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Host responses to cycles of climate change shape parasite diversity across North America's Intermountain West

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Abstract. Host-parasite cospeciation, in which parasite divergence occurs in response to host divergence, is commonly proposed as a driver of parasite diversification, yet few empirical examples of strict cospeciation exist. Host-parasite co-evolutionary histories commonly reflect complex mosaics of cospeciation, dispersal, lineage extinction and other phenomena. The episodic host-switching model of parasite diversification accounts for complexity by suggesting that diversification and faunal assembly is a consequence of fluctuation between environmental disruption and environmental stability. The phylogeographic predictions of the strict cospeciation and episodic host-switching models were tested using the North American pika/parasite assemblage, with a primary focus on the American pika, *Ochotona princeps* (Richardson, 1828), and a suite of its endoparasitic cestodes and nematodes. This approach integrating phylogeographic and demographic methods with inferences drawn from species distribution modelling revealed that the parasite community of pikas has been shaped by climate-driven range fluctuation of hosts and bouts of geographic and host colonization by parasites associated with transitions between glacial and interglacial phases.

Key words: comparative phylogeography, co-evolution, host-switching, historical demography, *Ochotona princeps*, Pleistocene

Introduction

Parasites represent an exceptionally diverse component of the biosphere (Poulin & Morand 2000), yet the processes that produced this diversity are not fully understood. One concept of parasite diversification with deep roots in parasitology is that parasite lineages, especially those that are strongly host-specific, diverge as a direct consequence of host differentiation (Brooks & McLennan 1993). This cospeciation model predicts that associated taxa speciate in concert, resulting in phylogenetic congruence between hosts and parasites. Such a clear phylogenetic prediction is relatively straightforward to test, and the growing database of co-phylogenetic studies demonstrates that perfect congruence between host and parasite phylogenies is uncommon (e.g. Brant & Gardner 2000, Brooks & Ferrao 2005, Huyse & Volckaert 2005, Zarlenga et al. 2006, Hoberg et al. 2012, Hoberg & Brooks 2013), even in host-parasite systems in which parasite life history characteristics might be predicted to maximize the potential for codivergence (e.g. phthirapteran chewing lice; Hafner & Page 1995, Johnson et al. 2002, Gomez-Diaz et al. 2007). For example, recent re-evaluation of the classical model for cospeciation revealed a complex history of host switching and geographic colonization over time (Brooks et al. 2014, 2015, Hoberg & Brooks 2015).

Until recently, studies of parasite diversification have primarily focused on interspecific or deeper taxonomic scales, with phylogenetic incongruence between host and parasite lineages explained in terms of coevolutionary phenomena such as host-switching, parasite lineage extinction or duplication (Page & Charleston 1998, Paterson & Banks 2001, Brooks & McLennan 2002). However, the roots of co-phylogenetic complexity lie at the interface of micro- and macroevolutionary history, which is most appropriately examined using phylogeographic tools (Riddle & Hafner 2004). Thus, investigating host-parasite relationships within a comparative phylogeographic framework has potential to provide insight into the processes that have led to parasite

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diversification (Nieberding et al. 2004, Criscione et al. 2005).

Parasites are ideal targets for comparative phylogeographic studies, which seek to uncover consistent patterns of genetic structure among co-distributed organisms to reveal general responses to past environmental influences (Bermingham & Moritz 1998). Possibly because the cospeciation model of host-parasite diversification makes essentially the same prediction as that made by comparative phylogeography (i.e. congruent phylogeographic structure between associated taxa), it has been embraced by researchers interested in host-parasite comparative phylogeography (e.g. Nieberding et al. 2004, Whiteman & Parker 2005, Gomez-Diaz et al. 2007). However, the interpretation of underlying causal mechanisms under cospeciation differs from that of comparative phylogeographic analyses of free-living species. In traditional comparative phylogeography, congruent genetic structure is typically seen as a consequence of extrinsic historical factors (e.g. climate change, vicariance) that affected multiple species in a similar way. Conversely, strict interpretation of the cospeciation model assumes that differentiation among parasite populations occurs exclusively as a consequence of host population structure. In the extreme view, a parasite represents the equivalent of an organellar genome, tracking hosts with such fidelity that incongruent genetic structure between host and parasite is assumed to reflect stochastic genealogical processes or different evolutionary rates rather than the possibility of semi-independent species histories (e.g. Štefka et al. 2011). However, numerous phylogeographic studies on host-parasite systems indicate that strict cospeciation (or "codivergence" which is the term that will hereafter be applied given that phylogeographic investigations typically focus on intraspecific patterns that may or may not result in speciation) fails to fully account for the complexity of host-parasite interactions (e.g. Perkins 2001, Wickström et al. 2003, Criscione & Blouin 2007, Gomez-Diaz et al. 2007, Whiteman et al. 2007, Mizukoshi et al. 2012). Additional coevolutionary events must be invoked (e.g. parasite dispersal among divergent host populations, which is analogous to inter-specific host-switching) to reconcile incongruent host-parasite relationships.

As an alternative to strict codivergence, recent insights about the nature of diversity have driven proposals for an integrated model or synthesis (termed the Stockholm Paradigm) for parasite diversification that seeks to accommodate the complexity of faunal assembly over evolutionary and ecological time (Hoberg & Brooks 2008, Agosta et al. 2010, Hoberg & Brooks 2010, 2013, Brooks et al. 2014, Hoberg & Brooks 2015). Understanding of diversification must include both codivergence and parasite dispersal (Brooks 1988), as well as other co-evolutionary events that can yield incongruent host-parasite lineage associations (e.g. parasite lineage extinction, "missing-the-boat", and independent differentiation of either parasite or host lineages; Brooks & McLennan 1993, Paterson & Gray 1997). In part, this "episodic host-switching model" is predicated on the idea that rather than tracking particular host species, parasites track specific resources that are provided by one or more potential hosts. Consequently, parasites may exist in a "sloppy fitness space" that represents the capacity for broad host-utilization in the context of Ecological Fitting (Janzen 1985, Agosta & Klemens 2008). Ecological Fitting effectively resolves the parasitological paradox between instances of apparent host-specificity and the propensity for parasites to readily switch among hosts, clearly indicated empirically across diverse host-parasite systems (Agosta et al. 2010). The potential for host colonization is mediated by opportunities for contact, usually driven by breakdown in ecological isolation, across an array of possible hosts that offer the appropriate suite of resources (Agosta et al. 2010). Such colonization events, often emanating from ecological transitions and environmental perturbation linked to climate, set the stage for complex phenomena involved in faunal assembly and diversification over space and time (Hoberg & Brooks 2008, Hoberg & Brooks 2015).

