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REVIEW PAPER

Origins and diversity of the Bering Sea Island fauna: shifting linkages across the northern continents

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Abstract

We synthesize the historical biogeography of non-marine fauna (mammals, birds, fish, non-parasitic and parasitic invertebrates) occurring across Bering Sea islands, considering endemism, species with origins in both North America and Far East Asia, and the impacts of introduced species through the Bering region. Insular communities often constitute assemblages of unique evolutionary lineages that reflect both neutral and selective processes of diversification as a consequence of isolation and through responses to in situ environmental change. However, current knowledge of the basic distribution, ecology, and evolutionary identity of the majority of terrestrial species through the Bering Sea region is still generally lacking. A preponderance of scientific effort associated with these islands has instead focused on conservation and management of marine-associated species and economically viable biological resources. Given the critical role that terrestrial environments play in maintaining evolutionary and ecological linkages between land and sea, a greater understanding of existing biodiversity, and the biological processes that influence community integrity through this remote region is warranted. Resolving responses of resident insular species to rapidly warming Arctic climate and to modern human-associated disturbances provides valuable insight for effective management of future population trajectories and for revealing the dynamics of intra- and inter-specific connectivity across the northern hemisphere and between marine and terrestrial ecosystems. The location of this region at a high-latitude cross-roads has led to a preponderance of island taxa having trans-Beringian distributions. Species associated with the Palearctic or the Nearctic occur across a strong longitudinal gradient, reflecting the role of the Bering Sea as a dispersal filter between mainland areas. Aleutian oceanic islands reflect different biogeographic histories among taxonomic groups from land-bridge islands of the Bering Sea. We discuss evidence of recent biodiversity responses to modern environmental perturbations, including continued colonisations and novel species interactions, and call for increased scientific scrutiny of terrestrial fauna across these remote outposts.

Keywords Beringia · Conservation · Climate change · Evolution · Introduced species · Island biogeography

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Introduction

Diversification of terrestrial faunas distributed across the biogeographic province of Beringia (Hultén 1937) epitomizes a dynamic history of biotic linkages between north-western North America and Far Northeast Asia. The Quaternary "ice age" (last 2.6 Myr) was characterized by an on-average colder global climate than the preceding Tertiary period, punctuated by a cyclic glacial-interglacial phase regime, with abundant literature documenting global impacts of this climatic variability on the evolution and ecology of biodiversity (Hewitt 1996; Avise et al. 1998; Hofreiter and Stewart 2009; Weigelt et al. 2016). At the cross-roads of the northern continents, repeated exposure of the Bering Isthmus (often referred to as the Bering Land Bridge) during glacial (cold) climate phases, as a result of terrestrial ice accumulation and corresponding lowered sea-levels, allowed for communities to continuously ebb and flow through this region (Sher 1999; Repenning 2001; Hoberg et al. 2012). Although ice sheets covered much of Europe and North America, displacing species during glacial times, vast areas within Beringia and central Asia remained ice-free, supporting predominantly arid polar steppe communities during glacial periods and mesic tundra or boreal forest biomes during interglacial (warm) stages, including at present (Pielou 1991; Elias et al. 1996; Guthrie 2001; Abbott and Brochmann 2003; Hewitt 2004; Haukisalmi et al. 2006). As such, species could periodically disperse between continents, generating Holarctic linkages (Hopkins 1959; Waltari et al. 2007; Eidesen et al. 2013).

Other Beringian species adapted in situ, diverging within isolated refugia and resulting in local endemism (Elias 1992; Brubaker et al. 2005; Pruett and Winker 2008; Sikes and Allen 2016). Beringian glacial environments also constituted a barrier or dispersal filter for many species due to habitat heterogeneity and climate severity, leading to detectable community turnover across longitude (DeChaine 2008; Elias and Crocker 2008). In contrast, during interglacials, terrestrial species were more isolated between Asia and North America across the Bering Strait (Sher 1999). Modern conditions exemplify this latter situation, with physical isolation of terrestrial faunas between Eurasia and North America, although dispersal has continued through various mechanisms.

Onset of interglacial climate led to inundation of the Bering Isthmus approximately 11,000 years BP (Elias et al. 1996; Jakobsson et al. 2017), loss of continental ice-sheets allowing for recolonisation of previously glaciated land, and fragmentation of land-bridge islands. In addition to Quaternary climate cycling and associated sea-level fluctuations, volcanism along the Aleutian arc at the subduction zone of the Pacific Tectonic Plate continues to impact the geology of oceanic islands that delimit the southern perimeter of the Bering Sea (Coats 1950). These islands maintain a barrier between cold sub-Arctic water and the more temperate Pacific Ocean (Ezer and Oey 2010). Aleutian terrestrial faunal biodiversity is a result of active or passive dispersal, or introduction via air or sea, reflecting biogeographic characteristics of oceanic island systems. However, being at high-latitude, this island arc was also subject to repeated glaciation coupled with volcanic events that reset local communities (e.g. Sikes and Slowik 2010; Walker et al. 2013), in contrast to the ice-free Bering Isthmus further north (see Bond 2019).

Beringia has also been a corridor for human movement through both terrestrial and coastal dispersal routes, from the earliest colonisation of North America to present-day habitation across mainland and island systems (Hoffecker et al. 2014; Graf and Buvit 2017). Local impacts from human-related stressors also span this timeframe and have been exacerbated by major climatic shifts (Wooller et al. 2018), including evidence for contributing to megafaunal overkill from the early Holocene (Mann et al. 2015; Lanoë et al. 2017).

Modern anthropogenic perturbations include settlement, industrial development, harvest of natural resources, and human-facilitated species invasions (Croll et al. 2005; Major et al. 2006; Huntington et al. 2015; Haynie and Huntington 2016). These are coupled by evidence for northward expansion of temperate biodiversity into the Bering Sea region associated with terrestrial and oceanic warming (Overland and Stabeno 2004; Chan et al. 2019).

Mainland Beringia has been the focus of extensive research associated with long-term geologic, climatic and biodiversity changes (Hopkins et al. 1982; Shapiro and Cooper 2003; Walsh 2008; Cooper 2014). Most terrestrial biodiversity research has emphasized (1) Warm phase (modern) ecology and population trends of species occurring through mainland areas, (2) Cold phase community dynamics across the Beringian Isthmus during the Wisconsinan glacial (~75 to 11 kya), or (3) Comparative phylogeographic evidence for evolutionary processes of diversification or extinction through the Quaternary, often with broad sampling across the Holarctic of wide-ranging taxa with distant origins. However, much less is known of faunal diversity occurring across land-bridge and oceanic island systems (Murie and Scheffer 1959). Island faunal communities are relatively depauperate compared with proximate mainland areas and are subject to classic island biogeographic consequences of immigration, extinction, extended isolation, and invasive species biology across both land-bridge and oceanic islands (Heaney 2007; Sax et al. 2007; Whittaker and Fernández-Palacios 2007). As such, resolving the historical biogeography of species including evolutionary origins, genetic demographic trajectories, and both ecological and co-evolutionary connections within the Bering Sea region in the context of contemporary environmental stressors will likely help in recognizing and interpreting continued biodiversity trends (Cook et al. 2017; Hoberg et al. 2017).

Here we synthesize data available from limited (and often old) literature concerning the diversity and origins of terrestrial fauna (mammals, birds, freshwater fish, non-parasitic and parasitic invertebrates) occurring across Bering Sea islands. We review the biogeographic history of discrete terrestrial habitats across latitudinal and longitudinal gradients, climatic thresholds, and variable geographic connectivity. Importantly, we focus on changing linkages among species and how complex species interactions may be important for future community integrity as anthropogenic environmental changes accelerate. This is particularly evident within the Bering Sea region given the intimate connections between islands and both marine ecosystems and avian migrants that encroach on terrestrial habitats and interact with resident species (Causey et al. 2005). These abundant marine and aerial resources are likely vital for the persistence of many terrestrial plants and animals, through dynamic biodiversity connections with terrestrial species through time (e.g., Polis and Hurd 1996, Wainright et al. 1998). The existing data highlight both predictable and idiosyncratic species responses to long term regional climate and geography, and importantly point to demonstrable gaps in our knowledge of basic biodiversity data from this region and how changing species associations may impact future community structure and functional diversity on islands (Boyer and Jetz 2014).

