

Future distribution of tundra refugia in northern Alaska

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Climate change in the Arctic is a growing concern for natural resource conservation and management as a result of accelerated warming and associated shifts in the distribution and abundance of northern species. We introduce a predictive framework for assessing the future extent of Arctic tundra and boreal biomes in northern Alaska. We use geo-referenced museum specimens to predict the velocity of distributional change into the next century and compare predicted tundra refugial areas with current land-use. The reliability of predicted distributions, including differences between fundamental and realized niches, for two groups of species is strengthened by fossils and genetic signatures of demographic shifts. Evolutionary responses to environmental change through the late Quaternary are generally consistent with past distribution models. Predicted future refugia overlap managed areas and indicate potential hotspots for tundra diversity. To effectively assess future refugia, variable responses among closely related species to climate change warrants careful consideration of both evolutionary and ecological histories.

Rapid warming in the Arctic^{1,2} is a strong impetus for investigating the responses of high-latitude species, particularly those considered at increasing risk of extinction or local extirpation^{3,4}. The northern tundra ecosystem is perhaps at highest risk as a result of Arctic amplification³, and because the Arctic Ocean dictates a finite limit for terrestrial species as tundra recedes⁵. Disturbances, such as increased industrial development and other anthropogenic stressors, compound impacts as the Arctic becomes more accessible^{6,7}. However, efforts to forecast the future extent and composition of northern ecosystems based on wildlife⁸ have generally not considered differential responses of species and populations to past climatic trends evident from genetic legacies⁹ (but see ref. 10). We introduce a modelling framework based on ecological and genetic criteria (Fig. 1) to aid in management planning that predicts the shifting potential distribution of target species through time in response to climate change and independently validates predictions using genetic demographic signatures and evidence of past community assembly from fossil and contemporary distributions.

Previous forecasting of changes to tundra biomes in North America concentrated on species exhibiting only seasonal occurrence within tundra⁸; however, non-migratory species may constitute more reliable indicators of environmental processes¹¹. Among vertebrates, resident small mammals such as shrews and voles are diverse, abundant species that respond rapidly to year-round seasonality and occur across broad environmental conditions. To introduce and demonstrate our methods, we chose two groups of congeneric species, each represented by multiple ecotypes within Alaska, including associations with the Arctic tundra biome, boreal biome or both. We include two shrews: the barren-ground shrew (*Sorex ugyunak*; tundra) and masked shrew (*S. cinereus*; boreal); and three rodents: the singing vole (*Microtus miurus*; tundra), meadow vole (*M. pennsylvanicus*; boreal), and root vole (= tundra vole; *M. oeconomus*; widespread).

Evaluation of future changes to ecosystem structure and function is informed by how past environmental change has influenced biomes through time^{12,13}, and by modelling future distributions¹⁴. Climatic variability through the Quaternary (2.6 Myr—present) can be quantified from isotopic measurements of sediment and ice cores^{15,16}, palaeoclimate models⁴, macrofossils^{17,18}, pollen data^{19–21} and genetic signatures of past demographic processes^{22,23}. In response to environmental change, species may exhibit variable strategies of range shifting, local adaptation to new environments, or extirpation^{24–26}. Within the next century, a significant reduction of Arctic tundra is predicted as boreal plant communities shift poleward^{3,27}. Through the Quaternary, tundra generally contracted during interglacial phases and expanded during glacial. Population genetic studies of tundra-dwelling small mammals¹⁰, birds²⁸ and plants²⁹ have revealed histories spanning multiple glacial cycles, indicating that some components of cold-adapted tundra communities persisted through interglacial warm phases such as the current Holocene period (11 kyr—present). Because past demographic trends reflect potential future trajectories for genetic diversity and population size and reveal relative risk of extirpation, historical records and genetic signatures are critical for predicting the future composition of tundra communities and identifying potential refugia⁹.

Species distribution models (SDMs) based on bioclimatic variables are developed to investigate biodiversity scenarios during discrete timeframes³⁰. Climate change studies using SDMs have provided numerous scenarios for future distributions^{13,14,31}, but distributional inference from abiotic variables alone is inherently difficult, given the range of possible climatic outcomes based on general circulation models (GCMs), spatial resolution issues, and potential synergistic effects^{6,32}. Potential synergies include biotic factors such as habitat disturbance, competition, host-parasite interactions and habitat affinities⁶. Predictions also rely

