	??	76, 78
<i>Dicrostonyx groenlandicus</i>	<i>Rauschoidea arctica</i> ★●	NA	BE	??	8, 76, 84
<i>Dicrostonyx torquatus</i> , <i>D.</i> <i>groenlandicus</i>	<i>Rauschoidea alternata</i> ★●	??	Holarctic	??	8, 76, 84
<i>Tamiasciurus hudsonicus</i>	<i>Douthittia primordialis</i> ★●	NA	N	N/A	70, 76, 80, 83
<i>Microtus miurus</i>	<i>Douthittia nordenskiöldi</i> ★●	??	Holarctic	??	76, 85
<i>Myodes rutilus</i>	<i>Douthittia nearctica</i> ★●	NA	e BE	??	76, 89
<i>Microtus xanthognathus</i>	<i>Rodentocestus freemani</i> ★◆	NA	e BE	??	74, 76
<i>Microtus</i> spp.	<i>Cookiella</i> c.f. <i>ondatrae</i> ★	NA	temperate	N/A	76, 77
<b>Hosts: Rodentia: Neotominae,</b> <b>Heteromyidae, Geomyidae,</b> <b>Sciuridae</b>	Eucestoda-Hymenolepididae				
<i>Peromyscus californicus</i> , <i>P. boylii</i> , <i>P.</i> <i>truei</i> , <i>Perognathus inornatus</i>	<i>Arostrilepis maritima</i> voegeae ◆	NA	LE (Cal)	N/A	64
<i>Thomomys bulbivorus</i>	<i>Arostrilepis schilleri</i> ◆	NA	LE (OR)	N/A	64
<i>Peromyscus polionotus</i> , <i>P. leucopus</i> , <i>P.</i> <i>mamiculatus</i> , <i>Ochrotomys nuttalli</i> , <i>Tamias striatus</i> , <i>T. amoenus</i> , <i>Ictidomys tridecemlineatus</i> , <i>Sciurus</i> <i>carolinensis</i> , <i>S. niger</i> , <i>Thomomys</i> sp.	<i>Hymenolepis folkertsii</i> ◆●	NA	Temperate	N/A	67, 68, 86
<i>Marmota caligata</i> , <i>M. broweri</i>	Eucestoda-Anoplocephalidae				
<b>Hosts: Lagomorpha</b>	<i>Diandrya composita</i> ●	NA	??	N/A	70
Ochotonidae	Eucestoda-Anoplocephalidae				
<i>Ochotona hyperborea</i>	<i>Schizorchis</i>	Asia	E	??	87, 88, 89
<i>Ochotona collaris</i>	<i>Schizorchis mongoliensis</i> ●	Asia	RE (Mongolia-e Siberia)	??	87, 88, 89
	<i>Schizorchis caballeri</i> ●	eBer	E to NWT	??	87, 88, 89



Table 2 (continued).