Study system and theory

Island groups

lsIands of the Bering Sea include the Aleutian archipelago, the Pribilof Island group, the Northern Islands, and numerous coastal land-bridge islands in proximity to mainland areas of both Far East Siberia and Alaska (Fig. 1). The Aleutian Islands constitute a narrow arc of mostly volcanic islands spanning the southern edge of the Bering Sea. They currently consist of ~200 named islands and numerous islets separated into six biogeographic groups by deep ocean passes connecting the Pacific Ocean and Bering Sea. Groups include (from west to east) the Russian Commander Islands, U.S. Near Islands, Buldir Island, Rat Islands, Andreanof Islands, and Fox Islands (including the Islands of Four Mountains group; Fig. 1). We consider these separately based on their connectivity through glacial cycling, whereby intra-group islands were connected by lowered sea levels during cold phases, but separated from other groups. The functional relevance of this for biodiversity is yet unclear, given the geological evidence indicating that glacial ice likely capped all Aleutian Islands in totality during glacial maxima (Thorson and Hamilton 1986). This effectively removed terrestrial biodiversity for extended periods with repeating cycles of ecosystem reassembly (Mann and Hamilton 1995). Most groups are true oceanic islands having never experienced mainland connections. As an exception, the Fox Islands group was connected to the mainland Alaska Peninsula by extensive ice from the northernmost projection of the Cordilleran Ice Sheet (Thorson and Hamilton 1986) as illustrated by Bond (2019) in a recent paleo-reconstruction map of Beringia during the last glacial maximum. It is possible the northern (Bering Sea) edge of this extended peninsula remained partially ice-free allowing for persistence of species, and for mainland connections of the Fox Islands (in the eastern Aleutian islands) as far west as Umnak and Anangula Islands (Black 1974).

Conversely, north of the Aleutian chain the glacial phase climate was colder and drier, leading to year-round sea-ice in the remaining Bering Sea, but ice-free conditions across the Bering Isthmus (Hopkins et al. 1982). As such, current land-bridge islands have supported terrestrial species continuously through successive glacial cycles (Rausch 1963; Garroutte and Ickert-Bond 2013). The Pribilof Island group consists of four islands located on the edge of the submerged Bering Isthmus. These islands are furthest south of the land-bridge groups, were first to be isolated from the mainland (~14–13 kyr; Colinvaux 1981;

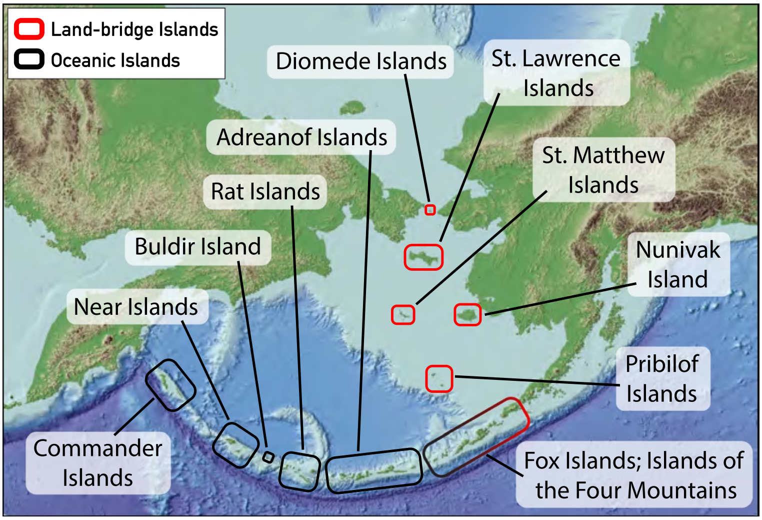

Fig. 1 Map of the Bering Sea Basin indicating the major island groups discussed. Islands are indicated as either land-bridge (red) or oceanic (black) in origin, where the Fox islands group may have been partially but not fully connected to the Bering Isthmus through time

Graham et al. 2016), and currently experience the warmest climate among land-bridge islands. As illustrated by Guthrie (2004: Fig. 1), the Northern Islands were sequentially isolated from mainland areas since the Last Glacial, including the St. Matthew group (10 kyr), Big and Little Diomede group (9 kyr), and St. Lawrence group (8 kyr) islands. Nunivak Island is situated in proximity to the southwestern Alaska mainland and was isolated most recently (5 kyr). These island groups are all characterized by Arctic-associated climate and biodiversity (Guthrie 2004).

Theoretical predictions for Bering Sea terrestrial faunal assembly

Islands of the Bering Sea region support species distributions that reflect multiple biogeographic histories, enabling application of predictions from island biogeographic theory to resolve processes influencing species richness and genetic diversity. MacArthur and Wilson (1967) posited that relative island area and isolation provide statistical power for explaining rates of colonisation, extinction, and patterns of insular species richness. Larger, less isolated islands are considered to receive more colonists and experience higher geneflow, resulting in greater richness, genetic diversity, and population carrying capacity, with correspondingly lower risk of extirpation or extinction through stochastic processes (Vellend 2003; Vitousek et al. 2013). Reflective of these dynamics, larger islands also tend to have greater habitat heterogeneity thus increasing opportunity for intra-island allopatry and divergence, particularly for species with low dispersal capabilities (Kisel and Timothy 2010). As such, a combined assessment of both ecological (area and isolation) and evolutionary evidence (addressing genetic diversity, phylogeographic history and phylogenetic relationships) might best explain the history of formation of native Bering Sea island faunas (Graham and Fine 2008).

Oceanic islands, formed from reef deposition, volcanism, or tectonic uplift, are originally devoid of terrestrial species, and communities assemble through colonisation (including introduction) and in situ diversification. Generally they exhibit lower richness compared to mainland or land-bridge islands of similar area, latitude, and isolation (Kier et al. 2009; Losos and Ricklefs 2009). Populations on oceanic islands generally also experience low gene flow from infrequent immigration of conspecifics, small initial population size and correspondingly rapid genetic drift following colonisation (Frankham 2008), often accompanied by low genetic variation from colonisation bottlenecks. However, lower richness on oceanic islands and vacant niche space may also allow for rapid proliferation, population growth, and local adaptive divergence. These combined dynamics can result in high island endemicity and the capacity for rapid radiations through an archipelago. Volcanic islands of the Aleutian arc have formed over the past 50 million years. However, the unique glacial history of this archipelago means that extant terrestrial diversity resulted from recent colonisation (<15 kyr), with expectations of non-equilibrium communities, low in situ endemism, low population genetic diversity, and low differentiation across islands (Hata et al. 2017). In addition, the geographic orientation of this island chain, coupled with local geology and location within productive seas, have enabled a major migration corridor between the northern continents with prolific breeding and feeding grounds for millions of sea-and shore-birds representing dozens of species (Henningsson and Alerstam 2005; Alerstam et al. 2007). Oceanic currents also flow along the island chain, both south of the chain (east to west; Alaskan Stream) and north (west to east; Aleutian North Slope Current) resulting in a steep temperature gradient between the Bering Sea and North Pacific (Stabeno et al.

1999; Sigler et al. 2011). Despite the young age of Aleutian terrestrial populations, flyways and surface currents have likely increased colonisation rates, providing expectations for linear connectivity and for longitudinal colonisation histories from multiple mainland areas (Emison et al. 1971; Winker and Gibson 2018) .