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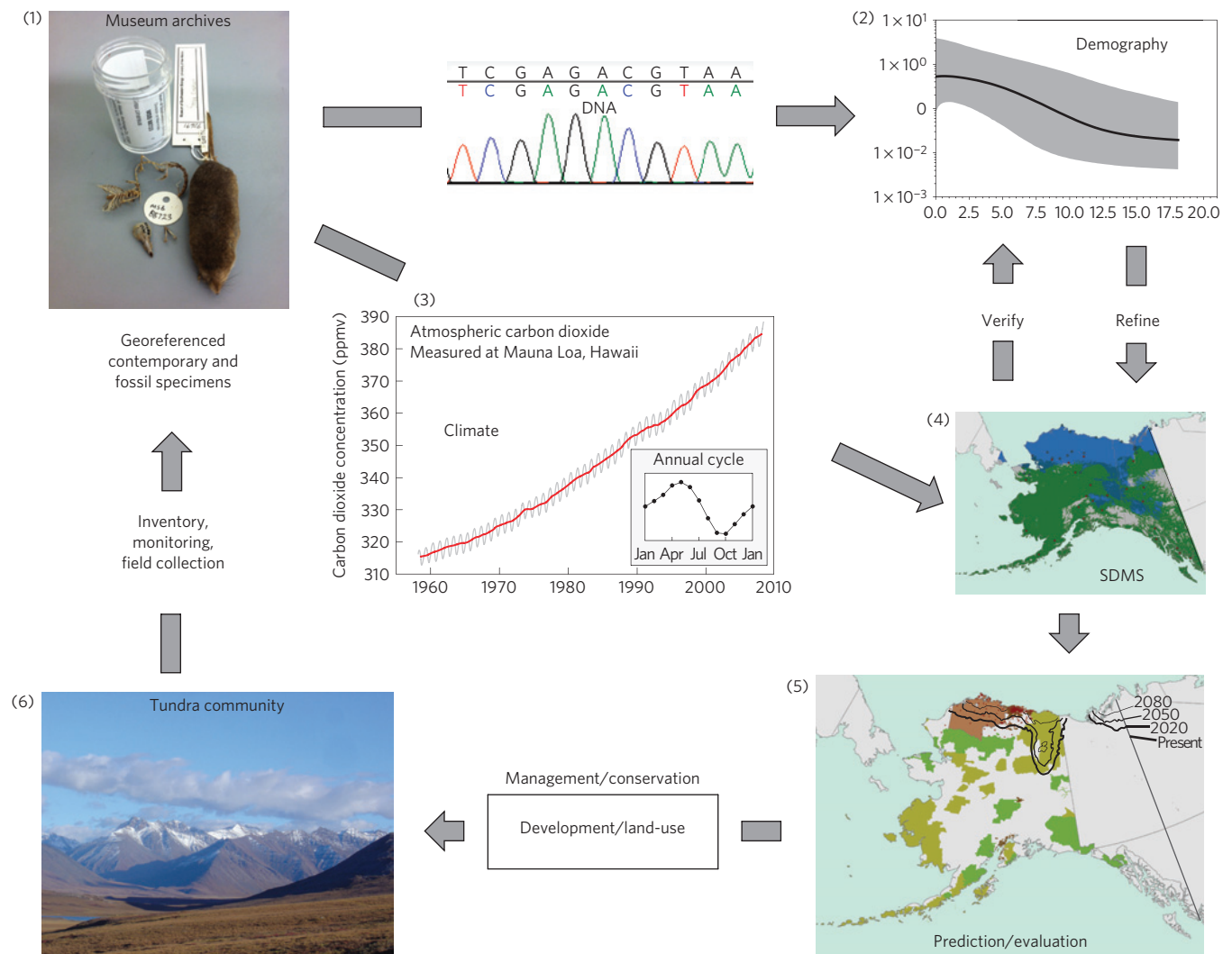


Figure 1 | Methodological summary. (1) Single or multiple species may be considered. Regional or rangewide geographic coverage of specimens increases statistical rigour for species distribution model and demographic analyses. (2) DNA sequence data from contemporary populations or fossil specimens informs phylogeographic investigations of spatial genetic structure, co-evolutionary relationships, genetic diversity and population size change through space and time. Specimen localities used for SDMs are determined from phylogeographic inference of discrete lineages, providing options for rangewide, geographically delineated, or lineage-based approaches. (3) Bioclimatic variables are compiled based on refined sets of georeferenced specimen localities, including fossils, to produce SDMs for present and past timeframes. (4) A process of verification and refinement using genetic signatures, specimen localities and SDMs increases the accuracy of SDMs. Extent, timing, and direction of population expansion/contraction inferred from genetic information may be statistically related to SDM predictions. (5) Refined distributional models are predicted into future timeframes to form hypotheses of expected changes for one to multiple study taxa. Overlaid hypotheses for multiple species may be used to refine potential future hotspots of diversity, and quantify community turnover through time. Methods may be adapted for various management or conservation applications related to future development and multiple land-use priorities. (6) Decisions based on this multi-disciplinary predictive process will impact future human interactions with local communities and increase knowledge of dynamic processes affecting diversity, distribution, and abundance through time. Continued long-term field work will increase geographic sampling and time-series will allow testing of future distributional hypotheses on an annual to decadal basis. This methodological cycle may be repeated for additional taxa, or adapted to address different research goals. The atmospheric carbon dioxide concentration in the central plot was created by Robert Rohde from NOAA published data and adapted by Nils Simon from Mauna Loa Carbon Dioxide-en.svg.

on assumptions including niche conservatism and the use of discrete lineages for studying taxa¹⁴. Contemporary climate is also influenced by the additive effects of anthropogenic stressors that have initiated a global warming trajectory with no analogue in the last 2 Myr (ref. 33), adding uncertainty to future predictions. Despite a novel climate trajectory, SDMs can accommodate environmental trends based on current climate data (including anthropogenic inputs), and thus still provide a valuable means of addressing future mitigation of climate change impacts^{34,35}. The uncertainty of SDM predictions may be reduced by incorporating an evolutionary genetic component to modelled data⁹ (Fig. 1).

Powerful advantages to using a historical framework include: past environmental conditions left multiple lines of palaeoclimatic evidence to support modelled distributions^{21,36}; and models can be validated independently through genetic analyses of community constituents^{9,37} and corroborated with fossil evidence^{11,35} (Fig. 1). Minimally, demographic evolutionary trends through time provide estimated trajectories of genetic diversity in response to ongoing and accentuated contemporary climate change.

We produce modelled species distributions for the past (Last Interglacial (LIG; 130 kyr); Last Glacial Maximum (LGM; 21 kyr)), present, and next century, using molecular signatures to confirm