The episodic host-switching model proposes that parasite diversification has occurred as a consequence of recurrent fluctuation between brief episodes of environmental disruption and long-term periods of environmental stability (Hoberg & Brooks 2008). Global episodes of environmental change (e.g. climatic cycles) provide a mechanism for cycling between these stages on landscape to regional scales, consistent with the Taxon Pulse hypothesis for faunal diversification (i.e. cycles of geographic expansion promoting adaptation and diversification, eventually concluding with lineage extinction; Erwin 1985). Under the episodic host-switching model, phylogenetic incongruence between hosts and parasites is predicted to be linked to environmentally-induced range shifts (by host, parasite, or both) that could produce complex host-parasite histories and faunal mosaics, representing a clear distinction from vicariance and strict cospeciation (Hoberg & Brooks 2010, 2013). For

example, novel interactions between host populations could trigger parasite dispersal from one host group to another (host-switching), while rapid geographic expansion of host populations could result in parasites failing to track their hosts ("missing-the-boat"). Conversely, concordant phylogenetic signatures between host and parasite lineages should correlate with the intervals of relative stability that fell between major episodes of environmental change, during which spatially structured populations could have diverged as a consequence of sustained geographic isolation. Further expectations of this dynamic include a tendency for parasites to undergo alternating trends toward specialization and generalization relative to hosts (described as Oscillation, Janz & Nylin 2008) and the complex assembly of faunal mosaics that result from recurrent patterns of geographic expansion and isolation on varying temporal and spatial scales (Geographic Mosaic Theory of Coevolution, Thompson 2005). Thus, the episodic host-switching model is a constituent component of the Stockholm Paradigm, an emerging synthesis that represents the interactions among Ecological Fitting, Oscillation, Taxon Pulses and the Geographic Mosaic Theory of Coevolution (Hoberg & Brooks 2008, Brooks et al. 2014, Araujo et al. 2015, Hoberg & Brooks 2015).

This study tests the predictions of the episodic host-switching model for Nearctic pikas (Ochotonidae), small lagomorphs that inhabit rocky alpine habitats in western North America, and a diverse suite of their endoparasitic helminths. Phylogeographic inferences are combined with perspectives drawn from species distribution modeling to assess the relative roles of climate-driven range fluctuation and long-term isolation in structuring diversity within the host-parasite assemblage. Specifically, the following are evaluated: 1) geographic distributions for 14 parasite species associated with pikas, 2) phylogeographic patterns within each parasite species, 3) signatures of demographic change that reflect recent population dynamics, 4) geographic corridors of relatively high dispersal probability for pikas and their parasites under environmental conditions of the Last Glacial Maximum and the current Interglacial Period, and 5) evidence of interspecific interactions between parasite species that could contribute to the structure of species distributions.

Material and Methods

Study system

Two pika species, the American pika, *Ochotona princeps* (Richardson, 1828), and collared pika, *O. collaris* (Nelson, 1893), are extant in North America, occurring in alpine environments of the Intermountain West and northwestern North America (Alaska and northern Canada), respectively (Hoffmann & Smith 2005). Pikas are sensitive to climate, with low tolerance for high temperatures (Smith 1974), and limited capacity for physiological thermoregulation (MacArthur & Wang 1974). This sensitivity played a role in historical range fluctuations in response to climatic oscillations, as demonstrated by fossil (Mead 1987, Hafner 1993, Grayson 2005) and phylogeographic (Galbreath et al. 2009, 2010) evidence. Pikas first arose in the Palearctic, and the North American species are probably descended from a single ancestral colonization across the Bering Land Bridge (Rausch & Ritter 1973, Niu et al. 2004, Formozov et al. 2006, Lissovsky et al. 2007).

This study focuses on reconstructing phylogeographic histories for the helminth parasites of *O. princeps*. However, the helminth fauna of *O. collaris* is descended from more southerly distributed ancestors associated with *O. princeps* (Galbreath & Hoberg 2012). Parasites of both *O. collaris* and *O. princeps* are therefore included in aspects of this phylogeographic analysis. Ten helminth parasite species have been formally described from these two host species, including anoplocephalid tapeworms of the genus *Schizorchis* Hansen, 1948, oxyurid nematodes of the genus *Cephaluris* Akhtar, 1947 and subgenera *Labiostomum* (*Labiostomum*) Akhtar, 1941 and *Labiostomum* (*Eugenuris*) (Schultz, 1948), and strongylid nematodes of the genera *Graphidiella* Olsen, 1948, *Murielus* Dikmans, 1939, and *Ohbayashinema* Durette-Desset, 1974. Hereafter these are referred to as the "major parasite lineages" associated with pikas. An additional eight genetically divergent clades have been identified within these major parasite lineages, which may represent additional species-level diversity (Galbreath & Hoberg 2012). This study focuses on six of these major lineages represented by a total of 14 parasite species that are specifically associated with *O. princeps*, including both formally described and putatively new species (Table 1). All helminths of *O. princeps* and *O. collaris* are restricted to these two host species (Grundmann & Lombardi 1976, Rausch & Smirnova 1984), and as is the case for the hosts, the closest relatives of the parasites occur in Asia. Therefore, all major parasite lineages presumably arrived in North America with pika colonists from the Palearctic, with subsequent diversification yielding further diversity (Hoberg et al. 2012).