Non-Aleutian Bering Sea islands are all land-bridge in origin, sharing glacial-phase terrestrial connections with the Bering Isthmus, and reflecting different ecological and evolutionary dynamics. At time of isolation through rising sea-levels, these islands would have supported a fuller complement of species that occurred locally within Beringia (Elias et al. 1996). Subsequent rapid reduction in land area, changing climate, and limiting resources, would have caused faunal relaxation, reducing species richness to new equilibria dependent on area, but with higher richness for a given area relative to Aleutian islands (Ickert-Bond et al. 2013; Garroutte et al. 2018). However, communities across these islands may have lacked uniform nestedness (where smaller islands theoretically support predictable subsets of the faunas of larger islands) as seen in other northern archipelagos including the Alexander Archipelago of Southeast Alaska (Conroy et al. 1999), given the stochastic nature of faunal relaxation coupled with high regional habitat heterogeneity across the intact Bering Isthmus through the last glacial phase (Elias et al. 2000). Relative isolation and position of Bering land-bridge islands should thus be a poor predictor of faunal similarity, although a lack of adequate data on faunal diversity and distributions across these islands precludes an accurate assessment of nestedness at this time. Similar to faunal relaxation, population genetic diversity should be higher at time of isolation, followed by periodic purging through repeated population fluctuations across a 5–12 kyr time-span, (Hewitt 1996; Eidesen et al. 2013). Environmental and demographic stochasticity through this period would have been high, given the northern latitude of these islands and Arctic climate. Both drift and adaptive change were potentially pervasive evolutionary processes. Finally, given data from changing bathymetry since the last glacial phase, connections with Siberia of northernmost land-bridge islands were severed prior to isolation from the Alaska mainland, indicating closer biogeographic affinities of insular species to the Nearctic, whereas the Pribilof Islands and St. Matthew were both isolated before the Bering Strait formed (Colinvaux 1981; Guthrie 2004; Graham et al. 2016).

From a comparative perspective, differences in non-marine faunas between the Aleutian and land-bridge archipelagos should include relative degree of endemicity, levels of divergence from mainland populations, and preponderance of local adaptation versus neutral divergence through drift (Hampe and Petit 2005). Land-bridge islands effectively constitute refugia for populations previously more widespread across the Bering Isthmus, retaining unique genetic signatures in legacy species that may help resolve origins (west, east, local endemic), species interactions (degree of co-evolution), and community assembly (ongoing colonisations/extinctions) through time (Conroy et al. 1999; Shafer et al. 2010).

All Bering Sea islands are remote from human population centres, with faunal communities that have developed through processes relatively free from modern anthropogenic influence. Despite this, the Bering Sea is increasingly impacted by human activities, through direct (livestock and wildlife introductions, human settlement, military installations), and indirect (anthropogenic environmental perturbations) influences, that increases species movements, community turnover, and novel interactions among species (Hoberg and Brooks 2015). An integrated faunal biodiversity assessment of the status and origins of species and populations on Bering Sea islands is necessary to resolve the comparative biogeographical history of this region and identify major knowledge gaps among existing communities in anticipation of more effective future conservation planning (Flagstad et al. 2019).

Studies of Faunal groups

Vertebrates

There are few terrestrial vertebrate species within the Bering Sea region although they are systematically diverse, consisting mostly of birds (only land and fresh water associated species are considered here), but including mammals and freshwater fish (Murie 1959. Rausch and Rausch 1968). Low richness among these groups is due to high-latitude isolation, harsh sub-Arctic climate, small island size, lower-diversity habitats, and a relatively young history of community assembly, particularly for Aleutian islands, resulting in few native species and recent colonisers of mainland origin (< 15 kyr). These criteria for a "simple" system present an opportunity to more clearly resolve geographic origin, demography, and biodiversity connections that might otherwise be obscured within more complex systems. Most non-avian vertebrates considered are small-sized, generally due to limited resources for supporting large-bodied species, coupled with a history of loss of larger species since isolation. However, extensive human introductions, particularly of medium and large mammals, have a widespread and continued presence through the region. Currently, no amphibians or reptiles occur within the study area.

Mammals

Terrestrial mammal species are few across the Bering Sea archipelagos (MacDonald and Cook 2010; Supplementary Materials Table S1), but provide disproportionately valuable insight for understanding biodiversity responses to ongoing environmental perturbation. These mammals are year-round residents, having evolved multiple adaptations for responding to all-season conditions at high latitudes in situ. Given the relative ease with which we can detect, sample, and quantify these species, relatively comprehensive data exists for most species across mainland Beringia. Extensive previous field sampling and specimen archives, have allowed for increased clarity of historical biogeography and ecology of Beringian mammals, making them an ideal group for investigating processes of change (Cook et al. 2005). However, knowledge gaps persist, particularly for rare species, for intricate co-evolutionary relationships among hosts and their associated biodiversity, for gene-flow dynamics across suture zones where multiple species pairs from distinct communities may hybridize, and from remote regions, such as Bering Sea islands, that are still under-sampled (Cook et al. 2017). For example, even basic information on genetic diversity and evolutionary divergence of island mammal populations from this region is still lacking. Increased sampling of mammals across Bering Sea islands should help to fill these gaps, providing valuable insight into Holarctic biodiversity dynamics. Finally, mammals often play a role of definitive hosts for a broad diversity of parasitic species that may exhibit complex life histories across multiple obligate or facultative host species from all of the higher-level groups discussed herein, and occupying all available habitats (Hoberg and Brooks 2015). As such, future sampling and research on the limited mammal diversity within the Bering Region has the potential to reveal intimate connections between both charismatic and enigmatic species that collectively maintain viable communities within this tenuous biological system and through time (Galbreath et al. 2019).

Although a relatively high diversity of small and medium-sized mammals persists across Greater Beringia, end-Quaternary regional extinctions of ice-age megafaunal species had mostly occurred before 12 kya (Mann et al. 2013). Wolf (*Canis lupus*), brown bear (*Ursus arctos*), polar bear (*Ursus maritimus*), caribou (*Rangifer tarandus*), muskox (*Ovibos moschatus*), and Dall's sheep (*Ovis dalli*) are the only species still extant, along with boreal taxa including moose (*Alces alces*) and black bear (*Ursus americanus*) that are expanding northward with boreal habitats. However, only polar bears have maintained populations on Bering Sea land-bridge islands due to their aptitude for crossing seasonal pack-ice. Janness (1929) and Ovsyanikov (2010) both noted the presence of polar bears on Diomede Islands although their occurrence there seemed to be transient. Rausch (1953) reported polar bears as uncommon but present on St. Lawrence Island during both summer and winter, and in addition reported single observations of both brown bear and wolf from the early 1900s, presumably having originated from Siberia via pack-ice. Additionally, Hanna (1920) noted a large year-round resident population of polar bears on the St. Matthew Islands up until ~ 1890 when they were extirpated by humans. This population likely maintained periodic gene flow across pack-ice, and may have been a source for rare migrants to the Pribilof Islands, considering several polar bear records from St. Paul Island dated from ~ 4.6 and ~ 3.6 kyr BP (Veltre et al. 2008) and most recently from the late-1800s (Ray 1971). No existing records of native mega-faunal species are evident from the Aleutian arc.

The Pribilof Islands provide a unique perspective on mega-faunal biogeography, with now clear evidence that St. Paul Island (100 km^2) supported a population of woolly mammoths (*Mammuthus primigenius*) until 5600 years ago, one of the last two extant populations along with Wrangel Island in the Arctic Ocean (up to 4000 years ago; Graham et al. 2016). The significance of these populations is reflected by timing of isolation of land-bridge islands from the Bering Isthmus in relation to both climatic transitions and human passage through Beringia (MacDonald et al. 2012; Guthrie 2004) noted that the Pribilof Islands were isolated from mainland areas by 13,000 years ago, potentially buffering St. Paul from human- or climatic-caused mainland extirpations of other mega-faunal populations, whereas Northern Islands remained connected to the eastern mainland until ~ 10,000 years ago. Eventual extirpation of St. Paul mammoths is now considered to be due to periods of local aridity and loss of fresh water sources, through evidence from isotopic, floral, and faunal reconstructions from St. Paul (Graham et al. 2016), and from ecological modelling (Wang et al. 2018).