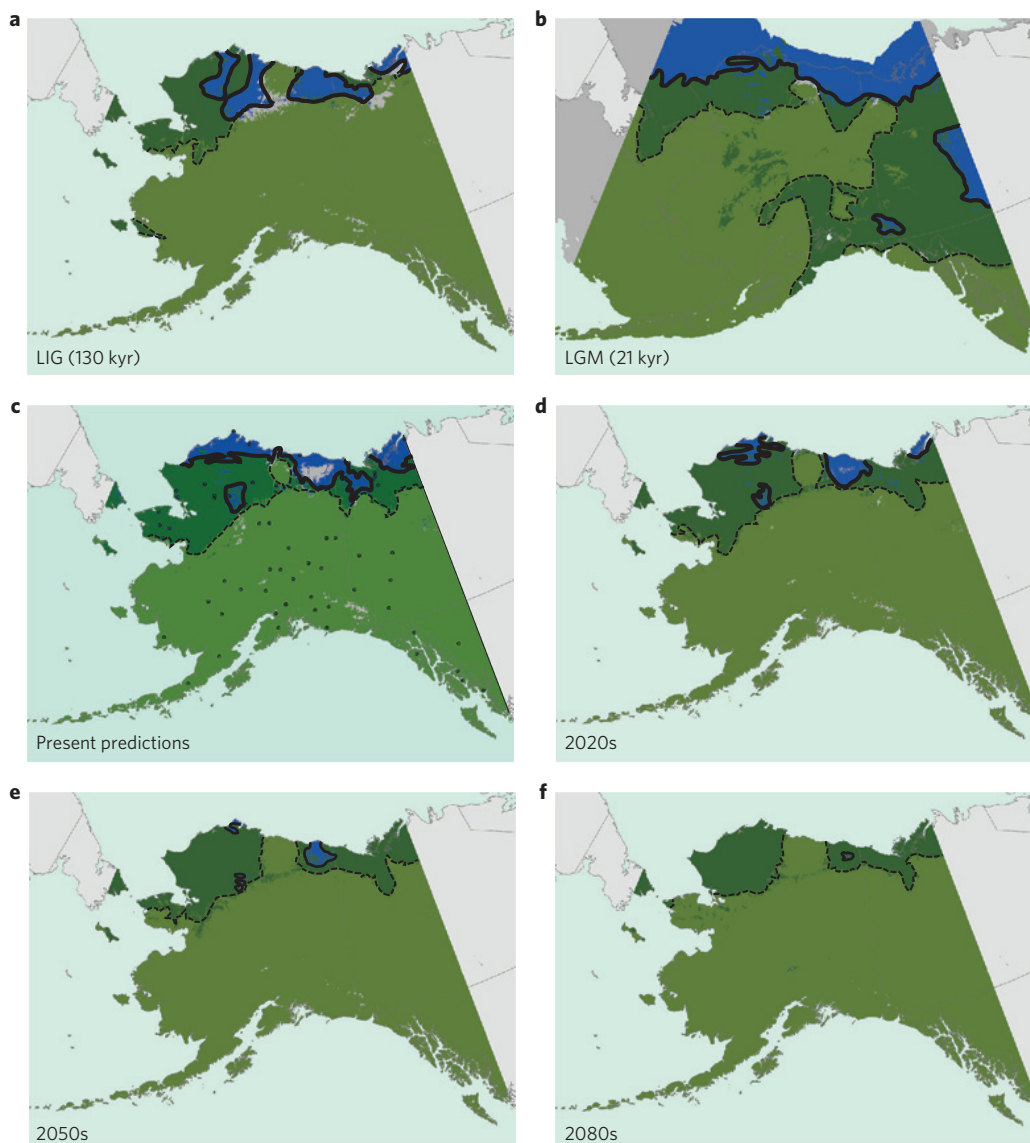


Figure 2 | SDMs for shrews. The study area depicting modelled potential distributions for barren-ground shrew (blue), masked shrew (light green), and both species (dark green) at different time frames from past to future. **a**, Last Interglacial projection to 130 thousand years ago. **b**, LGM projection to 21 thousand years ago. **c**, Present predictions using a climate envelope from 1950 to 2000, including locality records for each species used to create SDMs. **d-f**, Future predictions using climate envelopes for years 2010–2039, 2040–2069 and 2070–2099 respectively. Dashed lines indicate the extent of contact between the two study species and the broadest extent of tundra-associated barren-ground shrew prediction within the study area. Solid lines indicate areas where only the tundra-associated species is predicted through time (blue areas).

operational taxonomic units for models and to assess temporal changes in demography and distribution. We delimit regions of Arctic Alaska predicted to support species representative of the tundra community into the next century, and refer to these regions as potential hotspots for future diversity, considering the analysis of multiple cold-adapted species.

Recognition of diversity hotspots is challenging³⁸. Rapid distributional shifts may drive species out of reserves and into peripheral locations³⁹. Arctic tundra is limited to the north by the Arctic Ocean and this may facilitate detection of hotspots. We show that northernmost tundra areas may represent longest-term persistence, equating to highest suitability for future refugia. We also show that forecasted refugia are coincident with lands administered for both development opportunities and natural resource conservation. We assess the coincidence of predicted tundra hotspots with various land uses in northern Alaska, discuss the potential for optimizing predictions for refugial areas through meta-analysis of multiple

community constituents and highlight the utility of our methods for land management (Fig. 1).

Results

Species distribution models. Masked shrews and meadow voles are associated with boreal vegetation through southern and central Alaska, whereas barren-ground shrews and singing voles are associated with tundra (Fig. 2 and Supplementary Fig. S1). Root voles are widespread within Alaska (Supplementary Fig. S2). Present SDMs for all species closely match known distributions. SDMs projected to past timeframes and cross-calibrated using fossil localities for the LIG (Supplementary Fig. S3) indicate the presence of suitable habitats within the study area for all species. LGM predictions reveal expanded distributions to occupy exposed continental shelf with lowered sea levels, whereas LIG predictions closely match distributions predicted for the near future (2020s) with contracted ranges for tundra species and expanded ranges for