Several characteristics make the North American pika-helminth assemblage an excellent system to

investigate the factors that shape patterns of host and parasite diversity and to test predictions of the episodic host-switching model of parasite diversification. First, because these parasites are associated only with pikas, there is confidence that patterns of parasite diversity have not been influenced by dispersal mediated by other hosts. All nematode parasites in this assemblage have direct life cycles, with eggs shed to the environment before being ingested by the next pika host. Only the life cycle of *Schizorchis* includes an intermediate host, probably a soil-dwelling oribatid mite (Guan & Lin 1988), which is not likely to play a dominant role in parasite dispersal. Wind-mediated dispersal by oribatid mites has been observed, but for soil mites it is unlikely to occur over long distances (Lehmitz et al. 2011) and the probability of an infected mite being blown into the territory of (and then ingested by) a pika on a distant mountain range would be extremely small. The close association between North American pikas and their major parasite

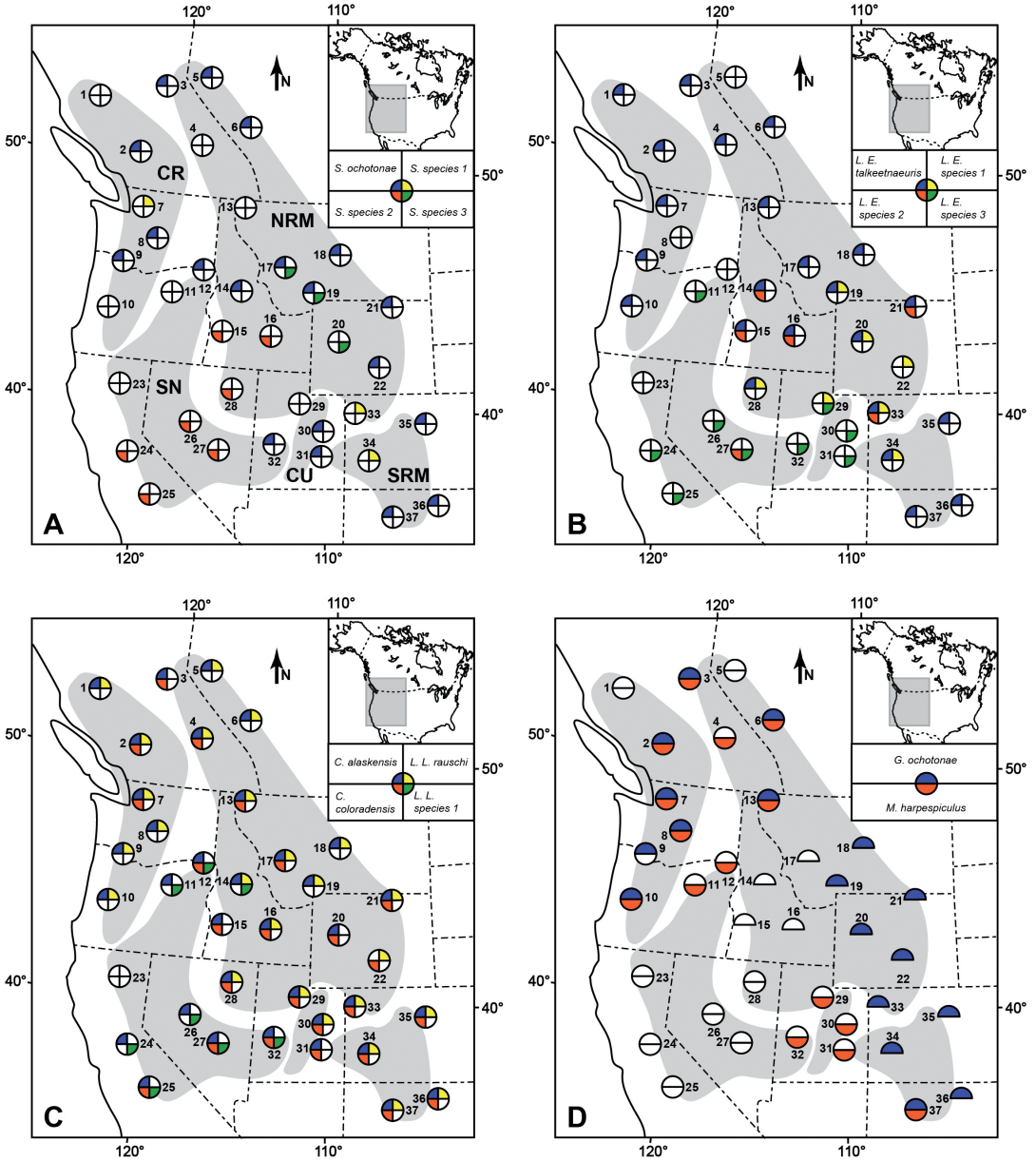

Fig. 1. Geographic distributions of species of A) *Schizorchis*, B) *Labiostomum* (*Eugenuris*), C) *Cephaluris* and *Labiostomum* (*Labiostomum*), and D) *Graphidiella* and *Murielus*. Numbers denote sampling localities and the adjacent segmented circles indicate presence (colored) or absence (white) of each parasite species. Gray patches on the primary maps show the distribution of major host lineages, which are identified in map A: Northern Rocky Mountains (NRM), Southern Rocky Mountains (SRM), Cascade Range (CR), Sierra Nevada (SN), Central Utah (CU). A gray box in the inset maps show the position of the primary map relative to North America. A key below each inset indicates the color and circle segment that denotes each species. The missing lower half of several circles in map D indicates that due to an error in sampling, those localities were not screened for *M. harpespiculus*.

lineages presumably dates back to their entry into the Nearctic, indicating a shared history that has spanned their co-tenure in North America. Second, American pikas exhibit strong phylogeographic structure as a consequence of isolation in separate mountain systems (Hafner & Sullivan 1995, Galbreath et al. 2009, Galbreath et al. 2010). Lineages are associated with the Northern Rocky Mountains (NRM), Southern Rocky Mountains (SRM), Cascade Range (CR), Sierra Nevada (SN), and Central Utah (CU) (Fig. 1), providing an opportunity to test for signatures of codivergence. Isolation among these host lineages is complete during interglacial periods when warm and dry climates restrict pika populations to fragmented sky islands. Periodic contact and limited gene flow among pika lineages has occurred during glacial periods when pika populations expanded to lower elevations (Hafner & Sullivan 1995, Galbreath et al. 2010). Though insufficient to break down genetic lineage boundaries, such contact may have provided opportunities for parasite dispersal among lineages as posited by the episodic host-switching model. Third, during the Quaternary the Intermountain West has been strongly influenced by periods of rapid climate change (e.g. glacial/interglacial transitions) alternating with periods of relative climatic stability (e.g. interglacial periods). Divergence time estimates for pika lineages indicate that *O. princeps* was distributed throughout the region prior to the glacial/interglacial cycles of the late Pleistocene (Galbreath et al. 2010), indicating that the species was exposed to repeated episodes of environmental disruption and establishing a context for testing predictions of the episodic host-switching model.