Medium-sized mammals occurring on Bering Sea islands are also capable of long-distance dispersal across available pack-ice, whereby occurrence on Northern Islands is more common and transient, with the Pribilof Islands further south experiencing greater isolation and fewer occurrences. Red fox (*Vulpes vulpes*; now considered *Vulpes fulva* in North America; Statham et al. 2014) is increasing in abundance across high-latitudes with more frequent occurrences through northern tundra regions (Killengreen et al. 2007; Savory et al. 2014) and occasional sightings on Northern Islands through bridging of pack-ice. Red foxes have the potential to compete with and replace native Arctic foxes (*Vulpes lagopus*) through the region (Post et al. 2009; Klein et al. 2015). Records of red fox on Diomede and St. Lawrence Islands are rare but consistent with transient occurrences and a Eurasian origin (Rausch 1953). Recent evidence of red fox colonisation and competitive displacement of Arctic foxes on St. Matthew Island may have severe consequences for the biological integrity of this isolated ecosystem (Klein et al. 2015). The origins of St. Matthew red fox are not yet resolved, and genomic sampling of this population through time could provide constructive insight into processes of contemporary community change and impacts on population demography of endemic island lineages. Historic sighting of red fox on St. Paul Island again indicates their ability for long-distance colonisations (Murie 1959). Finally, red fox are considered natural colonisers of the eastern Aleutians as far west as Unimak in the Fox Islands (Murie and Scheffer 1959).

Despite long-distance dispersal by red fox, recent genomic evidence indicates a lack of contemporary gene flow across the Bering Strait between *V. vulpes* and *V. fulva*, (Statham et al. 2014). Although Beringian sampling was limited in that study, circumstantial evidence suggests that modern access to Northern Islands is greatest from Eurasia, whereas access to the Aleutians in the south predominantly occurs westward from the Alaska Peninsula. As an exception, Arctic fox are reputed to have naturally colonised eastward through the western Aleutians, including Commander and possibly Near Islands (Murie 1959). The propensity for Arctic fox to move extensively through the Northern Islands (and the Arctic region in general) has received much attention McAtee and Preble 1923; Barabash-Nikiforov 1938; Rausch 1953; Murie 1959; Chesemore 1968; Fay and Rausch 1992; Geffen et al. 2007; Klein et al. 2015). Again, southern populations are less transient, and have persisted in isolation for longer. Murie (1959) posited that the abundance of dark morphs of both Arctic and red foxes from Bering Sea and Aleutian islands are a consequence of their extended isolation; a phenomenon consistent with genetic drift within small populations, having implications for adaptive capacity under future scenarios of change (e.g., Kawanishi et al. 2010), and possibly also deterministic selection (Uy and Vargas-Castro 2015), although with unknown adaptive significance. Both Commander and Pribilof Arctic fox are considered focal populations for future conservation assessment (Geffen et al. 2007).

Hares, including Eurasian mountain hares (*Lepus timidus*), and Alaskan hares (*Lepus othus*) are also considered to be genetically isolated across the Bering Strait, despite evidence for long-distance dispersal. The only verifiable island records of hares (species unconfirmed) are from Little Diomede with additional sightings from Big Diomede, and of aggregates of hares moving eastward across pack-ice from Little Diomede, as viewed from aircraft (Cason et al. 2016). In addition, unverified reports of *L. othus* exist from Unimak of the Fox Islands (Cason et al. 2016).

Unlike red fox and hares, Arctic ground squirrels (*Urocitellus parryii*) are a Holarctic species, exemplifying a trans-Beringian taxon endemic to Arctic tundra habitats (Galbreath et al. 2011). These hibernating squirrels are associated with deep xeric (dry) soils allowing for burrow construction. Their distribution reflects a history of more expansive steppe environments through glacial phase Beringia (Zazula et al. 2003). Xeric habitat requirements likely precluded squirrel occurrence on some land-bridge islands coincident with a “mesic buckle” through east-central Beringia, described as a discontinuity of polar steppe across Beringia due to mesic tundra habitats in this region, and as evidenced from both fossils and climatic reconstructions (Guthrie 2001; Yurtsev 2001; Elias and Crocker 2008; Bond 2019). Although the complex mosaic of these heterogeneous glacial phase environments is still not well resolved, absence of squirrel records from the Pribilof Islands, St. Matthew Islands, and particularly from Nunivak Island, coupled with deep genetic and geographic partitioning of lineages through Beringia (Galbreath et al. 2011) lends support to long-term disjunct distributions. As with multiple other taxa, *U. parryii* is considered native to the Fox Islands only as far west as Unimak.

Small mammals collectively provide evidence of biogeographic and evolutionary processes throughout the study region. Only three mammal species are endemic to Bering Sea islands, all small mammals occurring on land-bridge islands (Fig. 2). The St. Lawrence Island shrew (*Sorex jacksoni*) and Pribilof Island shrew (*Sorex pribilofensis*) are putative sister taxa most closely related to mainland forms within both Eurasia (*Sorex portenkoi, Sorex leucogaster*, and *Sorex camtschatica*), and North America (*Sorex ugyunak*; Jong 1982; Demboski and Cook 2003). Speciation within this complex

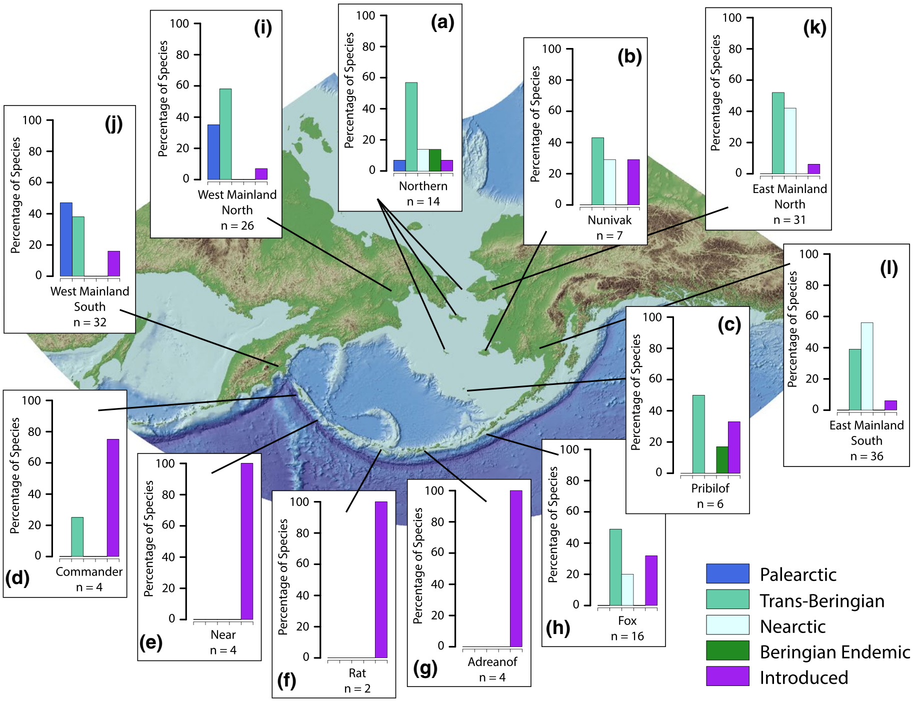

Fig. 2 Map of the Bering Sea Basin indicating occurrence of 'non-human' terrestrial mammals and biogeographic origins. Data for Alaska was compiled from MacDonald and Cook (2010), and for Siberia was compiled from the IUCN Red List (https://www.iucnredlist.org/) and from the Full List of Kamchatka Mammals (http://www.travelkamchatka.com/animalmore.htm), both accessed 4 December 2019. Number of species (n) are indicated below island group names