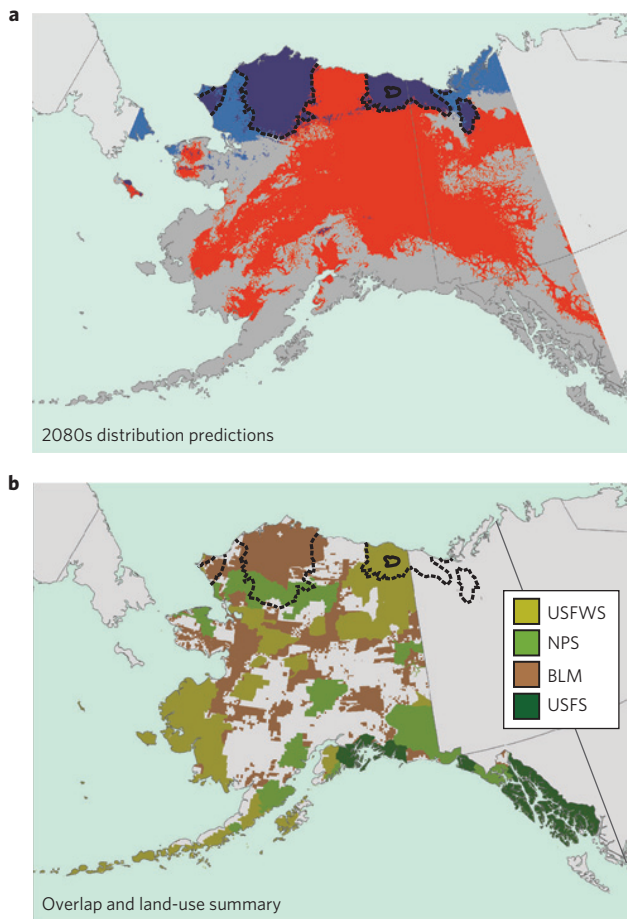


Figure 3 | Future (2080s) species distribution models for tundra-associated species. **a**, Study area overlaid with modelled potential distributions for barren-ground shrew (blue), singing vole (red), and both species (purple) using a climate envelope for 2070–2099 AD. **b**, Current Federal lands in Alaska. USFS, US Forest Service. Dashed lines indicate future refugial areas where both tundra-associated study species are predicted. Solid line indicates refugial area where only tundra-associated species are predicted without overlapping boreal species' predictions.

boreal species compared with present distributions (Fig. 2a,d and Supplementary Fig. S1a,d). Future distributions indicate a rapid expansion of masked shrews and meadow voles northward, to occupy most of the study area by 2080. Barren-ground shrews

are predicted to contract in range, but with a slower velocity than expanding masked shrews (Fig. 2d–f). The total predicted area for singing voles remains fairly constant through time, but shifts spatially from west to east (Supplementary Fig. S1d–f). In both shrews and voles, predictions reflect increasing proportions of overlap between boreal and tundra taxa, representing broadening contact zones through time, disparate rates of change among different ecological associations, and consequently a reduction in total area predicted solely for tundra species (Fig. 3). The refugial area for only tundra species consists of a small region within the Arctic National Wildlife Refuge, although total overlap of tundra species is fragmented into four larger refugial areas in the northern Brooks Range and Arctic Coastal Plain (Fig. 3). Distribution of widespread root voles decreases slightly into the future, particularly in central Alaska (Supplementary Fig. S2d–f). The area predicted for barren-ground shrews without boreal masked shrews within the next century (2080s) amounts to <1% of present SDM predictions (Fig. 2; Supplementary Table S1) and the total area for barren-ground shrews including the zone of contact with masked shrews is reduced to ~60% of present. Of this 60%, ~36% is coincident with Bureau of Land Management (BLM) lands, including the National Petroleum Reserve-Alaska currently managed for multiple uses, ~12% and ~15% is coincident with US Fish and Wildlife Service (USFWS) and National Park Service (NPS) lands, respectively, currently managed as natural areas, and ~37% is coincident with 'other' land uses, including private and Native lands in Alaska, but primarily in Canada near the Mackenzie River Delta (Fig. 3). Of predicted future refugia for barren-ground shrews and singing voles (hotspots for multiple tundra species) in the 2080s, ~47% is coincident with BLM lands, ~17% is coincident with USFWS lands, ~14% is coincident with NPS lands, and 22% is coincident with 'other' land uses (Fig. 3; purple areas). Models for both tundra species indicate a marked exodus from areas representing western and southern extents of Arctic tundra, including the Seward Peninsula. For full details of distributional predictions as related to land-management categories see Supplementary Table S1.

Demographic analyses. Genetic evidence from previous phylogeographic assessments facilitated compilation of specimens representing independent lineages for demographic analyses, and defined the full geographic extent and coalescent history of lineages within the study area⁹. Only singing voles did not exhibit significant genetic signatures of range expansion over all demographic analyses (Table 1 and Fig. 4c). However, the degree and timing of population change differs despite similar genetic diversity within each group (shrews and voles; Table 1).

Table 1 | Demographic statistics for all study species.

Statistic	Barren-ground shrew	Masked shrew	Singing vole	Root vole	Meadow vole
<i>n</i>	68	114	81	78	27
π	0.00255	0.00235	0.0113	0.0053	0.0053
Hd	0.864	0.880	0.985	0.957	0.963
θ	0.0464	0.362	0.0640	0.0210	0.443
<i>D</i>	−1.891 (0.0068)	−2.680 (\ll 0.0001)	−1.297 (0.087)	−1.685 (0.018)	−1.708 (0.023)
<i>F</i> ₅	−21.370 (\ll 0.0001)	−85.722 (\ll 0.0001)	−21.394 (\ll 0.0001)	−9.505 (0.012)	−14.974 (\ll 0.0001)
<i>R</i> ₂	0.0386 (0.0069)	0.0151 (\ll 0.0001)	0.0603 (0.099)	0.0511 (0.039)	0.0544 (\ll 0.0001)
<i>g</i>	2978.960	3349.408	340.391	278.555	2242.385
s.d.(<i>g</i>)	626.761	444.590	36.053	51.088	415.904
s.d.(<i>g</i>) > 0	4.878	8.068	9.441	5.452	5.392

n = number of specimens; π = nucleotide diversity; Hd = haplotype diversity; θ = effective population size given taxon specific mutation rate; *D* = Tajima's *D*; *F*₅ = Fu's *F*₅; *R*₂ = Ramos-Onsins and Rozas *R*₂; *g* = best maximum likelihood estimate of the growth parameter; s.d.(*g*) = standard deviation of the growth parameter; s.d.(*g*) > 0: number of standard deviations above zero of the mean growth value. *P*-values are provided in parentheses.