Data collection

Mitochondrial DNA (mtDNA) sequence datasets were assembled for helminths obtained from 222 *O. princeps* specimens collected during a survey of 37 field localities distributed across the full geographic

Table 1. Summary statistics and model selection for molecular data from parasites of *O. princeps*. The first column lists major parasite lineages (genera or subgenera) in bold and the morphospecies identified from each. The remaining columns list the number of specimens sequenced (N), the number of haplotypes (N_H), haplotype diversity (h), percent nucleotide diversity (π), effective population size calculated using IM scaled by per generation per sequence mutation rate (μN_e) with lower (–CL) and upper (+CL) 95 % confidence limits, Tajima's D statistic, Fu's F_s statistic, and the nucleotide substitution models used in Bayesian phylogenetic (major lineage) and skyline (individual species) analyses.

	N	N_H	h	π (%)	μN_e	–CL	+CL	D	F_s	Model
Schizorchis										GTR + I + G
S. ochotonae	94	41	0.96	1.60	13.71	9.49	20.34	–0.59	–4.74	HKY + I + G
S. species 1	9	4	0.69	2.08	8.32	3.83	22.49	–1.52	6.32	HKY
S. species 2	19	8	0.81	2.40	10.08	5.78	18.69	0.80	4.49	HKY + I
S. species 3	13	4	0.62	0.29	1.19	0.42	3.32	0.17	1.49	HKY
Cephaluris										HKY + G
C. alaskensis	118	56	0.98	3.94	38.41	26.65	55.71	–0.37	–15.32**	HKY + I
C. coloradensis	47	29	0.98	1.95	19.22	12.48	29.91	–0.64	–12.45**	HKY + I
***Labiostomum* (*Eugenuris*)**										GTR + G
L. (*E.*) *talkeetnaeu*ris	76	22	0.92	0.98	8.32	4.81	14.18	–0.60	–7.54*	HKY + G
L. (*E.*) species 1	16	7	0.86	1.10	3.71	1.54	8.95	0.79	0.30	HKY
L. (*E.*) species 2	7	6	0.95	2.49	15.86	6.43	49.57	0.13	0.00	GTR
L. (*E.*) species 3	24	9	0.88	1.08	4.96	2.35	10.01	0.20	–0.28	GTR
***Labiostomum* (*Labiostomum*)**										GTR + G
L. (*L.*) *rauschi*	68	31	0.96	1.53	12.92	7.98	20.75	–0.32	–13.45**	HKY[a]
L. (*L.*) species 1	17	5	0.62	0.26	2.43	0.88	6.57	–1.52*	–1.41	HKY
Murielus										HKY + I + G
M. harpespiculus	43	30	0.95	4.22	40.36	27.65	60.06	–0.46	–4.59	HKY + I + G
Graphidiella										HKY + I
G. ochotonae	72	29	0.94	1.44	13.09	8.16	21.06	–1.10	–11.09**	HKY

[a] DT-MODSEL chose the HKY + I model for the Bayesian skyline analysis of *L.* (*L.*) *rauschi*, but inclusion of the invariant sites parameter caused terminal errors in BEAST. We therefore removed the parameter for this analysis. * Significant at α = 0.05. ** Significant at α = 0.005.

range of the host (Fig. 1, Supplementary material). These molecular datasets consisted of a portion of the cytochrome oxidase I (*COI*, 369 bp) gene and a region overlapping sections of the 12 s and 16 s ribosomal genes (rDNA, ~810 bp) from the nematodes and cestodes, respectively. A subset of these data, in addition to sequences representing parasites acquired from other pika species (*O. collaris*, *O. hyperborea*, *O. cansus*), were published previously in a study on North American pika-parasite biogeography (Galbreath & Hoberg 2012) and obtained from GenBank: *Cephaluris* (*COI*, n = 92 parasite individuals, Genbank # HQ189841-HQ189932), *L.* (*Eugenuris*) (*COI*, n = 55, HQ189933-HQ189987), *L.* (*Labiostomum*) (*COI*, n = 49, HQ189988-HQ190036) and *Schizorchis* (rDNA, n = 64, HQ189777-HQ189840). Additional DNA sequences were acquired for the major nematode lineages using primers BpCoxI-F1/BpCoxI-R1 (Sato et al. 2005), and for the major tapeworm lineage using primers Hym16sF/Hym12sR (von Nickisch-Rosenegk et al. 2001). Reaction conditions were as described elsewhere (Galbreath et al. 2009, Galbreath & Hoberg 2012). This yielded the following additional sequence data: *Cephaluris* (*COI*, n = 85 parasite individuals, Genbank # KP876060-KP876144), *L.* (*Eugenuris*) (*COI*, n = 77, KP876217-KP876293), *L.* (*Labiostomum*) (*COI*, n = 44, KP876294-KP876337) and *Schizorchis* (rDNA, n = 82, KP876383-KP876464). DNA sequences were also collected from specimens representing two additional nematode (strongylid) genera using the same nematode primers and conditions: *Murielus* (*COI*, n = 45, KP876338-KP876382) and *Graphidiella* (*COI*, n = 72, KP876145-KP876216). All of these strongylid specimens represent populations associated with *O. princeps*, with the exception of two samples obtained from *O. cansus* that are referable to *Murielus tjanschaniensis* (Gvozdev, 1962) and are included here to place the North American *Murielus* diversity within its broader Holarctic context. Parasites were identified to species using methods appropriate for each taxon (Hoberg et al. 2009, Galbreath & Hoberg 2012). Vouchers and frozen tissues for host and parasite specimens are archived in appropriate research collections (hosts – University of Alaska Museum, Museum of Southwestern Biology, Cornell University Museum of Vertebrates, parasites – United States National Parasite Collection, Museum of Southwestern Biology; Supplementary material Table S1).