Focal group/host	Taxon	Origin	Colonization	Contact	Citation(s)
<i>Ochotona cansus</i>	<i>Schizorchis yamashitai</i> ●	Asia	RE	??	87, 88, 89
<i>Ochotona princeps</i>	<i>Schizorchis ochotona</i> complex ★●	NA	N	N/A	87, 88, 89
	Nematoda-Protostrongylidae				
Leporidae	<i>Protostrongylus</i>	EuA	Multiple expansions	??	90
<i>Lepus othus</i>	<i>Protostrongylus</i> c.f. <i>pulmonalis</i> ●	EuA	E	??	90
	Nematoda-Heligosomoidea				
Ochotonidae	<i>Oibayashinema</i>	EuA	Multiple expansions?	N/A	91
<i>Ochotona princeps</i>	<i>Oibayashinema aspeira</i> ◆●	NA	LE (WY)	N/A	91
<i>Ochotona princeps</i>	<i>Oibayashinema nearctica</i> ◆●	NA	LE (WA)	N/A	91
<i>Ochotona cansus</i>	<i>Oibayashinema patriciae</i> ★	Asia	CA endemic	N/A	91
	Nematoda-Molineoidea				
Ochotonidae	<i>Murielus</i>	EuA	W to E	N/A	89
<i>Ochotona cansus</i>	<i>Murielus tjanchiensis</i> ●	Asia	CA endemic	N/A	89
	Nematoda-Oxyuroidea				
Ochotonidae	<i>Cephaluris</i>	Asia	Multiple expansions	??	87, 88, 89, 92
Ochotonidae	<i>Lablostomum</i> ( <i>Eugenuris</i> )	Asia	Multiple expansions	??	87, 88, 89, 92
Ochotonidae	<i>Lablostomum</i> ( <i>Lablostomum</i> )	Asia	E	??	87, 88, 89, 92
<i>Ochotona hyperborea</i>	<i>Cephaluris</i> c.f. <i>coloradensis</i> n. sp. ★●	Asia	Siberian endemic	??	87, 89
<i>Ochotona collaris</i> / <i>O. princeps</i>	<i>Cephaluris alaskensis</i> complex ★●	NA	N	??	87, 88, 89
<i>Ochotona collaris</i>	<i>Cephaluris</i> n. sp. ★	NA	e BE	??	87, 88, 89
<i>Ochotona cansus</i>	<i>Cephaluris</i> c.f. <i>hashimi</i> ●	Asia	CA endemic	N/A	89
<i>Ochotona hyperborea</i> , <i>O. collaris</i> , <i>O. princeps</i>	<i>Lablostomum</i> ( <i>Eugenuris</i> ) <i>talkeetnae</i> complex ★●	NA	N	??	88, 89
<i>Ochitona collaris</i> / <i>O. princeps</i>	<i>Lablostomum</i> ( <i>Lablostomum</i> ) <i>rauschi</i> complex ★●	NA	N	??	87, 88, 89, 92
<i>Ochotona hyperborea</i>	<i>Lablostomum</i> ( <i>Lablostomum</i> ) n. sp. ★	Asia	w BE	??	88, 89
<i>Ochotona cansus</i>	<i>Lablostomum</i> ( <i>Lablostomum</i> ) c.f. <i>akhtari</i> ●	Asia	CA endemic	N/A	89
	Hosts: Artiodactyla				
Artiodactyla	<i>Marshallagia</i>	EuA	Multiple, W to E	??	93
Artiodactyla	<i>Teladorsagia</i>	EuA	W to E expansion w Cordillera	??	94
<i>Oreamnos americanus</i>	<i>Marshallagia lichtenjeisi</i> ★◆	NA	Arctic to w Cordillera	??	93, 95
<i>Ovibos moschatus</i> , <i>Rangifer tarandus</i>	<i>Teladorsagia boreoarcticus</i> ★●	NA?		??	94, 96, 97, 98

Table 2 (continued).

Focal group/host	Taxon	Origin	Colonization	Contact	Citation(s)
<i>O. moschatus</i> , <i>R. tarandus pearyi</i> , <i>R.t. groenlandicus</i>	<i>Teladorsagia boreoarcticus/davittiani</i> ★●	NA?	RE (Canadian Arctic)	??	97, 99
Artiodactyla	Nematoda-Protostrongylidae				
Artiodactyla	<i>Protostrongylus</i>	EuA	Multiple E expansions	??	97, 100, 101
Artiodactyla	<i>Varestrongylus</i>	EuA	Multiple E expansions	??	97, 102, 103, 104
Artiodactyla	<i>Umingmakstrongylus</i>	EuA	??	??	97, 103, 105
Artiodactyla	<i>Parelaphostrongylus</i>	EuA	W to E expansion	??	97, 100, 102, 103, 106, 107
<i>Oreamnos americanus</i>	<i>Protostrongylus rushi</i> ●	NA	w Cordillera	??	98
<i>Ovis dalli</i> , <i>Ovibos moschatus</i>	<i>Protostrongylus stilesi</i> ●	NA	Arctic to w Cordillera	??	97, 98, 100, 101
<i>Ovibos moschatus</i> , <i>Rangifer tarandus pearyi</i> , <i>R.t. groenlandicus</i> , <i>R.t. caribou</i> , <i>R.t. grantii</i> , <i>Alces alces gigas</i>	<i>Varestrongylus elegunniensis</i> ★●	NA	BE? Recent to CHA Isles	??	97, 102, 103, 104, 108
<i>Ovibos moschatus</i>	<i>Umingmakstrongylus pallikaukensis</i> ●	NA	Recent to CHA Isles	??	97, 103, 105, 108
<i>Odocoileus virginianus</i> , <i>Rangifer tarandus</i> subspecies	<i>Parelaphostrongylus andersoni</i> ●	NA	Nearctic endemic	??	97, 98, 102, 103, 106
<i>Odocoileus hemionus</i> , <i>Ovis dalli</i> , <i>Ovis canadensis</i>	<i>Parelaphostrongylus odocoilei</i> 25C9	NA	N along W Cordillera, coastal	??	97, 100, 107, 109
<i>Odocoileus hemionus</i> , <i>Rangifer tarandus grantii</i>	Nematoda-Dictyocaulidae <i>Dictyocaulus eckerti</i> ●	EuA?	Holarctic	??	98
<i>Rangifer tarandus grantii</i> , <i>Alces alces gigas</i>	Nematoda-Filarioidea <i>Onchocerca cervipedis</i> ●	EuA?	Holarctic into Neotropics	??	97, 110
<i>Alces alces</i>	<i>Alceffilaria abramovi</i> ●	Asia	RE (ne Siberia)	??	111
<b>Host group: Carnivora, Mustelidae</b>	<b>Eucestoda-Taeniidae</b>				
Mustelidae	<i>Versteria</i>	EuA?	Multiple expansions, W and E, N	??	112
<i>Mustela erminea</i> , <i>Neovison vison</i> , ( <i>Ondatra zibethicus</i> )	<i>Versteria</i> n. sp. ★●	NA	RE (OR-NWT)	??	90, 112
<i>Mustela erminea</i> , <i>M. nivalis</i>	<i>Versteria</i> n. sp. ★●	Asia?	Holarctic (Chukotka-WI)	??	90, 112
Mustelidae	Nematoda-Dioctophymatoidea <i>Soboliphyme</i>	EuA?	E; N	??	32, 62, 63