of sibling species has occurred through fragmentation of Beringia since the last glacial phase, and subsequent rapid allopatric divergence (Hope et al. 2012, 2013). Preliminary assessment of genetic diversity among Pribilof Island shrews indicates extremely low variability across multiple microsatellite loci and reduced representation genome sequencing (Hope, unpublished data). The precise sequence of differentiation among these shrew taxa along with systematic relationships are yet unresolved, although collectively they share Nearctic origins (Peterson 1967). The insular vole (*Microtus abbreviatus*) occurring on St. Matthew Island is likewise a peripheral endemic with low genetic diversity, belonging to the singing-vole complex (including *Microtus miurus* occurring through tundra regions of Alaska) with Nearctic origins (Rausch and Rausch 1968; Weksler et al. 2010). Finally the black-footed brown lemming (*Lemmus trimucronatus*) found only on St. George Island (Pribilof group) has been considered an endemic species (Davis 1944). However, it shows minimal genetic divergence from mainland populations, and is most closely related to populations from both Alaska and Chukotka in Far East Siberia, confirming this species as having a true Holarctic phylogroup distributed across the Bering region (Fedorov et al. 2003). In addition, brown lemmings are found on Nunivak Island, but not along the Aleutian arc or within the Northern Islands. Conversely, collared lemmings (*Dicrostonyx groenlandicus*) are distributed both within the eastern Aleutians as far west as Unalaska (Fox Islands) and also on St. Lawrence

Island (MacDonald and Cook 2010). Although the mainland genetic affiliation of the St. Lawrence population is not resolved, it was considered by Rausch (1953) to be most closely related to Nearctic populations. This is supported by more recent isolation of St. Lawrence Island from North America than from Siberia following the last glacial (Guthrie 2004).

The distribution of mammal diversity through the Bering Sea region provides some generalizable biodiversity patterns that are shared across other terrestrial groups (Figs. 2 and 3). Species with trans-Beringian distributions are over-represented within this region, reflecting strong biogeographic connections between Eurasia and North America. Trans-Beringian species are also more prevalent at northern latitudes, associated with Arctic tundra habitats (Hope 2019), whereas species with Palearctic or Nearctic origins are more numerous at southern latitudes, reflecting a prevalence of boreal-associated species, and higher incidence in western or eastern Beringia respectively (Fig. 2; Supplementary Materials Table S2, S3). Mainland areas support the vast majority of Beringian mammal diversity whereas islands are highly depauperate. Only small mammals still exhibit Beringian endemism with species found only on land-bridge islands, reflecting extended isolation and persistence since fragmentation of the Bering Isthmus. Finally, few mammal species are found on oceanic Aleutian islands and most are a consequence of human introduction (Barabash-Nikiforov 1938; Fig. 2; Supplementary Materials Table S1). The Fox Islands group supports the greatest mammalian

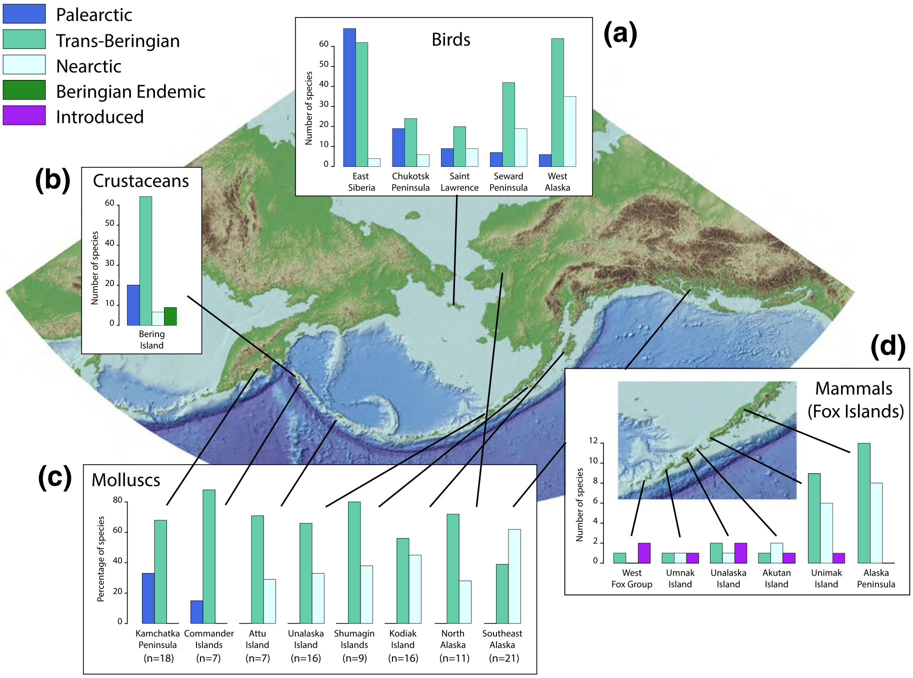

Fig. 3 Map of the Bering Sea Basin indicating occurrence of terrestrial fauna and biogeographic origins. Faunal groups include data for: **a** birds (adapted from Sealy et al. 1971); **b** Crustaceans from Bering Is. (adapted from Novichkova and Chertoprud 2016); **c** Molluscs (adapted from Roth and Lindberg 1981); and **d** Mammals on the Fox islands group (adapted from Peterson 1967)

diversity (Fig. 3), consistent with at least partial land connections with the Bering Isthmus through the last glacial phase (Hoffmann and Peterson 1967).

Birds

Bird diversity through Beringia is high compared with other vertebrate groups due to their propensity for aerial dispersal and long-distance migration coupled with abundant regional marine resources. Beringian geography provides both natural corridors as part of multiple global flyways and extensive breeding habitats that are in proximity to marine food and isolated from predators. Winker et al. (2002) reported 125 species of birds from the St. Matthew Islands, reflecting migratory connections with both the Palearctic and Nearctic, coupled with endemism, and contemporary climate-induced distributional changes. Given the difficulty of sampling from this remote region, the diversity of life-histories among sea- and shore-birds, and the complexity of both intra- and inter-specific origins and of biodiversity connections, an accurate generalization of avian faunal assembly within the Bering Sea region is as yet unfeasible (Winker et al. 2002). We consider here only the primary literature addressing land and freshwater birds that more closely rely on terrestrial habitats and resources within the study region (e.g., as defined and summarized by Sealy et al. (1971); Fig. 3). The natural history of Bering Sea terrestrial birds nonetheless reflects a diverse assemblage that includes resident taxa, regular seasonal migrants, and occasional occurrences of many other species (Winker et al. 2002). The roles of these avian species in transporting biodiversity across the northern continents, or in impacting native species are still largely unknown. However, genetic diversity, endemism, biogeographic history and the unique ecology of many species have been assessed to varying extents.

Sealy et al. (1971) provided a comprehensive biogeographic summary of birds occurring on St. Lawrence Island that, similar to mammals, reflects regional diversity patterns with a high prevalence of trans-Beringian species, and greater representation of Palearctic and Nearctic species in relation to western or eastern mainland areas respectively (Fig. 3). In addition, many insular bird populations exhibit signs of extended isolation, with low genetic diversity and high divergence. For instance, Aleutian Island bird populations have been shown to exhibit genetic diversity ranging from 7 to 70 % lower than nearest mainland populations for terrestrial species (Pruett et al. 2018). Unlike mammals, ancient colonisation of birds along the Aleutian arc and subsequent evolutionary differentiation from mainland populations has occurred repeatedly among birds, including song sparrows (*Melospiza melodia*; (Pruett and Winker 2005a), pacific wrens (*Troglodytes pacificus*; Pruett et al. (2017) and rock ptarmigan (*Lagopus mutus*; Pruett et al. 2010), suggesting little modern dispersal among major island groups and limited capacity for natural genetic rescue of the smallest and most remote populations (Pruett et al. 2017). Lower genetic diversity and greater isolation by distance also increasingly justify consideration of island populations as independent conservation units (Kier et al. 2009). A population genetic assessment of common ravens (*Corvus corax*) on the Aleutian arc again highlights endemism, with the Near Islands (Attu) exhibiting refugial isolation dated to the last glacial phase, indicating the possibility of exposed continental shelf and terrestrial population persistence at these times (Pruett and Winker 2008; Pruett et al. 2018). Rock ptarmigan (*Lagopus mutus*) offer an alternative historical biogeography for Aleutian birds whereby trans-Beringian distributions reflect isolated populations that are considered to have diversified through vicariance in multiple cryptic glacial refugia followed by redistribution among the Aleutian Islands from a Eurasian origin followed by sustained isolation and divergence (Holder et al. 1999, 2000). These case studies make evident that biogeography of Aleutian birds has been highly dynamic with multi-directional colonisation through time, although with most from east to west.