COI sequences were aligned by eye. Several indels were evident in the rDNA dataset, so these data were aligned using CLUSTALW (Thompson et al. 1994) as implemented in MEGA 3.1 (Kumar et al. 2004) under default parameters. The alignment was checked by eye and indels were removed, yielding a final rDNA dataset of 805 bp. To quantify patterns of genetic diversity among species, haplotype and nucleotide diversity were calculated for each species using DNASP 4.10.4 (Rozas et al. 2003). Because many population genetic methods rely on the assumption of neutral evolution, DNASP was used to test each intraspecific dataset for selective neutrality by calculating Tajima's D statistic and assessing significance based on coalescent simulations of 1000 neutrally evolving populations.

Data analysis

To characterize phylogeographic structure within and among all species in the six major parasite lineages for which genetic data are available, a Bayesian phylogenetic approach using MRBAYES 3.0b4 (Huelsenbeck & Ronquist 2001) was applied to reconstruct relationships among unique haplotypes. An appropriate model of nucleotide substitution for each haplotype dataset was chosen using DT-MODSEL (Minin et al. 2003) (Table 1), and analyses included five chains that were each run for five million steps. Sampling took place every 100 steps and the first 10000 samples were discarded as burn-in. Analyses were repeated three times from different starting seeds to confirm topological convergence, and support for relationships was assessed based on nodal posterior probabilities. Nematode phylogenies were rooted using one representative sequence from the most closely related lineage(s) available in the dataset. Thus, the pinworms *Cephaluris*, *L.* (*Labiostomum*), *L.* (*Eugenuris*) provided outgroups for each other, as did the strongylids (*Graphidiella*, *Murielus*). The *Schizorchis* tree was rooted with *Hymenolepis diminuta* (Rudolph, 1819) (GenBank #AF314223).

Phylogenetic methods assume that existing sequences occupy tip positions in a tree rather than ancestral nodes and branching is strictly bifurcating. However, at the population level both ancestral and descendant haplotypes may be present and a single haplotype may give rise to multiple descendant haplotypes. Therefore, TCS 1.21 (Clement et al. 2000) was used to construct minimum spanning networks (MSNs) for all species based on the statistical parsimony method described by Templeton et al. (1992). The probability of parsimony was set to 99 % to conservatively infer parsimonious relationships and avoid over-interpreting relationships between more distantly related haplotypes that may be better reconstructed via phylogenetic methods.

Effective population size (N_e) plays an important role in determining the distribution of population genetic diversity (Nadler 1995, Criscione & Blouin 2005), and may offer insight into differences in phylogeographic structure observed in parasites that share the same host. Extensive sampling of American pika populations provides an opportunity to assess demographic trends for a diverse array of parasites associated with a single host species. Therefore, relative estimates of long-term N_e were obtained for populations of parasites associated with *O. princeps* using IM (Hey & Nielsen 2004). Each parasite species was analyzed separately based on a maximum of 50 representative DNA sequences, which were randomly selected from the full sequence dataset if a greater number of individuals had been sequenced. Datasets were limited to 50 individuals to reduce the computational intensity of the analysis. Species were treated as a single population by setting the population divergence time to zero (flag –j5), and simulations ran for 10 million generations following a 100 thousand generation burn-in. Each analysis included 10 chains which followed a two-step heating scheme (h1 = 0.05, h2 = 0.7). The infinite sites model of nucleotide substitution was applied if it was consistent with the data, but in most cases the data required the HKY model. Pika populations fluctuated in size as a consequence of climate change (Galbreath et al. 2009), indicating that associated parasites might also experience changes in N_e over time. The genetic signature of recent changes in N_e was assessed for each species associated with *O. princeps* based on complete sequence datasets rather than unique haplotypes. First, the F_s (Fu 1997) statistic was calculated, which has been shown to be sensitive to demographic growth under a model of sudden expansion (Ramos-Onsins & Rozas 2002). Significant departures of the observed test statistic from the simulated data, potentially indicative of recent population expansion, were assessed using DNASP 4.10.4 (Rozas et al. 2003) to generate null distributions from 1000 coalescent simulations of a neutrally evolving, large population of constant size. Second, Bayesian skyline plots (Drummond et al. 2005) were generated using BEAST 1.4.8 (Drummond et al. 2002, Drummond & Rambaut 2007). Rather than test for a single demographic event (e.g. recent population growth), skyline plots assess fluctuations in effective population size over time. Further, skyline plots take into account coalescent stochasticity associated with genealogical processes that summary statistics cannot address. For skyline analyses, separate models of nucleotide substitution were selected for each species using DT-MODSEL (Minin et al. 2003) (Table 1). Lacking information on whether or not nucleotide evolution in the parasites is clock-like, a relaxed, uncorrelated lognormal molecular clock model was applied (Drummond et al. 2006). Each analysis used the constant Bayesian skyline tree prior (10 groups) with default priors for model parameters. For all but one species the model was run for 50 million generations with trees and parameters sampled every 1000 generations. For *C. alaskensis* the analysis was run for 110 million generations and sampled every 10000 generations. Skyline plots were generated in TRACER 1.4 (Rambaut & Drummond 2004) after discarding 10 % of samples as burn-in and ensuring that effective sample size values for all parameters were greater than 200. For all datasets that produced informative results (i.e. skyline plots that did not simply reflect the prior distribution), a second analysis (10 million generations for most species, 100 million for *C. alaskensis*) was run to confirm the initial result.