**Table 2** (concluded).

Focal group/host	Taxon	Origin	Colonization	Contact	Citation(s)
<i>Martes caurina</i> , <i>Martes americana</i> , <i>Martes zibellina</i> , <i>Neovison vison</i>	<i>Soboliphyme baturini</i> ●	Asia?	Holarctic	??	32, 61, 62, 63
<i>Martes</i> spp.	Nematoda-Trichinellidae <i>Trichinella</i> spp. ●	EuA	Holarctic, multiple E	??	113, 114, 115

**Note:** NA, North America; EuA, Eurasia; B, Beringia; CA, Central Asia; CHA, Central High Arctic; HA, High Arctic; W, westward; E, eastward; N, northward; RE, regional endemic; BStrait, Bering Strait; BE, Beringian endemic; AK, Alaska; BC, British Columbia; Cal, California; IA, Iowa; NWT, Northwest Territories; OR, Oregon; WA, Washington; WI, Wisconsin; WY, Wyoming; YK, Yukon Territory.

★Species recognized and described based on BCP specimens;

◆species recognized and described based on archival specimens related to BCP collections;

♣higher-level taxon established based on BCP specimens;

●substantially new geographic or host range recognized based on BCP specimens.

- 1) Waltari and Cook 2005; 2) Lanier and Olson 2009; 3) Galbreath and Hoberg 2011; 4) Melo-Ferreira et al. 2015; 5) Fedorov et al. 1999; 6) Fedorov and Goropashnaya 1999; 7) Fedorov and Stenseth 2002; 8) Wickström et al. 2003; 9) Hope et al. 2013; 10) Fedorov et al. 2003; 11) Conroy and Cook 2000; 12) Galbreath and Cook 2004; 13) Cook et al. 2004; 14) Runck and Cook 2005; 15) Kohli et al. 2014; 16) Kohli et al. 2015; 17) Fedorov et al. 2008; 18) Hope et al. 2016; 19) Galbreath et al. 2011; 20) McLean et al. 2015; 21) Malaney et al. 2015; 22) Demboski and Cook 2004; 23) Hope et al. 2010; 24) Hope et al. 2011; 25) Hope et al. 2012; 26) Weckworth et al. 2010; 27) Weckworth et al. 2011; 28) Cook et al. 2001; 29) Stone et al. 2002; 30) Small et al. 2003; 31) Stone and Cook 2002; 32) Karpenko et al. 2007; Koehler et al. 2009; 33) Fleming and Cook 2002; 34) Dawson et al. 2014; 35) Waltari and Cook 2005; 36) Cook et al. 2006; 37) Runck et al. 2009; 38) Brunhoff et al. 2003; 39) Iwasa et al. 2009; 40) Eddingsaas et al. 2004; 41) Weckworth et al. 2015; 42) Cronin et al. 2015; 43) Fedorov 1999; 44) Conroy and Cook 2000; 45) Sawyer and Cook 2016; 46) Jackson 2016; 47) Hope et al. 2016; 48) Malaney and Cook 2015; 49) Malaney et al. 2013; 50) Sawyer 2014; 51) Hope et al. 2014; 52) Stone and Cook 2000; 53) Peacock et al. 2007; 54) Demboski et al. 1999; 55) Greiman et al. 2013; 56) Gulyaev et al. 2007; 57) Cook et al. 2016; 58) Gulyaev et al. 2010; 59) Kormienko and Dokuchaev 2012; 60) Mel'nikova and Gulyaev 2004; 61) Koehler 2006; 62) Koehler et al. 2007; 63) Hoberg et al. 2012; 64) Makarikov et al. 2012; 65) Makarikov et al. 2013; 66) Makarikov et al. 2016; 67) Makarikov et al. 2015; 68) Hoberg et al. 2016; 69) Makarikov and Hoberg 2016; 70) Wickström et al. 2005; 71) Haukisalminen et al. 2009a, 72) Haukisalminen et al. 2008, 73) Haukisalminen and Henttonen 2003, 74) Haukisalminen et al. 2006, 75) Haukisalminen et al. 2007, 76) Haukisalminen et al. 2014, 77) Haukisalminen and Henttonen 2000, 79) Haukisalminen and Henttonen 2007, 80) Haukisalminen et al. 2009b, 81) Haukisalminen et al. 2016, 82) Haukisalminen et al. 2008, 83) Haukisalminen et al. 2004, 84) Wickström 2004; 85) Haukisalminen et al. 2001; 86) KE Galbreath unpub. data; 87) Galbreath 2009; 88) Galbreath and Hoberg 2012; 89) Galbreath and Hoberg unpub. data; 90) BCP unpub. data; 91) Durrrette-Desset et al. 2010; 92) Hoberg et al. 2009; 93) Hoberg et al. 2012b, 2012d; 94) Hoberg et al. 1999; 95) Jenkins et al. 2004; Hoberg et al. 2012d; 96) Streele et al. 2013; 97) Kutz et al. 2012; 98) Hoberg and Beckman unpub. data; 99) Hoberg et al. 2012a, 2012c; 100) Kutz et al. 2001b; 101) Hoberg et al. 2002; 102) Kutz et al. 2007; 103) Kutz et al. 2013; 104) Verocai et al. 2007; 105) Kutz et al. 2014; 106) Asmundsson et al. 2008; 107) Jenkins et al. 2005; 108) Kafle et al. 2015; 109) Hoberg et al. 2005; 110) Verocai et al. 2012; 111) Dokuchaev and Atrashkevich 2001; 112) Lee et al. 2016; 113) Zarlenga et al. 2006; 114) Pozio et al. 2009; 115) Korhonen et al. 2016; 116) Galbreath et al. 2013.