Pruett and Winker (2005b) considered genetic signatures from divergent populations of the rock sandpiper (*Caladris ptilocnemis*) as evidence of regional refugia within Beringia, with the Commander Islands biogeographically associated with southern Siberian mainland, Pribilof and St. Matthew Islands associated with a central Beringian refugium, and the remainder of the Aleutian Islands and Northern Islands most closely associated with the Nearctic. These affiliations are again reflective of high regional heterogeneity through glacial phase Beringia and dynamic change through time. A central Beringian refugium is also considered to have facilitated allopatric divergence of McKay's bunting (*Plectrophenax hyperboreus*), isolated on the Bering Isthmus and subsequently on St. Matthew Islands from more widespread snow buntings (*P. nivalis*), although genetic divergence between the two species is minimal (Maley and Winker 2010). Beringia has evidently been an important driver of diversification among birds (Klicka and Zink 1999), although this relatively vagile group offers both predictable biogeographic associations as well as high levels of discordance in the timing of diversification, species origins, and distributional limits (Humphries and Winker 2011).

Fish

Marine fish within the Bering Sea region are diverse and abundant, constituting a vital resource for both wildlife and humans, supporting marine bird populations that in turn maintain terrestrial systems through nutrient exchange and increased community complexity (Croll et al. 2005; Zeglin et al. 2016). However, as with birds, freshwater fish faunas are depauperate as existing freshwater habitats have been isolated, limited in extent, and dynamic through time due to recent glacial history. Most freshwater fish occurring within the Bering Sea region have colonised via marine pathways rather than through fragmentation of previously more widespread Beringian terrestrial waterways (Neuhold et al. 1974). Some species are fully or potentially anadromous, including salmonids (*Oncorhynchus* spp.) and Dolly Varden (*Salvelinus malma*). Other species such as nine-spined (*Pungitius pungitius*) and three-spined (*Gasterosteus aculeatus*) sticklebacks may exhibit multiple life-histories, associated with saltwater, freshwater, or some combination. Other species such as the coastrange sculpin (*Cottus aleuticus*) are euryhaline, capable of tolerating saltwater environments. A survey of freshwater fish of the Aleutian Islands by Kenney and Von Hippel (2017) identified only 9 species, all with capabilities to colonise via marine corridors.

Conversely, glacial phase river systems across the Bering Isthmus are considered to have been extensive, highly interconnected, and important corridors for dispersal of freshwater fish between Eurasia and North America through the Quaternary (Marincovich and Gladenkov 1999; Bond 2019). Such connectivity might be reflected by high genetic diversity among extant land-bridge populations but with lack of regional structure. These characteristics are shared by fish on St. Lawrence island, including a population of Arctic grayling (*Thymallus arcticus*), with historic connections through mainland Alaska, Yukon Territory, and British Columbia (Redenbach and Taylor 1999), and Alaska blackfish (*Dallia pectoralis*) with trans-Beringian genetic affiliations (Campbell and Lopéz 2014).

The limited available comparative evidence for the historical biogeography of Bering Sea freshwater fish contrasts somewhat with terrestrial mammals. Whereas mammal movement across the Bering Isthmus has been predominantly eastward, and movement through the Aleutian chain westward, evidence from fish generally indicates closer affiliations to North America of land-bridge island populations (St. Lawrence Islands) and closest ancestral connections with Eurasia for Aleutian Island populations. For instance, both Dolly Varden (Yamamoto et al. 2014) and nine-spined sticklebacks (Aldenhoven et al. 2010) are hypothesized to have colonised the Aleutians from western regions including Kuril Islands and Sea of Okhotsk, with the Near Islands supporting the greatest diversity of fish among all Aleutian and Pribilof Islands (Redenbach and Taylor 1999). However, it is evident, that both the evolutionary histories and the contemporary ecology of Bering region freshwater fish remain understudied.

Invertebrates

Non-parasitic invertebrates

The earliest synthetic work on the Bering Sea terrestrial non-parasitic invertebrates dates from the 1960s and focused on ground beetles and spiders, both primarily predatory arthropods. Lindroth (1963, 1979) documented high latitude ground beetles (Coleoptera: Carabidae, ~260 Alaskan species) in Beringia with a focus on understanding biogeographic trends. He determined that movement of ground beetles from the Palearctic to the Nearctic across northern Beringia was more common than the opposite. He also noted that more Holarctic species could be found in western and northern Alaska than in interior or south coastal Alaska. This led him to conclude that dispersal across the northern portion of the land bridge was more important than along the southern portion. However, we note that the western and northern portions of Alaska, dominated by tundra, are also likely now more climatologically and ecologically similar to the former land bridge than interior and southern Alaska, which are now densely forested at lower elevations. Lindroth's conclusions about the importance of northern Beringia for dispersal are therefore confounded by the fact that all regions of Alaska were not, or at least now are not, equally hospitable to species adapted to the climate of the land bridge.

In contrast, Lindroth's analysis (1963) of the Aleutian carabid fauna (31 species) led him to conclude these islands have had a small role to play, relative to the land bridge, in the dispersal of ground beetles across Beringia. This is despite these islands having maintained a warmer climate than the land bridge. One explanation for this is that even with lower sea levels, the main island groups remained disconnected from each other and the mainland. Another explanation is that these islands experience sufficient cloud cover and strong winds to make conditions more challenging for life than the Arctic north slope of Alaska. Arctic Alaska has numerous insect taxa that are absent from the Aleutians, such as dragonflies, butterflies, grasshoppers, and ants – all highly vagile but likely excluded by the harsher climate of the Aleutians. In contrast to the land bridge, and as seen in the birds and mammals, the predominant direction of ground beetle dispersal in the Aleutians is from the Nearctic towards the Palearctic. Holm (1960), focusing on spiders performed a similar investigation of the Aleutian archipelago. Lindroth (1963), interpreting Holm's (1960) work, concluded the Aleutian spider fauna showed a similar pattern to the ground beetle fauna—no Palearctic spiders were found in the Aleutians. The spider fauna was composed of primarily Nearctic species with some Holarctic species and dispersal from the Nearctic towards the Palearctic dominated. Terrestrial molluscs show a similar pattern to spiders and ground beetles (Fig. 3). The terrestrial mollusc fauna within the Aleutian arc has a

Nearctic origin, except for species found on the Commander islands which have a Palearctic origin (Roth and Lindberg 1981). The strait between Attu and the Commander Islands in the far west of the island chain has apparently acted as a barrier to dispersal of terrestrial invertebrates across the Aleutians, even during times of much lower sea levels. These predominantly Nearctic-origin patterns seen in terrestrial invertebrates of the Aleutians are not mirrored in the flora (Hultén 1960; Lindroth 1963), which show more evidence of movement in both directions across the Aleutians. Recent analysis of the Aleutian flora by Garroutte et al. (2018) found that species with a Nearctic origin (141 spp.) outnumber species with a Palearctic origin (131 spp.) but to a much lesser extent than that seen in the terrestrial invertebrate fauna.