To understand how environmental conditions contributed to shaping the distributions of the parasites of *O. princeps*, an approach based on species distribution modelling was used to infer corridors of highest dispersal probability for pikas across North America's Intermountain West (Chan et al. 2011). The Create Friction Layer > Invert SDM tool of SDMtoolbox 1.1a (Brown 2014) was used in conjunction with ArcMap 10.2.2 to invert species distribution predictions that had previously been generated for pikas under current and Last Glacial Maximum (LGM, ~21 thousand years ago) conditions (Galbreath et al. 2009). Species distribution models under LGM conditions were based on simulated climate data generated using two alternative general circulation models: Community Climate System Model (CCSM3, Collins et al. 2006) and Model for Interdisciplinary Research on Climate (MIROC, Hasumi & Emori 2004). Inverted species distribution models produce friction layers with highest values in cells where probabilities of species occurrence are lowest (i.e. highest resistance to colonization). Next, the Least-Cost Corridors and Paths > Pairwise: All Sites tool of SDMtoolbox was used with ArcMap to calculate corridors that minimize the cost of dispersal between sampling localities by following paths of lowest friction. Calculation of these least-cost corridors, which predict zones of highest connectivity among populations, was conducted using default settings. Sampling locality 23 (Fig. 1) was excluded from this analysis because no parasites were observed at this locality.

Finally, in addition to host history, competitive interactions between parasites have potential to

influence the geographic distribution of parasite species. Though such interactions cannot be assessed directly with available data, it is possible to calculate the probability that two or more randomly distributed species will occur in a single host population (Haukisalmi & Henttonen 1998). Species occurrences were randomly resampled 10000 times for each parasite species detected in the 37 *O. princeps* populations that are represented in the dataset. Pairwise comparisons between simulated species occurrences yielded a frequency distribution for the number of times two parasite species occurred in the same population, which was compared to field observations to determine if the species occurred together less often than expected by chance alone. Due to the large number of pairwise comparisons, a Bonferroni correction was applied. For two of the major parasite lineages, *Schizorchis* and *L.* (*Eugenuris*), which each include four putative species, this approach was extended to simulate distributions for all four species simultaneously before calculating the probability of observing two species together in a single host population. An R script used to perform this resampling procedure is available on request from the authors.

Results

All DNA sequences exhibited characteristics consistent with expectations for true mtDNA (e.g. variant sites in *COI* concentrated at first and third codon positions). Tajima's D tests indicated that one species exhibited a weakly significant signature of selection, *L.* (*L.*) species 1, but the remaining 13 tests were non-significant (Table 1). Haplotype diversity was universally high within all species, showing that species are not dominated by a small number of high-frequency haplotypes. In contrast, nucleotide diversity varied considerably among lineages, though there was no obvious taxonomic or geographic pattern among species with high or low diversity.

Morphological and molecular identification of new parasite material included in this study indicate no new species-level diversity relative to that which has been reported previously (Table 1, Galbreath & Hoberg 2012). Four of the major parasite lineages (including cestodes and oxyurid nematodes) associated with *O. princeps* are distributed widely across most of the host's range (Fig. 1A-C), contrasting with the apparent absence of the two strongylid genera, *Murielus* and *Graphidiella*, from many southwestern populations (Fig. 1D). This highlights a biogeographic distinction between the parasite communities of southwestern populations (primarily associated with the SN host lineage) and those that are distributed across the Cascade Range and Rocky Mountain cordilleras. Three species, *S.* species 2, *L.* (*E.*) species 3, and *L.* (*L.*) species 1, are primarily associated with southwestern populations, while the remaining seven species representing *Schizorchis*, *L.* (*Eugenuris*), and *L.* (*Labisotomum*) are found in populations distributed in an arc across the northern and eastern portion of the host's range (Fig. 1A-C). The two species of *Cephaluris* are relatively widespread throughout. Despite these patterns, there is no clear concordance between parasite species boundaries and those of the major pika lineages. All but one species was associated with two or more host lineages.

Phylogenetic analyses confirmed the results of the morphological examination, showing that all morphospecies represent genetically distinct, and in most cases unambiguously monophyletic, lineages (Fig. 2). In the most speciose lineages, *Schizorchis* and *L.* (*Eugenuris*), relationships among species are generally well-resolved. In contrast, phylogenetic resolution within most species was relatively poor. To illustrate intraspecific relationships, a composite phylogeny is presented that incorporates MSNs onto the phylogenetic framework provided by the Bayesian analysis (Fig. 2). In this way a phylogenetic context is established for unlinked networks, while retaining information regarding fine-scale relationships among haplotypes separated by few mutations. In general, species are represented by many haplotypes of roughly equal frequency, and haplotypes are rarely shared among more than two populations. Notable exceptions include widespread, high-frequency haplotypes of *L.* (*E.*) *talkeetnaeuris* Akhtar, 1956, *L.* (*L.*) *rauschi* Akhtar, 1956, and *G. ochotonae* Olson, 1948 (Fig. 2B, C, F). Approximately 16 % of all nematode haplotypes were shared among two or more localities. In contrast, only around 5 % of *Schizorchis* haplotypes were shared, suggesting a higher level of geographic structuring in the tapeworms. Of the shared haplotypes, most are geographically clustered, though *L.* (*L.*) *rauschi* again provides an exception. In this species, one haplotype is found in two localities that span nearly the full *O. princeps* distribution (1 and 22, Fig. 2), but not in intervening localities.