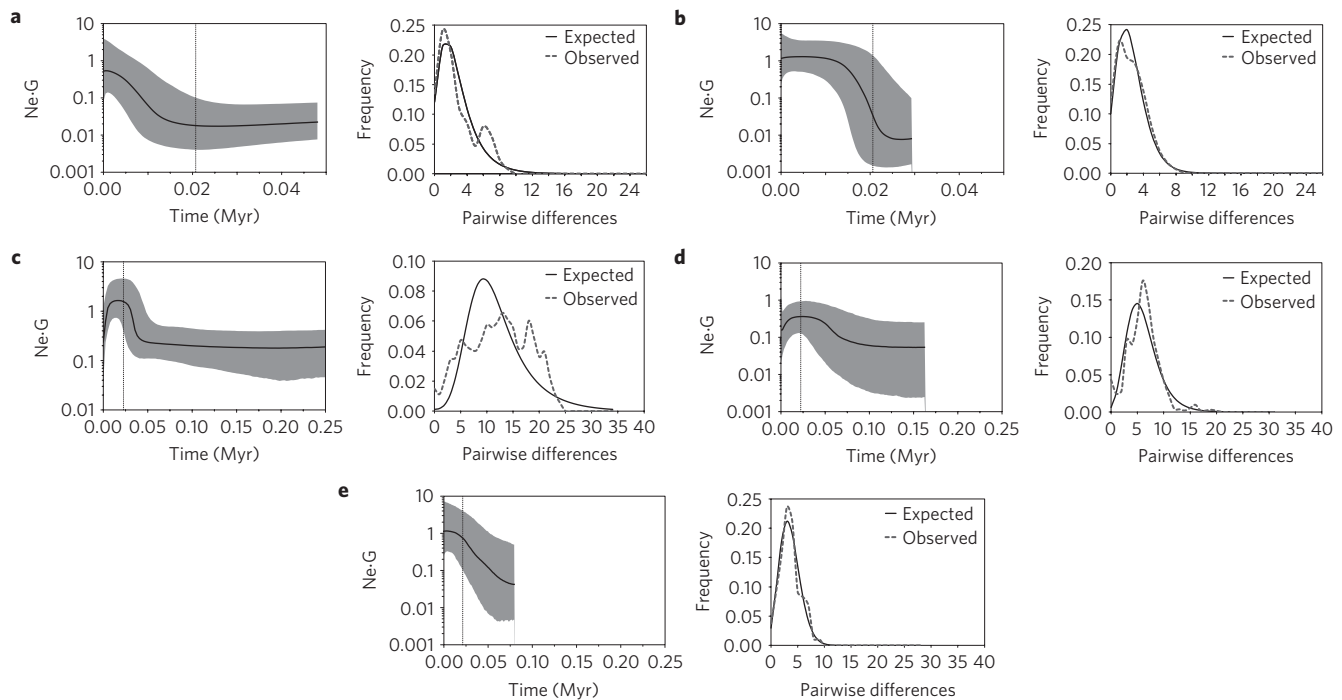


Figure 4 | Demographic results. BSPs (left plot) and mismatch distributions (MDs; right plot) for **a**, barren-ground shrew **b**, masked shrew **c**, singing vole **d**, root vole and **e**, meadow vole. BSPs indicate population growth from past (right) to present (left) including median population size through time (black line) and 95% highest probability distribution (grey interval). Log-transformed y-axes represent population size as a function of effective population size (Ne) and generation time (G). Vertical dotted lines intersect plots at the LGM (21 kyr). MDs indicate expected and observed curves for the number of pairwise differences under an exponential population growth scenario.

Smooth mismatch distributions with few pairwise differences for shrews and meadow voles indicate recent expansion, and Bayesian skyline plots (BSPs) reflect population growth since the LGM (Fig. 4a,b,e). Ragged mismatch distributions for singing and root voles, with more pairwise differences, indicate earlier expansion in these species, corroborated by a signal of population growth deeper in their coalescent histories, coincident with interstadial events of the mid- to late-Wisconsinan glacial (~75–25 kyr; Fig. 4b,c). The growth parameter (g) indicated significant population growth for all species, although the effective population size, reflected by theta (θ), was much higher for boreal species than for tundra or widespread species. BSPs from singing and root voles indicate recent population declines since the LGM.

Discussion

Using a combination of geophysical, atmospheric, evolutionary and palaeontological approaches²⁴, we have revealed distinctive spatial, ecological and evolutionary responses of different community components within Alaska to environmental change¹⁰. This integrated framework can be applied more broadly throughout the Arctic and across multiple biomes to forecast future scenarios and identify common processes, responses, and distributions, particularly for future refugial areas. Analytical rigour is increased by incorporating inference from multiple disciplines. Our conceptual framework may also be adapted to incorporate additional methods, for instance applying coalescent simulated hypothesis tests of spatial evolutionary processes¹¹. Fossil evidence, particularly from pollen data, has traced the expansion of tundra during cooler periods and its contraction during warmer periods^{4,19–21}. Fossils also verify times of occupation for study taxa (Supplementary Fig. S3). Previous phylogeographic assessments for multiple Arctic taxa provide knowledge of the evolutionary origins of species, lineage relationships, and regional

variability, yielding data for multi-species analyses⁹. For instance, assessment of the two shrew species indicates that barren-ground shrews persisted in Alaska during the LGM whereas masked shrews were restricted south of continental ice sheets⁴⁰, despite predictions of a suitable climate within Alaska at that time for both species. Molecular investigations contribute to interpreting differences between ecological responses (realized niche) versus theoretical responses (fundamental niche) based on abiotic climate variables alone.

The species we explored represent multiple life-history strategies that are reflected by molecular demographic responses. Importantly, all species show signals of range expansion and/or population growth, but with the timing and magnitude differing as a result of factors such as differences in the timing and severity of regional climate shifts, mutation rate differences between taxa, and variable evolutionary origins (for example, Palaearctic, Nearctic, or Beringian endemic). By using multiple lines of evidence to assess demography, we discriminate along both temporal and spatial axes. For instance, singing voles exhibit marked population growth (g -statistic > 9 s.d. above 0; Table 1) coincident with a cooling climate preceding the LGM (BSP; Fig. 4c), and, based on fossil localities, a corresponding increase in the extent of tundra. These voles then experienced a decline coincident with climate warming following the LGM, as evident from SDMs (Supplementary Fig. S1) and molecular signatures (BSP, Tajima's D and Fu's F_s ; Fig. 4 and Table 1). This downward trajectory in population size coincident with warming implies possible future declines of singing voles and associated tundra species¹¹. Dramatic population growth and expansion of meadow voles and masked shrews (boreal species; Table 1) is consistent with recent movement into Alaska⁴¹, tracing northward shifts in associated habitat as early as 12 kyr. Both BSPs (Fig. 4b,e) and high values of θ (Table 1) are consistent with leading edge expansion and massive proliferation of these boreal species^{21,42}. New records of the masked shrew within open