suggests that these species did not disperse from Beringia after the last ice age and implies limited importance of Beringia as a source of post-glacial colonization.

Phylogeographic analyses based on broad BCP sampling are revealing concordant zones of genetic differentiation (Fig. 5) that help interpret the impact of the boundaries of the Beringian refugium, such as the Upper Kolyma region of Siberia in the west (e.g., Galbreath and Cook 2004; Kohli et al. 2015; Haukisalmi et al. 2016) and near the Yukon–Alaska border in the east (Dawson et al. 2014). In addition, the influence of smaller peripheral refugia in the Canadian Arctic (Fedorov and Stenseth 2002; Fedorov et al. 2003; Cook et al. 2016b), southeast Alaska (Cook et al. 2001; Sawyer and Cook 2016), and in the periglacial zone south of the Laurentide and Cordilleran ice sheets (Fedorov et al. 2003) is being explored. Early attempts to unravel the evolutionary history of arctic ground squirrels (*Urocitellus parryii*), one of the quintessential high-latitude mammals, relied on a view of Beringia as a vast steppe with few natural barriers to gene flow (e.g., Nadler and Hoffmann 1977). However, our work to test those ideas in *U. parryii* elucidated range-wide phylogeographic structure and a dynamic history of diversification spanning the Bering Land Bridge (Eddingsaas et al. 2004; Galbreath et al. 2011; McLean et al. 2016b), suggesting that late Pleistocene environmental changes within central Beringia supported significant regional differentiation in this species. Such insights establish a template for testing hypotheses of fine-scale phylogeographic structure in other northern taxa.

Five groups of cyclophyllidean tapeworms represented by the genera *Arostrilepis*, *Anoplocephaloides*, and *Paranoplocephala* among cricetids, *Versteria* among small to medium mustelids and rodents, and *Staphylocystoides* in shrews further serve as critical exemplars demonstrating the importance of Beringia as a center of diversification. Based on patchy geographic and host sampling, *Arostrilepis* was historically thought to be represented by a single geographically widespread and hypervariable species with a considerable host range across the Holarctic (Schiller 1952; Ryzhikov et al. 1978). By contrast, recent morphological and molecular investigations of *Arostrilepis* specimens collected primarily through the BCP led to the formal description (or redescription) of 13 species spanning the Holarctic and centered on Beringia (e.g., Makarikov et al. 2013). Further, the discovery of at least 15 unnamed genetic lineages appears consistent with a yet broader cryptic assemblage of species among cricetid, geomyid, heteromyid, and dipodid rodents extending into Boreal and Temperate zones in the Nearctic (Haas et al., unpublished data). A complex history involving recurrent expansion events across Beringia (intercontinental) and also from multiple refugia within Eurasia or North America (intracontinental) has driven geographic and host colonization and was the primary determinant of diversification through considerable faunal mixing over time (e.g., Hoberg et al. 2012a).