Strong concordance between pika genetic lineages and intraspecific genetic structure in parasites is not evident. Though some parasite haplotypes associated with specific host lineages form monophyletic clades within parasite species (e.g. *S.* species 2 – NRM cluster, *L.* (*E.*) species 3 – CU cluster, *M. harpespiculus* Dikmans, 1939 – NRM cluster, Fig. 2A, B, G), the

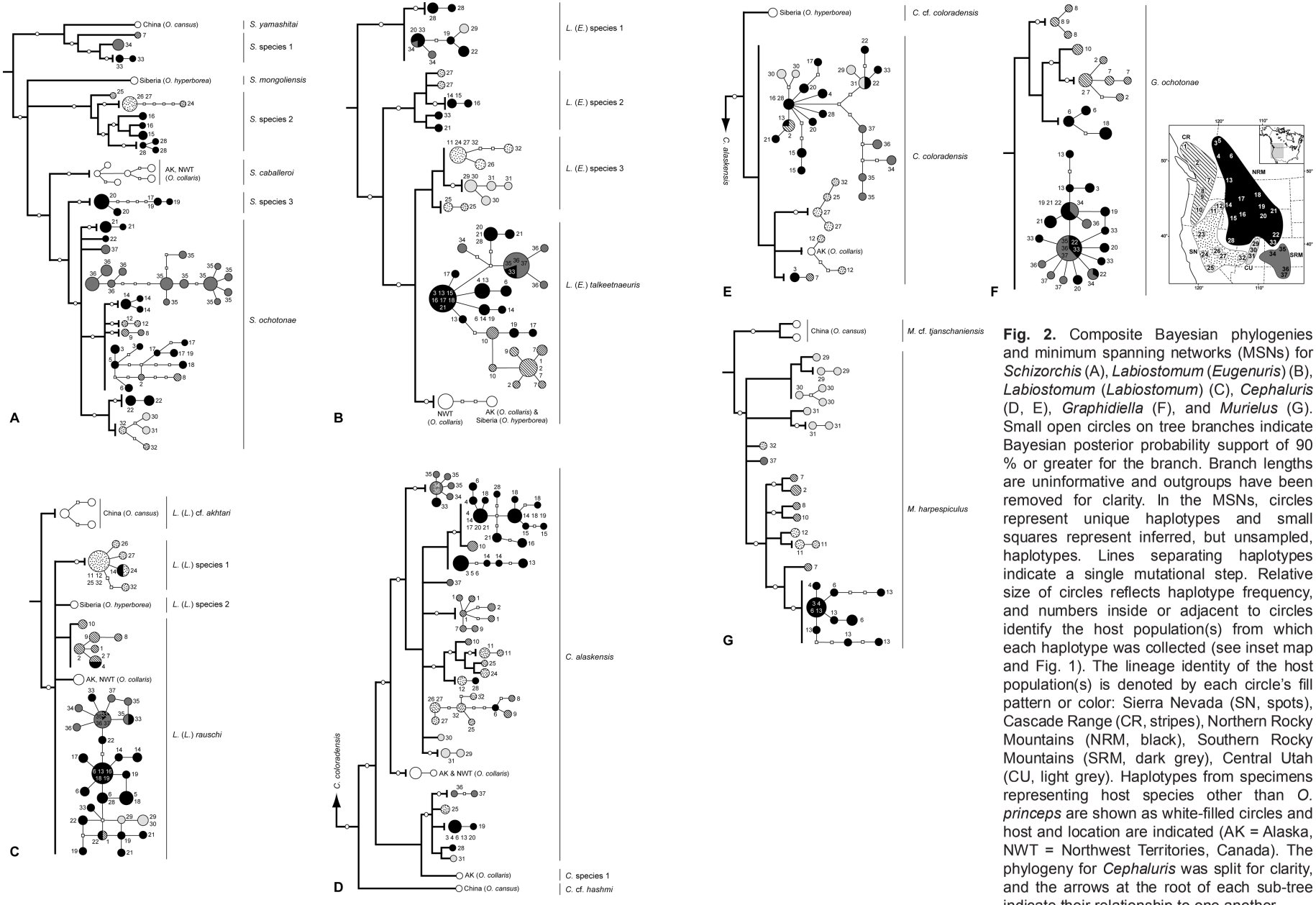

Fig. 2. Composite Bayesian phylogenies and minimum spanning networks (MSNs) for *Schizorchis* (A), *Labiostomum* (*Eugenuris*) (B), *Labiostomum* (*Labiostomum*) (C), *Cephaluris* (D, E), *Graphidiella* (F), and *Murielus* (G). Small open circles on tree branches indicate Bayesian posterior probability support of 90 % or greater for the branch. Branch lengths are uninformative and outgroups have been removed for clarity. In the MSNs, circles represent unique haplotypes and small squares represent inferred, but unsampled, haplotypes. Lines separating haplotypes indicate a single mutational step. Relative size of circles reflects haplotype frequency, and numbers inside or adjacent to circles identify the host population(s) from which each haplotype was collected (see inset map and Fig. 1). The lineage identity of the host population(s) is denoted by each circle's fill pattern or color: Sierra Nevada (SN, spots), Cascade Range (CR, stripes), Northern Rocky Mountains (NRM, black), Southern Rocky Mountains (SRM, dark grey), Central Utah (CU, light grey). Haplotypes from specimens representing host species other than *O. princeps* are shown as white-filled circles and host and location are indicated (AK = Alaska, NWT = Northwest Territories, Canada). The phylogeny for *Cephaluris* was split for clarity, and the arrows at the root of each sub-tree indicate their relationship to one another.