tundra in northern Alaska (ARCTOS—<http://arctos.database.uaf.edu>) further indicate their propensity to occupy peri-glacial areas, facilitating northward expansion with a large effective population size⁴². The relatively lower contemporary effective population size in tundra-associated species is also accompanied by a less extreme population size change through time than for expanding boreal-associated species (Fig. 4a,c), and reflects higher average genetic diversity than boreal species in most instances (Table 1). The current occurrence of boreal small mammals (masked shrews and meadow voles) north of the extent of boreal forest, as predicted from present day SDMs, indicates that many species are not restricted to preferred habitats, provided the prevailing climate is amenable^{32,43}. Barren-ground shrews recently expanded to occupy tundra in North America, including extensive areas previously covered by continental ice sheets. Delayed population growth until post-LGM probably reflects the occurrence in lower densities during coldest periods (sub-optimal conditions for this species) in Alaska. Population growth may reflect a transition to more mesic tundra from arid steppe since the LGM (refs 17, 18). A slightly bimodal mismatch distribution may also indicate expansion from multiple source areas (Fig. 4a). There is growing evidence from phylogeographic studies that incremental specialization to Arctic conditions among tundra community constituents is a process that requires persistence through multiple glacial cycles¹⁰. We might expect tundra species with a relatively long coalescent history within Alaska (eastern Beringia) to more predictably respond to climate trends than recent additions to the community such as barren-ground shrews⁴⁰. Although our unprecedented current warming trajectory may conceivably test the ecological limits of persistent tundra species, even ecological equivalents may exhibit idiosyncratic demographics and distributional predictions³²—differences that again may be predicted by comparative genetic analyses.

Predictions from SDMs indicate habitat suitable for both boreal and tundra community constituents within the study area during the LGM. However, purely climate-based predictions belie historical distributions based on both genetic and palaeontological evidence. No genetic or fossil evidence supports the persistence of masked shrews or meadow voles through a glacial phase within the study area, although the Arctic fossil record documents that other boreal-associated species did persist⁴⁴. Instead, our target boreal species probably occupied southern temperate refugia, and expanded into Alaska only during interglacials. Past SDMs therefore illustrate the potential distribution (= fundamental niche) based on abiotic variables projected back in time, demonstrating that the use of climatic variables alone without considering habitat/community components may not effectively represent the realized niche^{43,45}. Preliminary comparative demographic evidence from >20 small mammal species with boreal, tundra or widespread distributions reveals predictable variability in the timing or extent of major evolutionary responses that typify these different ecological associations (unpublished data—current authors).

Future distributional and demographic scenarios provide initial bases for land-management planning while generating hypotheses for future ecological investigations³⁴. These projections are founded on our understanding of present and past environmental processes that leverage multiple historical timeframes and spatiotemporal evolutionary responses of species. We have shown that for two tundra species, persistent predicted habitat in northern Alaska is largely coincident with areas designated for multiple-use activities, particularly within BLM lands associated with northern portions of the National Petroleum Reserve-Alaska (Fig. 3 and Table 1). The highest concentration of current industry activities (near Prudhoe Bay) is not, however, coincident with these refugial predictions (Fig. 3). Modelling future predictions for tundra species may

therefore assist in management planning that will inform both conservation and development priorities⁴⁶. The other persistent refugium predicted for both barren-ground shrews and singing voles in Alaska is coincident with USFWS lands administered as the Arctic National Wildlife Refuge (Fig. 3). As change in northern Alaska accelerates¹³, unfragmented and protected natural areas such as this probably represent valuable future refugia for the Arctic tundra community³¹. Evaluation of additional tundra-associated species using these methods should help clarify and refine relationships between refugial areas and land-use designations. Common areas for both tundra and boreal species, as predicted by shifting contact zones (Fig. 2 and Supplementary Fig. S1), could represent a potential increase in both species richness and genetic diversity as a consequence of changing climate⁴³. The relative importance of refugial areas for obligate tundra species versus potential diversity hotspots where biomes overlap should be carefully assessed, as each provides distinct conservation opportunities^{12,32}. The coastal position of predicted hotspots for tundra species, for instance, also warrants the incorporation of other components of Arctic biodiversity, such as migratory bird breeding grounds (for example, ref. 47) and factors influencing the terrestrial/marine ecotone.

The methods used here constitute a multi-disciplinary framework for future climate change investigations. This framework can be adapted for different research priorities and to incorporate methodological developments from constituent scientific fields. Inference for a particular community (for example species inhabiting Arctic tundra hotspots) may be improved by including other tundra-associated species along with boreal species, widespread generalists, and non-resident migratory components. Phylogeographic investigations will allow comparative assessments of demography and, in conjunction with SDMs, can provide multiple perspectives on community change within Alaska and more broadly the Arctic¹⁰. These analyses illustrate the potential for biological interactions among species predicted to experience differential, and potentially punctuated, velocities of distributional change^{25,48}. Initial predictions for small mammals reveal a shifting zone of contact for boreal and tundra species into the future (Fig. 2 and Supplementary Fig. S1) that is not necessarily congruent with rates of change for other components of these biomes. For instance, boreal conifer species do not exhibit a steady northward advance at the same rate as these small mammal species, although forest shifts along a leading edge of expansion may be sudden and rapid when a critical climatic threshold is exceeded⁴⁸. Such dynamic contact zones may increase the potential for competition, gene flow through hybridization of closely related species¹², co-evolution versus transfer of parasites, including pathogens⁴⁹, and community turnover, depending on the relative resilience of populations and species^{32,45}.

Methods

A summary of integrated methods is provided (Fig. 1). For full details of all methods see Supplementary Information.