There are a number of terrestrial invertebrate species endemic to the Bering Sea region. A flightless snow scorpionfly, *Boreus borealis*, is known only from the Pribilof Islands (Penny and Byers 1979). Two species of flightless beetles in the family Salpingidae, *Aegialites saintgeorgensis* and *Aegialites saintpaulensis*, are each known only from the Pribilof Islands (Zerche 2004). The flightless carrion beetle *Lyrosoma opacum*, is restricted to coastal habitats from the Kuriles, through the Aleutians to Kodiak, Alaska (Yoo et al. 2013). A more complete list of the 64 non-marine arthropod taxa known predominantly from the Bering Sea region, and not yet known from outside Alaska, is supplied in Supplementary Materials (Table S4). However, given the sparse sampling of these taxa, it's likely that some will eventually be documented outside Alaska or the Bering Sea region. Additionally, a number of these taxa are known only from their type specimen(s) and have yet to receive further taxonomic scrutiny (e.g., McAtee and Preble 1923), thus it is also possible that some might be found to belong to different, more widely distributed taxa. Conversely, most island populations of the Bering Sea region have not been studied genetically, and numerous cryptic and endemic species may remain undiscovered. Preliminary genetic study of the arthropod fauna of St. Matthew Island (Fig. 1) discovered one such possible overlooked endemic – a species of weevil in the genus *Lepidophorus* most closely related to *Lepidophorus lineaticollis* of mainland Alaska, rather than *Lepidophorus inquinatus*, which is widespread in the Aleutians (Sikes et al. 2016). The glacier-free Beringian refugium in interior Alaska is the presumed cause of many of the, often flightless, arthropod species potentially endemic to Alaska, as summarized in Sikes and Allen (2016).

Recent investigations into the status of Holarctic arthropods in Beringia have overturned many prior conclusions. Numerous species previously thought to be Holarctic have since been determined to be mistaken combinations of distinct Palearctic and Nearctic lineages that are often sister species. Brunke et al. (2019) focused on subcortical rove beetles and found complete allopatric divergence across Beringia. Schär et al. (2018) focused on ants and found the majority of species previously thought to be Holarctic were not. Kimsey and Carpenter (2012) came to similar conclusions regarding the yellowjacket fauna (subfamily Vespinae), recognizing no Holarctic species. The majority of Holarctic species have also yet to receive modern molecular investigation, so this is a ripe area for future research.

Novichkova and Chertoprud (2016) summarised the freshwater crustaceans on the Commander Islands, demonstrating a largely trans-Beringian fauna, but also indicating an endemic species component (Fig. 3). Documentation of freshwater arthropod faunas elsewhere across Bering Sea islands are sporadic (e.g., Neuhold et al. 1974 for Amchitka Island indicating predominance of fly larvae). An appraisal of freshwater molluscs across Bering Sea islands is also warranted given high mainland diversity (Dall 1905) coupled with relative sensitivity of this group to cold temperature limits (Vinarski et al. 2016), and thus potential for establishment of invasive populations in a warmer Arctic. Soil-dwelling invertebrate groups, including nematodes (Willerslev et al. 2014) and annelids (Nurminen

1973; Shurova 1978; Booysen et al. 2018) have likewise been assessed to some extent on mainland areas but there are few records from Bering Sea islands. These latter groups may readily be unintentionally transported across vast distances by humans and migratory animals, with high invasive potential. Preliminary genetic analysis from St. Paul Island indicates the presence of non-native earthworms (Genus *Dendrobaena*) as well as recent origins for multiple species of terrestrial molluscs (e.g., Genus *Deroceras*; Hope unpublished data).

In summary, the terrestrial invertebrate fauna of the Bering Sea region islands is depauperate (even in contrast to Arctic mainland Alaska), and shares biogeographic patterns more closely with the mammals than birds, freshwater fishes, or plants. Relative to all of these taxonomic groups, terrestrial invertebrates are poorly studied. Similarly, freshwater invertebrates have been afforded only minimal attention through the study region.

Species introductions

Our synthesis provides a new comparative insight into Beringian biodiversity, although a primary finding is lack of detailed information on existing species diversity, relative genetic diversity, population connectivity, and evolutionary origins, particularly among invertebrates. Among island vertebrate populations, low population genetic diversity coupled with high regional structure indicates these populations may deserve high conservation priority. An additional concern for conservation of native populations is the prevalence of species introductions, particularly of mammals, for which most information is available, and which has been previously reviewed (e.g., Bailey 1993; Ebbert and Byrd 2002; MacDonald and Cook 2010; Figs. 2 and 3). Human introductions of mammals occurred broadly through the region to provide furs, food, and recreational hunting resources from as early as the mid-1700s (Ebbert 2000). Unintentional mammalian introductions, particularly of Norway rats (*Rattus norvegicus*) to multiple islands (Supplementary Table S1) have also been pervasive through the last 200 years (Renner et al. 2018), with severe impacts on marine bird colonies and intertidal communities (Jones and Byrd 1979; Kurle 2005; Harris 2009). The combined impact of non-native large-bodied ungulates and small to medium sized introduced predators have devastated native habitats and wildlife, and generated financial and ecological burdens through recovery efforts that are challenged by remote geography and extreme environments (Ebbert and Byrd 2002; Jones et al. 2008). Despite costs, mammalian eradication efforts on Aleutian islands have seen successful re-establishment of native communities in some cases (e.g., sea bird recovery, Croll et al. 2016), but not others, depending in part on the introduced species' ecology.

For instance, grazing caribou were introduced to St. Matthew Island and experienced dramatic population fluctuations in the absence of natural predators and within the confines of a small island, with cascading impacts on both vegetation and wildlife (Klein 1968). Despite rapid extirpation of this herd through stochastic processes, the depleted climax lichen communities and altered flora have yet to recover (Klein 1987). A similar succession and lagged recovery, coupled with contemporary climate shifts, has been documented for lichen communities on St. Paul (Klein and Shulski 2011). One might assume that following post-glacial fragmentation of the Bering Isthmus, the process of faunal relaxation on multiple new land-bridge islands would have seen potentially catastrophic community restructuring through time that would have strongly influenced the evolutionary trajectories of surviving populations as isolated interglacial communities equilibrated. Caribou and Arctic fox, both native species to Beringian mainland areas, offer an additional perspective as they are among the most frequently introduced species throughout the Bering region, and their evolutionary history has been strongly shaped by Beringian environments (Polfus et al. 2017). Despite Arctic adaptations of these mammals, they still may exert negative impacts on island communities that have restructured through time in their absence (Croll et al. 2005; Ricca et al. 2016). Unfortunately, there was little foresight for considering the origin and genetic stock of source populations for historic introductions, or the suitability of islands to support even locally adapted introduced species (see MacDonald and Cook 2010 for a summary of mammalian source information).

The impacts of more cryptic invaders such as invertebrate species has been difficult to assess. As the Bering Sea warms, a northward shift of sub-Arctic biodiversity is increasingly able to withstand local year-round conditions (Overland and Stabeno 2004). Evidence of community turnover within marine systems is emerging over a multi-decadal timeframe (Schumacher et al. 2003; Thorson et al. 2019), for which increasing attention and funding is being afforded to understand ecosystem consequences (Grebmeier et al. 2006; Stabeno et al. 2019), particularly considering the commercial importance of Bering Sea fisheries (Sigler et al. 2011) and the potential negative impacts for subsistence and livelihoods of indigenous communities (Huntington et al. 2013; Druckenmiller et al. 2019). Altered marine ecosystems, sea-ice extent, atmospheric shifts, and sea-bird community turnover (Stempniewicz et al. 2007) may be strong predictors of changing terrestrial systems (Bhatt et al. 2010) but minimal effort has been afforded to document and study the impacts of climate change on sea-locked terrestrial islands for which movement of faunal species is often not an option.