Similarly, *Paranoplocephala* and *Anoplocephaloides* continue to represent complicated and taxonomically problematic assemblages of species with broad geographic ranges in the Holarctic (Haukisalmi and Henttonen 2003; Haukisalmi 2009; Haukisalmi et al. 2009b, 2014, 2016). With important contributions from BCP collections, tapeworms that are predominately associated with northern arvicolines and previously assigned to the *Paranoplocephala omphalodes* complex are now recognized as at least 14 distinct genera based on integrated morphological and molecular data (Haukisalmi et al. 2014). Phylogenies for these cestodes suggest that episodes of host colonization by parasite lineages contributed to diversification while they created novel host–parasite interactions due to past episodes of range expansion from multiple refugia (e.g., Wickström et al. 2003; Makarikov et al. 2013; Haukisalmi et al. 2016).

Parasite diversity, in combination with phylogenetic and population data, is critical to revealing otherwise cryptic histories for mammalian hosts. For example, *Rauschoides arctica* (formerly *Paranoplocephala*) found in *Dicrostonyx* lemmings contains subclades that are

either geographically widespread or restricted to islands of the Arctic archipelago (Wickström et al. 2003), a pattern consistent with isolation of multiple populations of hosts and parasites north and south of the continental glaciers during glacial maxima. Post-glacial expansion from south to north tracked deglaciation (Lessa et al. 2003) and brought previously isolated parasite populations into contact. Further, the boundaries for Nearctic and Eurasian host populations were not always at the Bering Strait, as indicated by *Dicrostonyx* of Neartic origin on Wrangel Island (Fedorov and Stenseth 2002), while *R. arctica* in these collared lemmings is represented by two discrete clades of Palearctic origin. Among lemmings, this may be another example of complex lineage persistence through host colonization prior to the local extinction of the original host group (Hoberg and Brooks 2008), in this case Eurasian *Dicrostonyx*. Complex signatures of geographic colonization are also indicated in *Anoplocephaloides* in lemmings (Haukisalmi et al. 2016) and in the nematode *Soboliphyme baturini* in marten (Koehler et al. 2009a; Hoberg et al. 2012b).

In its role as a high-latitude refugium, Beringia has long been recognized as stimulating the evolution of endemic northern faunas (Sher 1984, 1999). However, as population histories and species distributions become more fully resolved across Beringia, a more nuanced picture is emerging that links climatic oscillations, opening and closing of dispersal barriers, and geographic range fluctuations as major drivers of diversification in the region (Cook et al. 2004; Galbreath et al. 2011; Hoberg et al. 2012a; Hoberg and Brooks 2013). This new concept of Beringia as both a facilitator of intercontinental dispersal and a venue for in situ diversification significantly extends our view of land bridges and their importance in biotic diversification, including in expansion into the Americas by ancient humans (Hoffecker et al. 2014). This complex history is evident especially in some northern rodents (e.g., Fedorov et al. 2003) as well as in the tremendous diversity of their helminths, the full extent of which is only now becoming apparent through investigation of extensive BCP collections (e.g., Wickström et al. 2003, 2005; Haukisalmi et al. 2006, 2007, 2014; Lee et al. 2016).