Species distribution models. For SDM development, we used current, past, and future monthly climate data (2.5 arc-minutes; 4 km). Bioclimatic variables, representing summaries of means and variation in temperature and precipitation (Supplementary Table S2), were first examined for multicollinearity, excluding those with a Pearson's $R^2 > 0.8$ with another variable. SDMs were developed within three masks: for *Microtus miurus* and *Sorex ugunak* a mask bounded by 129° W, 162° W, 50° N, and 72° N was used; for *M. pennsylvanicus* and *S. cinereus* a mask bounded by 50° W, 179° W, 25° N, and 72° N was used; for *M. oeconomus* a mask bounded by 32° E, 162° W, 36° N, and 85° N was used. In all cases, bounds correspond to the distribution of study lineages. For species locality data, we collated georeferenced occurrence points for the two shrew species (masked shrew, $n = 223$; barren-ground shrew, $n = 21$) and three vole species (meadow vole, $n = 217$; root vole, $n = 145$; singing vole, $n = 72$), using natural history collection data. Multiple options are available for assessing model uncertainty from SDMs, including examination of results across multiple algorithms (for example, ref. 50).

We focus on the optimization of present-day models using Maxent by calibrating initial past projections using fossil data, and then incorporating multiple future climate GCMs. We generated SDMs using only presence records, contrasted with pseudo-absence data resampled from the remainder of the study area. We used five replicates under the 'crossvalidate' option, and selected when possible a fossil-based threshold for determining suitable habitat. We generated summary maps in ArcGIS 9.3 by averaging Maxent outputs (see Supplementary Information). Past models were made for the LGM and the LIG. Future predictions were made for three timescales: 2010–2039 (referred to as 2020s), 2040–2069 (referred to as 2050s), and 2070–2099 (referred to as 2080s). For the LGM and future time periods, we show the predicted habitat for which 50% or more of the GCM models indicate suitable habitat.

Demographic analyses. Cytochrome *b* gene sequences were obtained from GenBank or sequenced for the current study from frozen (−80 °C) heart or liver tissue through standard salt extraction, polymerase chain reaction, and cycle sequencing methods, with sequence data deposited in GenBank (Supplementary Appendix S1). Samples from masked shrews ($n = 114$; 1,075 bp; 34 localities), barren-ground shrews ($n = 68$; 1,075 bp; 14 localities), meadow voles ($n = 27$; 672 bp; 17 localities), root voles ($n = 78$; 1143 bp; 32 localities) and singing voles ($n = 81$; 1,072 bp; 17 localities) were each grouped as a single population for demographic analyses, all representing distinct lineages based on previous phylogeographic investigations. For each population, genetic diversity statistics (nucleotide diversity [π] and haplotype diversity [Hd]) and tests of demographic expansion (Tajima's D , Fu's F_s , and R_2) were calculated. We also investigated θ and the population growth parameter (g), each run with a starting value of $g = 1$, using 1,000 short chains, 10 long chains, and a random starting seed, within a maximum likelihood framework (F84 substitution model; empirical base frequencies; Tv/Ti ratio = 15). To avoid potential upward bias we calculated the standard deviation (s.d.) from each mean value of g and inferred significant population growth if $g > 3$ s.d. (g) (ref. 41). Pairwise mismatch distributions were produced in DnaSP to visually assess demographic expansion. We produced Bayesian skyline plots to calculate population size change through time using a mutation rate of 5.5% per million years for shrews and 4% per million years for voles¹⁰.