Documenting species introductions and resolving the origins, timing, and causation of specific events is inherently difficult. However, Gaston et al. (2003) recorded surprisingly high incidence of winged insect species introductions coincident with human visitations to Gough Island in the South Atlantic, demonstrating the value of comprehensive biodiversity surveys for determining rates and consequences of human mediated community turnover for native insular faunas.

Host-parasite dynamics

Invasion of species on islands may significantly influence host-parasite dynamics. Introduction and proliferation of host species such as terrestrial molluscs, annelids and other invertebrate groups can facilitate establishment of obligate linkages within complex parasite lifecycles (Laverty et al. 2017). Coupled with the potential for ecological fitting to facilitate new and potentially harmful host-parasite associations (Araujo et al. 2015; Hoberg and Brooks 2015) there is a need to resolve the diversity of, in particular, helminth parasite diversity across the Bering Sea Islands.

Although a relatively large amount of published information is available on parasites of terrestrial mammals across Beringia (for reviews see Jellison and Neiland 1965; Cook et al. 2005, 2017; Hoberg et al. 2012, 2013), very little research has been performed on Beringian islands. The most attention by far has been given to species of parasites that pose threats to human health, such as *Echinococcus multilocularis* in Arctic foxes and rodent intermediate hosts on St. Lawrence, Bering and Pribilof Islands (Barabash-Nikiforov 1938; Afanas'ev 1941; Rausch 1953; Fay and Williamson 1962; Davidson et al. 2016). Some of these surveys, however, provided information on other parasites, e.g., Fay and Williamson (1962) reported 7 species of helminths (2 nematodes, 1 trematode and 4 cestodes) from Arctic fox on St. George Island. Interestingly, the trematode *Maritrema afanassiewi*, found in the Pribilof shrew (*S. pribilofensis*) on St. Paul Island (our unpublished data) is normally parasitic as adult in seabirds and uses aquatic snails and arthropods as intermediate hosts; however, the specific environment of the Beringian islands creates conditions for regular infection of mammalian hosts with these avian parasites. The only known specific parasite of shrews on any of the Beringian Islands is the cestode *Lineolepis pribilofensis* (Olsen 1969; Hope et al. 2016) which reaches high intensity and prevalence of infection (our unpublished data). McPherson and Tiner (1952) described a new nematode species *Rictularia microti* in St. Lawrence Island voles. In the same year, Rausch (1952) examined 4 species of rodents from St. Lawrence, Nunivak, Bering and St. George Islands for parasitic worms and reported 3 species of adult cestodes, 2 species of larval cestodes and 2 species of nematodes. Schiller (1952) found 5 species of helminth parasites (2 cestodes, 3 nematodes) in the introduced rats from Adak Island (Aleutians). There have been almost no studies of parasitic worms of terrestrial vertebrates on Beringian islands in the past several decades. As a result, genetic data that would reveal their phylogenetic affinities and trace their origin to either Nearctic or Eastern Palearctic, are completely lacking.

Bering sea biodiversity conservation and future research directions

We have highlighted the importance of Bering Sea terrestrial environments for maintaining biogeographic associations within the region even though they constitute relatively small and remote habitats. These islands support some of the world's largest colonies of marine birds and mammals that maintain connections between marine and terrestrial species, and within terrestrial communities. These islands also support local endemics, and act as filter corridors for contemporary dispersal between continental mainland areas. However, much of the terrestrial faunal diversity is discrete, cryptic, and still either understudied or completely undocumented. Without even periodic regional monitoring of these communities, it is not possible to accurately establish the dynamics of species movements, in situ population demographic and evolutionary trajectories, or rates and timing of colonisations and introductions. As such, even given well-established theory from which to test biogeographic predictions, sufficient data are not available for rigorous analysis.

Existing biodiversity accounts do however provide some insight into regional patterns and processes, including (1) higher trans-Beringian (Holarctic) species associations at higher latitudes with stronger affinities of species to either Palearctic or Nearctic in the south of the Bering region; (2) a predominant clock-wise gyre for species movement among mammals and invertebrates (west to east across northern Beringia, and east to west along the Aleutian arc; (3) more idiosyncratic origins for birds and freshwater fish but with strongest evidence for movement from maritime northeast Asia eastward into the Bering region; (4) reduced faunal species richness on islands and low genetic diversity among populations; (5) endemism of mammals and invertebrates across land-bridge islands but endemism of birds prevalent across Aleutian islands, reflecting the history of Holocene fragmentation of the Bering Isthmus coupled with differential dispersal ability; and 6) extensive evidence for the detrimental impacts of mammalian species introductions but conversely, little documentation of introductions from other taxonomic groups, or their impact on native biodiversity.

The importance of species interactions for maintaining community processes is exemplified by parasite lifecycles that rely on multiple hosts. Loss of terrestrial biodiversity may disrupt functional connections among species, and similarly, species introductions may facilitate development of new host-parasite relationships, where the role that parasites fulfil for host fitness or conversely disease is still unclear. It is therefore of interest that our review of existing literature documents biogeographic concordance among mammals and invertebrates through the study region, given their combined importance for parasite lifecycles through time. Future targeted surveys of terrestrial and freshwater invertebrates as well as comprehensive parasite surveys across host taxa would help to resolve much of the biotic complexity across Bering Sea islands. Similarly, little is understood about the function of microbial community dynamics for driving whole community processes, although evidence indicates critical linkages between microbes and higher-level community assembly among oceanic islands (Stempniewicz et al. 2007). Both parasites and microbes are among the most sensitive indicators of biotic responses to contemporary environmental change and warrant future study.

This synthesis demonstrates that Bering Sea islands support unique genetic diversity, community composition and ecological function. However, this international region is also administered by multiple jurisdictions, and management or conservation efforts for wildlife and native species habitats is varied (Meltofte et al. 2013; IPCC 2019). Bering Sea islands may act as refuges for existing terrestrial species contending with modern environmental disturbance. However, limited ability to disperse in response to directional climate shifts or increasing human-mediated disturbance may increase local vulnerability. As such, enhanced efforts are required for terrestrial faunal discovery, description, and long-term monitoring within the Bering region, as has been recently promoted more broadly through the Arctic (Christensen et al. 2020). Of particular importance will be implementation of a modern genetic toolset for diagnosing the distribution and genetic diversity of often cryptic species assemblages across this phylogeographically complex region (Hebert et al. 2003; Colella et al. 2020). With rapidly improving genomic and metagenomic methods, biodiversity discovery and monitoring, including detection of introduced species, can be enhanced through sequencing of environmental DNA (eDNA; e.g., Garlapati et al. 2019) or through targeted metabarcoding for broad taxonomic groups (Greiman et al. 2018). Similar methods may also be applied for detecting ancient DNA to understand community turnover through time, better reconstruct past environments (Pedersen et al. 2015) and trace species origins within Beringia (Loog et al. 2020). An additional consideration for future research will be towards clearer resolution of biotic linkages between terrestrial, freshwater and marine ecosystems. The Bering Sea region is an ideal system to investigate these connections, that are also clearly demonstrated through human subsistence practices, allowing for opportunities to enhance and integrate socio-cultural priorities of indigenous communities with conservation initiatives (Mustonen and Ford 2013).

An emerging view of Beringian diversity is that populations from most species occurring on Bering Sea islands occupy only a small component of total species ranges and are often peripheral to core distributions. The remoteness of these populations coupled with knowledge that peripheral populations are often distinct, both indicate that native Bering Sea faunas are likely locally adapted, and constitute unique biodiversity. However, these peripheral populations are also least readily sampled, and poorly represented within biorepositories. One of the most effective future actions for enhancing our knowledge of the rates, trajectories, and impacts of biodiversity change will be to more comprehensively sample, document and preserve robust specimen materials across the spatial extent of the Bering region, and through time (Schmitt et al. 2019). Effective continued monitoring of communities and growth of archives coupled with emerging genetic and analytical techniques will enhance both conservation and management of Bering Sea biodiversity and more broadly across the Arctic.

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