### **Beringia's long reach — extending the temporal and geographic influence of the crossroads**

Beringia has had a strong influence not only on Eurasian and Nearctic faunas but also on faunal dynamics in the Neotropical region (e.g., proboscideans: Shoshani and Tassy 1996). Our understanding of these biogeographic linkages is improving due to increased availability and geographic and taxonomic coverage of mammal and parasite specimens (e.g., Conroy et al. 2001; Hoberg 2005; Pozio et al. 2009; Esteva et al. 2010; Hoberg et al. 2012a; Korhonen et al. 2016). For example, assemblages of *Trichinella* nematodes that circulate through carnivory or scavenging by various mammals (e.g., carnivores, suids, and rodents) provide insights into colonization processes from Eurasia through the Nearctic and extending into the tropics (e.g., Pozio et al. 2009; Korhonen et al. 2016). The clade of “encapsulated” *Trichinella* initially diversified in central Eurasia with subsequent history dominated by sequential events of geographic and host colonization that account for the distribution of nine recognized species (Zarlenga et al. 2006). A single species, *T. patagoniensis*, is endemic to southern South America among small felids that radiated near 8 MYBP (Johnson et al. 2006). Distribution and phylogeny are consistent with geographic expansion from Eurasia with small felids, across a proto-Beringia during the late Miocene, through the Nearctic, and across an emergent or nascent Panamanian Isthmus near 10 MYBP prior to the Great American Interchange that ensued about 3–5 MYBP (Bacon et al. 2015).

Subsequently, the temporal duration and spatial history for radiation of an assemblage of *Trichinella* at high latitudes appear constrained by events in the late Pliocene and through the Quaternary. Climatological forcing and ecological perturbation served as determinants of recurrent episodes for expansion, colonization, and the origins of extensive faunal

mosaics (e.g., Hoberg et al. 2012a; Korhonen et al. 2016). Contact zones and a broad geographic boundary demonstrated between *T. nativa* and the currently unnamed T-6 genotype among wolverines in northwestern Canada may reflect the most recent post-glacial expansion events following the last glacial maximum about 11 KYBP (e.g., Dunams-Morel et al. 2012).

### **Beringia: tracking the pulse of change — impacts of accelerated warming in the Arctic**

Global climate warming is having a disproportionate influence on Arctic ecosystems (IPCC 2013) and the consequences of this change are yet to be fully realized. BCP collections are helping us to understand the implications of climate change for species distributions and community diversity (e.g., Baltensperger and Huettmann 2015; Hope et al. 2015) and to monitor fundamental biological attributes such as life histories, life cycles, and parasite transmission dynamics (e.g., Kutz et al. 2005; Jenkins et al. 2006; Laaksonen et al. 2015). For example, a series of discoveries based on field collections radically altered our understanding of the ungulate lungworm fauna in the Beringian region and broadly across the Holarctic (e.g., Hoberg et al. 1995, 2008, 2017; Kutz et al. 2001b, 2007; Jenkins et al. 2005). Links between lungworm demography and climate were elucidated through the development of DNA sequence-based diagnostic methods that probed extensive archival samples from across the North American Arctic (e.g., Kutz et al. 2012; Hoberg et al. 2013; Verocai et al. 2014). Application of these methods demonstrated recent range expansion onto Victoria Island from the mainland of the central Canadian Arctic by the lungworms *Umingmakstrongylus pallikuukensis* in muskoxen and *Varestrongylus eleguneniensis* primarily in barren-ground caribou (Kutz et al. 2013; Hoberg and Brooks 2015). Global warming that led to a climatological tipping point contributed to this expansion as development and transmission of *Umingmakstrongylus* shifted from a 2- to a 1-year cycle (Kutz et al. 2005). Accelerated development by larvae in gastropod intermediate hosts resulted in increasing abundance and infection pressure for parasites in muskoxen. Changing infection dynamics, in conjunction with a shifting balance in the distribution of permissive environments in the low Arctic islands, facilitated northward expansion since 2000 (Kutz et al. 2013; Hoberg and Brooks 2015). Lungworms provided the first examples of climate-related changes in development and distribution for any macroparasite in a large mammal (Kutz et al. 2005).

The generality of climate as an important determinant for host–parasite assemblages emerges from insights derived from specimens. Climate change influences population establishment and subsequent range shifts, structuring diversity across both temporally shallow (e.g., as demonstrated on Victoria Island) and deep time (e.g., episodic events linked to climate oscillations throughout the Quaternary). On the periphery of expanding geographic ranges, ecological perturbation drives the opportunity for colonization due to a shifting balance in the range of permissive environments suitable for parasite development and opportunities for expansion and establishment that are directly limited by capacities for transmission, resilience, and persistence in an array of host species (Agosta et al. 2010; Hoberg and Brooks 2015; Laaksonen et al. 2015). Further, these signify the Beringian nexus as a fundamental exemplar of biotic assembly as addressed in the Stockholm Paradigm (e.g., Hoberg and Brooks 2008, 2013, 2015; Hoberg et al. 2012a; Araujo et al. 2015).