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References

- Callaghan, T. V. *et al.* Biodiversity, distributions and adaptations of Arctic species in the context of environmental change. *Ambio* **33**, 404–417 (2004a).
- Callaghan, T. V. *et al.* Responses to projected changes in climate and UV-B at the species level. *Ambio* **33**, 418–435 (2004b).
- IPCC *Climate Change 2007: Impacts, Adaptation, and Vulnerability* (Cambridge Univ. Press, 2007).
- Harris, S. A. Thermal history of the Arctic Ocean environs adjacent to North America during the last 3.5 Ma and a possible mechanism for the cause of the cold events (major glaciations and permafrost events). *Prog. Phys. Geog.* **29**, 218–237 (2005).
- MacDonald, G. M. Some Holocene palaeoclimatic and palaeoenvironmental perspectives on Arctic/Subarctic climate warming and the IPCC 4th assessment report. *J. Quat. Sci.* **25**, 39–47 (2010a).
- Brook, B. W., Sodhi, N. S. & Bradshaw, C. J. A. Synergies among extinction drivers under global change. *Trends Ecol. Evol.* **23**, 453–460 (2009).
- Forbes, B. C. *et al.* High resilience in the Yamal-Nenets social-ecological system, West Siberian Arctic, Russia. *Proc. Natl Acad. Sci. USA* **106**, 22041–22048 (2009).
- Fuller, T., Morton, D. P. & Sarkar, S. Incorporating uncertainty about species' potential distributions under climate change into the selection of conservation areas with a case study from the Arctic Coastal Plain of Alaska. *Biol. Conserv.* **141**, 1547–1559 (2008).
- Pauls, S. U., Nowak, C., Bálint, M. & Pfenninger, M. The impact of global climate change on genetic diversity within populations and species. *Mol. Ecol.* **22**, 925–946 (2012).
- Hope, A. G., Takebayashi, N., Galbreath, K. E., Talbot, S. L. & Cook, J. A. Temporal, spatial and ecological dynamics of speciation among the amphiberingian small mammals. *J. Biogeogr.* **40**, 415–429 (2013).
- Prost, S. *et al.* Losing ground: Past history and future fate of Arctic small mammals in a changing climate. *Glob. Change Biol.* **19**, 1854–1864 (2013).
- Parnesan, C. Ecological and evolutionary responses to recent climate change. *Ann. Rev. Ecol. Syst.* **37**, 637–639 (2006).
- Sandel, B. *et al.* The influence of Late Quaternary climate-change velocity on species endemism. *Science* **334**, 660–664 (2011).
- Peterson, A. T. *et al.* Future projections for Mexican faunas under global change scenarios. *Nature* **416**, 626–629 (2002).
- Lisiecki, L. E. & Raymo, M. E. A Pliocene–Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. *Paleoceanography* **20**, PA1003 (2005).
- Miller, G. H. *et al.* Temperature and precipitation history of the Arctic. *Quat. Sci. Rev.* **29**, 1679–1715 (2010).
- Elias, S. A. & Crocker, B. The Bering Land Bridge: A moisture barrier to the dispersal of steppe-tundra biota? *Quat. Sci. Rev.* **27**, 2473–2483 (2008).
- Guthrie, R. D. New carbon dates link climatic change with human colonization and Pleistocene extinctions. *Nature* **441**, 207–209 (2006).
- Bigelow, N. H. *et al.* Climate change and Arctic ecosystems: 1. Vegetation changes north of 55 °N between the last glacial maximum, mid-Holocene, and present. *J. Geophys. Res.* **108**, 1–25 (2003).
- Fréchette, B. & Vernal, A. Evidence for large-amplitude biome and climate changes in Atlantic Canada during the last interglacial and mid-Wisconsinan periods. *Quat. Res.* **79**, 242–255 (2012).
- Fritz, M. *et al.* Late glacial and Holocene sedimentation, vegetation, and climate changes from easternmost Beringia (northern Yukon Territory, Canada). *Quat. Res.* **78**, 549–560 (2012).
- Hewitt, G. M. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biol. J. Linn. Soc.* **58**, 247–276 (1996).
- Hewitt, G. M. The genetic legacy of the Quaternary ice ages. *Nature* **405**, 907–913 (2000).
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* **15**, 365–377 (2012).
- Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. *Annu. Rev. Ecol. Syst.* **41**, 321–350 (2010).
- Walker, M. D. *et al.* Plant community responses to experimental warming across the tundra biome. *Proc. Natl Acad. Sci. USA* **103**, 1342–1346 (2006).
- Hinzman, L. D. *et al.* Evidence and implications of recent climate change in northern Alaska and other Arctic regions. *Climatic Change* **72**, 251–298 (2005).
- Sahlman, T., Segelbacher, G. & Höglund, J. Islands in the ice: Colonization routes for rock ptarmigan to the Svalbard archipelago. *Ecography* **32**, 840–848 (2009).
- Brochman, C. & Brysting, A. K. The Arctic—an evolutionary freezer? *Plant Ecol. Divers.* **1**, 181–195 (2008).
- Guisan, A. & Thuiller, W. Predicting species distributions: Offering more than simple habitat models. *Ecol. Lett.* **8**, 993–1009 (2005).
- Loarie, S. R. *et al.* The velocity of climate change. *Nature* **462**, 1052–1055 (2009).
- Gillson, L., Dawson, T. P., Jack, S. & McGeoch, M. A. Accommodating climate change contingencies in conservation strategy. *Trends Ecol. Evol.* **28**, 135–142 (2012).
- MacDonald, G. M. Global warming and the Arctic: A new world beyond the reach of the Grinnellian niche? *J. Experiment. Biol.* **213**, 855–861 (2010b).
- Wiens, J. A., Stralberg, D., Jongsomjit, D., Howell, C. A. & Snyder, M. A. Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proc. Natl Acad. Sci. USA* **106**, 19729–19736 (2009).
- Roberts, D. R. & Hamann, A. Predicting potential climate change impacts with bioclimate envelope models: A palaeoecological perspective. *Glob. Ecol. Biogeogr.* **21**, 121–133 (2012).
- Brigham-Grette, J. Contemporary Arctic change: A paleoclimate déjà vu? *Proc. Natl Acad. Sci. USA* **106**, 18431–18432 (2009).
- Carstens, B. C. & Richards, C. L. Integrating coalescent and ecological niche modeling in comparative phylogeography. *Evolution* **61**, 1439–1454 (2007).
- Cabeza, M. *et al.* Combining probabilities of occurrence with spatial reserve design. *J. Appl. Ecol.* **41**, 252–262 (2004).
- Araújo, M. B., Cabeza, M., Thuiller, W., Hannan, L. & Williams, P. H. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Glob. Change Biol.* **10**, 1618–1626 (2004).
- Hope, A. G., Speer, K. S., Demboski, J. R., Talbot, S. T. & Cook, J. A. A climate for speciation: Rapid spatial diversification within the *Sorex cinereus* complex of shrews. *Mol. Phylogenet. Evol.* **64**, 671–684 (2012).
- Lessa, E. P., Cook, J. A. & Patton, J. L. Genetic footprints of demographic expansion in North America, but not Amazonia, during the Late Quaternary. *Proc. Natl Acad. Sci. USA* **100**, 10331–10334 (2003).
- Nullmeier, J. & Hallatschek, O. The coalescent in boundary-limited range expansions. *Evolution* **67**, 1307–1320 (2013).
- Hof, A. R., Jansson, R. & Nilsson, C. Future climate change will favour non-specialist mammals in the (sub)Arctic. *PLoS ONE* **7**, e52574 (2012).
- Harington, C. R. Pleistocene vertebrates of the Yukon Territory. *Quat. Sci. Rev.* **30**, 2341–2354 (2011).
- Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X. & Karanewsky, C. J. *et al.* How does climate change cause extinction? *Proc. R. Soc. B* **280**, 20121890 (2013).
- Truett, J. C. & Johnson, S. R. (eds) *The Natural History of An Arctic Oil Field* (Academic, 2000).
- Flint, P. L. *et al.* Changes in abundance and spatial distribution of geese molting near Teshekpuk Lake, Alaska: Interspecific competition or ecological change? *Polar Biol.* **31**, 549–556 (2007).
- Scheffer, M., Hirota, M., Holmgren, M., Van Nes, E. H. & Chapin, F. S. Thresholds for boreal biome transitions. *Proc. Natl Acad. Sci. USA* **109**, 21384–21389 (2012).

49. Hoberg, E. P., Galbreath, K. E., Cook, J. A., Kutz, S. J. & Pottey, L. Northern host-parasite assemblages: History and biogeography on the borderlands of episodic climate and environmental transition. *Adv. Parasitol.* **79**, 1–97 (2012).
50. Araújo, M. B. & New, M. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* **22**, 42–47 (2007).

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Author contributions

A.G.H., J.A.C., E.W. and S.L.T. conceived the study, collected and provided samples, and performed genetic laboratory work. A.G.H and E.W. compiled data, designed and performed analyses. D.C.P. managed aspects of policy and land-use. S.L.T., A.G.H., J.A.C., and D.C.P. secured funding. A.G.H. led writing. All authors discussed the results and implications and contributed to writing the manuscript at all stages.

Additional information

Genetic sequence data were deposited in GenBank (Accession numbers JQ778853-JQ778955; KC473470-KC473496). Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to A.G.H.

Competing financial interests

The authors declare no competing financial interests.