### **Beringia: a model for reframing priorities — conservation genetics and genomics**

The global climate is changing with an expected irreversible state shift that may already be in play (Barnosky et al. 2012). Northern high latitudes are a special focus because the biota is currently experiencing heavy impacts from three directions: competition from invasive and nonnative species, habitat conversion, and climate warming. Both intentional

and accidental introductions of nonnative species have already led to significant changes in northern environments. BCP collecting efforts identified introductions of *Peromyscus maniculatus* in the Copper River Basin (MacDonald et al. 2009) and red squirrels (*Tamiasciurus hudsonicus*) to several islands in southeast Alaska (MacDonald and Cook 2007) as well as a series of new distributional records of mammals (e.g., Cook et al. 2016b). We also provided further documentation of introduced populations of Nearctic *Neovison* and *Ondatra* in the Palearctic. These and other anthropogenic introductions have considerable implications for host and parasite diversity and should be carefully monitored (e.g., Hoberg et al. 2015). BCP collections provided the critical sampling required to test questions related to how introduced populations expand with considerable impacts on native, often naïve organisms.

Of particular concern are populations isolated on islands, especially those of the Aleutian Islands, Alexander Archipelago, and Canadian Arctic Archipelago. Fur “ranchers” introduced fur-bearers such as arctic and red fox, marten, and mink and their prey, especially arctic ground squirrels, to more than 450 islands in Alaska (Bailey 1993) in the 20th century. These introductions had devastating impacts on the native fauna, including nesting waterfowl such as geese (Bailey 1993). Molecular genetic analyses of BCP samples of 17 arctic ground squirrel populations (including 12 North Pacific islands) throughout southwestern Alaska (Cook et al. 2010) provided a framework for disentangling recent human-mediated introductions from older endemic populations, with the study largely corroborating the written record of early explorers. Such specimen-based projects allow federal managers to prioritize eradication efforts while also protecting endemic populations.

Conversely, some species that show deep phylogeographic structure in northwestern North America occur naturally on the western islands of the Alexander Archipelago (e.g., Dawson et al. 2014). Some of these distinctive lineages of mammals and associated parasites represent paleoendemics, meaning that their DNA signatures reflect long-term persistence and divergence in glacial refugia along the North Pacific Coast (Koehler et al. 2009a; Hoberg et al. 2012b; Sawyer and Cook 2016), and these signatures are consistent with the Coastal Refugium Hypothesis. Phylogeographic studies along the North Pacific Coast, combined with insight from fossils recovered from the extensive karst systems (Heaton and Grady 2003), suggest that a suite of terrestrial species persisted nearby in coastal ice-free refugia during glacial advances. Identification of these endemic taxa in the region brings them to the attention of natural resource managers, increasing the likelihood of their persistence (Dawson et al. 2007).

In the early 1900s, the Alaska Game Commission introduced American marten (*Martes americana*) from the mainland to select islands of Southeast Alaska’s Alexander Archipelago to strengthen local economies under the assumption that no marten species previously inhabited these islands. Genetic (Stone et al. 2002; Small et al. 2003; Dawson et al. 2017) and parasitological (Koehler et al. 2007; Hoberg et al. 2012b) investigations stemming from BCP collections now suggest that several islands in the Alexander Archipelago harbor a different species, the endemic Pacific marten (*Martes caurina*), and that some of their populations may have been negatively impacted by competition and hybridization with introduced *M. americana*. Salvaged marten carcasses collected annually over the last two decades, if bolstered by continued specimen collecting, will offer rare opportunities to explore the dynamics of these human-mediated hybrid zones. Because translocated, endemic, and hybrid populations occur across a series of islands, the Alexander Archipelago provides a powerful series of independent experiments that can illuminate outcomes of species introductions and other perturbations (e.g., industrial logging) on these insular mesocarnivore populations.

Another mustelid example from high latitudes hinges on a series of studies of ermine across the Holarctic that revealed four independent phylogenetic lineages with disparate demographic and evolutionary histories (Fleming and Cook 2002; Dawson et al. 2014; Colella et al., unpublished data). Two ermine lineages are widely distributed across the Arctic and meet in south coastal Alaska. Fine-scale BCP sampling within that region and including the Alexander Archipelago shows that a third distinctive lineage is endemic to just a few islands (Prince of Wales Archipelago and Haida Gwaii). This island lineage roughly corresponds to the subspecies *Mustela erminea haidarum*, and is federally protected in Canada; however, in Alaska, these ermine are not protected within their restricted range. Given the history of intensive habitat conversion that these coastal regions have experienced, combined with change underway due to warming climate (Hennon et al. 2012), informed wildlife management depends on a solid understanding of both the distribution and the biogeographic history of species because an unusually high percentage of taxa have been identified as endemic along the North Pacific Coast (Cook and MacDonald 2001). This foundation can only be provided by spatially extensive and site intensive archives like those of BCP (Cook et al. 2006; Cook and MacDonald 2013).

### Specimens, synergy, and synthesis — a role for integrative field sampling

Museum collections that are temporally deep and include multiple specimens of multiple species from each sampling location provide key infrastructure for addressing a series of biodiversity-based challenges headed into the middle of the 21st century. First, museums house considerable primary data (e.g., species identity, date of collection, georeferenced collection locality, and standard measurements) that can immediately inform biodiversity assessments and form the basis for predictive models of the future (Hope et al. 2013, 2015). Second, as specimens and the sampling they represent are used in future investigations, large amounts of new or derivative data (e.g., genomes, stable isotopes, morphometric data, or parasite–host associations) become associated with the specimen record and can be readily accessed by research communities. Museums are increasingly tracking and linking (e.g., arctos.database.museum) these web-accessible derivative data (e.g., GenBank), with each specimen providing a powerful nexus between distinct research agendas and allowing for more integrated views of high-latitude biodiversity under a regime of climate change (Fig. 4). Recent policy changes in federal science agencies (e.g., NSF and US Geological Survey (USGS)) require greater data sharing and will be facilitated by the linking of derivative data with museum collections.

Our current Arctic snapshots reveal substantial insights about biodiversity, connectivity, and continuity of these high-latitude systems. Specimens, data, interpretations, and biodiversity informatics across complex assemblages tell us about the history and provide a pathway to anticipate the outcomes of change and perturbation at high latitudes. The geographic and taxonomic scale of the BCP collections are to a degree unprecedented and as such provide considerable capacity as baselines against which to recognize and measure accelerating perturbation across scales in the Holarctic and extending into the Boreal–Temperate zones of North America and Eurasia (e.g., Cook et al. 2013; Hoberg et al. 2013). The scope and depth of collections, however, are both a blessing and a challenge. Although integrated studies have contributed to a deeper understanding of the historical processes that have shaped northern systems, considerable gaps remain. Extracting meaningful information from specimens such as those generated by BCP will rely on forward-looking museum staff, resource managers, and researchers, but also on a diminishing number of systematists, taxonomists, and biogeographers. Given the current level of taxonomic instability (Morrison et al. 2009) across parasite taxon groups, such efforts will



require sweeping species-level resolution of diversity. In most cases, this demands integration of molecular and morphological criteria (e.g., Makarikov et al. 2013; Haukisalmi et al. 2014, 2016). Connecting the dots that link historical processes and ecological explanations has implications for our basic understanding of northern ecosystems in perturbation.

Tapeworms infecting shrews in the genus *Sorex* provide an example of the magnitude of the challenge that remains. In North America alone, there are over 40 species of cestodes, with many taxa yet to be described (Greiman et al. 2013). Indeed, the tapeworm fauna of eulipotyphlan shrews is probably among the most diverse of any group of mammals. Given that a single *Sorex* individual may harbor hundreds of individual cestodes representing more than a dozen species, identifying samples by classical methods (staining and slide mounting) is a monumental undertaking. Fortunately, next-generation sequencing technologies have made accurate and efficient identification of helminth taxa possible by means of metagenomics (Tanaka et al. 2014; Hino et al. 2016). Metagenomics approaches that use not only fecal samples but also whole gastrointestinal tracts of historic fluid-preserved samples will complement classic techniques and generate a more complete picture of parasite diversity and dynamics in the Arctic. These emerging tools are especially important as we track how parasite communities are changing across the immense Arctic region.

Data derived from specimens collected over the past two decades have yielded considerable insights about and recognition of new diversity at all levels across carnivore, artiodactyl, rodent, lagomorph, and soricid hosts and their parasites. The BCP is changing the narrative about Beringia, shifting from single-species investigations to explorations of faunal structure and assembly over time. This capacity to examine assemblages through time emerges from strongly hypothesis-oriented frameworks for the project, the powerful concept of integrated field collections (specimens and archives) to explore diversity, and a combination of phylogenetic/phylogeographic/population approaches used to recover the histories of a series of northern organisms across the variable landscapes of Quaternary Beringia, but the effort has only just begun. Much remains to be elucidated regarding how species expanded and contracted, contributing to the reshuffling of ancient communities and the evolution and assembly of parasite faunas. This information is paramount for predicting and interpreting biotic responses to rapidly shifting environments. Specimens and data archived through the BCP and incorporated into biodiversity informatic pipelines will continue to be capable of strong contributions to our understanding of perturbation in northern ecosystems at scales ranging from species to ecosystems.

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