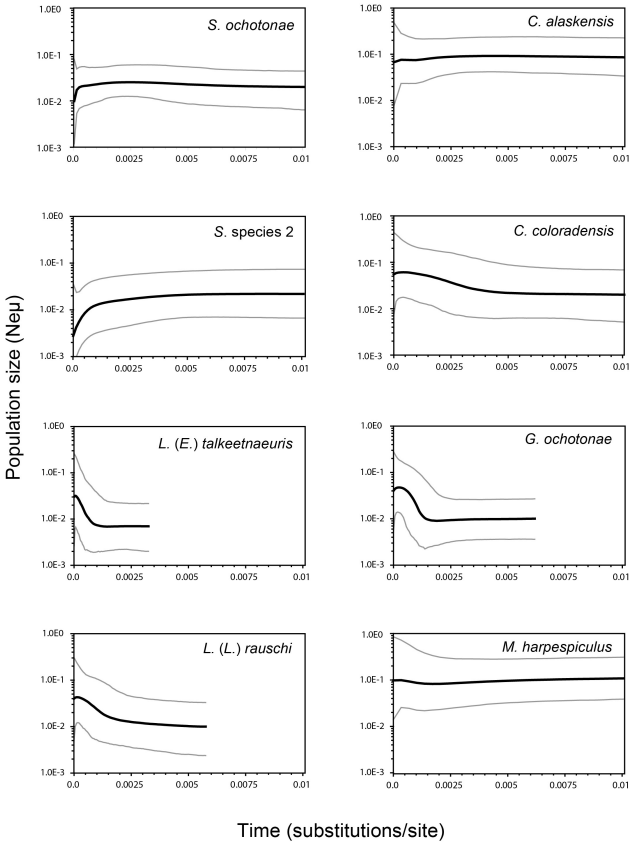

Fig. 3. Bayesian skyline plots for parasite species showing effective population size scaled by mutation rate and plotted as a function of time. A heavy black line indicates the median value of effective population size. Gray lines denote the 95 % highest posterior probability interval. The horizontal axis has been scaled to show the same interval (0-0.01 substitutions/site) for all plots.

overall pattern is one of paraphyly with respect to host lineages. Further, individual haplotypes of six species are shared between two different host lineages. Sharing between the NRM and SRM lineages is most extensive (seven haplotypes), followed by NRM and CR (three haplotypes), NRM and SN (one haplotype), and NRM and CU (one haplotype).

Estimates of N_e scaled by mutation rate are relatively consistent across most parasite species (Table 1), but values for one pinworm (*C. alaskensis* Hobbs, 1976) and strongylid (*M. harpespiculus*) appear to be significantly higher than those recorded for most of the other species. Tests of recent demographic change revealed varied results, though some general patterns were evident. Fu's F_s test detected a signature of recent expansion in five species (Table 1), while Bayesian skyline plots provided additional perspective on the history of demographic change for several species (Fig. 3). Consistent with the F_s tests, *C. coloradensis* Hobbs, 1976, *L.* (*L.*) *rauschi*, *L.* (*E.*) *talkeetnaeuris*, and *G. ochotonae* all exhibited signatures of recent population growth. *Cephaluris alaskensis* and *M. harpespiculus* showed evidence of long-term stability in population size, and two tapeworms, *S. ochotonae* and *S.* species 2, exhibited signatures of recent population decline. Skyline analyses for six species represented by the smallest DNA sequence datasets (7 to 24 individuals) yielded uninformative results in the form of skyline plots that did not differ substantially from the prior distribution (not shown).

Examination of least-cost corridors between pika populations indicate that fewer barriers to pika dispersal existed during LGM environmental conditions relative to the present (Fig. 4). In particular, both LGM reconstructions suggest a relatively high degree of connectivity between the CR, NRM, and CU host lineages, establishing a potential dispersal corridor across the northern and eastern portions of the American pika's distribution. Strong linkages to populations representing the SN host lineage are not evident under any scenario.

Simulations to estimate the probability that parasite species pairs occur together less frequently than expected by chance failed to detect non-random

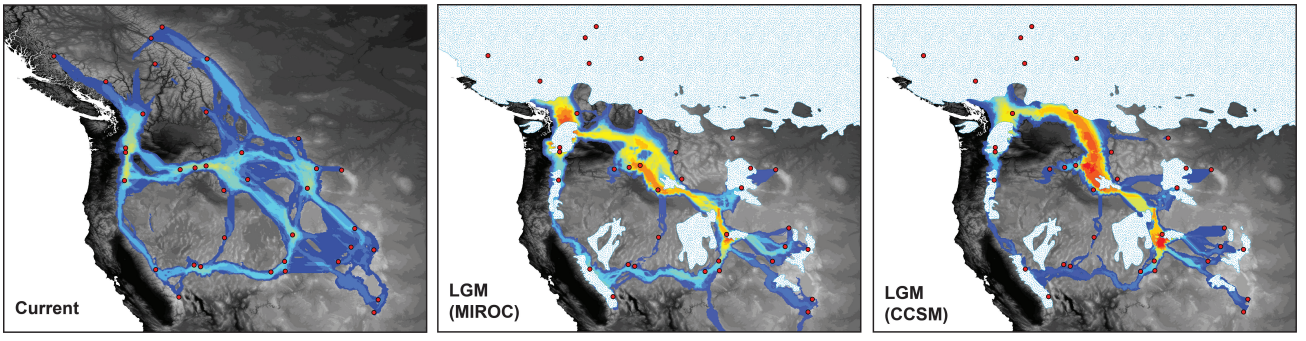

Fig. 4. Least-cost corridors calculated between sampling localities based on current and Last Glacial Maximum (LGM) climate conditions. Least-cost corridors are represented using a color spectrum ranging from blue (high dispersal cost) to red (low dispersal cost). Color spectra are set to the same scale for the three panels to aid in comparison between them. Red-filled circles denote sampling localities. On the LGM maps, the distribution of glacial ice and major pluvial lakes has been masked (blue speckles). Gray background shading represents elevation contours. Separate results are presented for LGM conditions simulated under two different climate models (see text).

associations in all but two cases after correcting for multiple comparisons ($\alpha = 0.05$). Only the *L.* (*E.*) *talkeetnaeuris*/*L.* (*E.*) sp. 3 ($P < 0.0001$) and *L.* (*L.*) *rauschi*/*L.* (*L.*) species 1 ($P = 0.0002$) species pairs exhibited significant negative associations. Of the simulations that evaluated associations in the distributions of four species simultaneously, a significant negative relationship among species of *Schizorchis* was observed ($P = 0.0151$), but this was not the case for *L.* (*Eugenuris*) ($P = 0.5644$).

Discussion

If strict codivergence (or co-speciation sensu Brooks 1979) was the dominant process driving diversification within the major parasite lineages associated with American pikas, host and parasite phylogeographic structure should be strongly concordant. Given minimal evidence of concordance, alternative processes have presumably contributed to the complex pattern of relationships between host lineages and parasite diversity. Though parasite dispersal between host lineages is one common cause of incongruence between host and parasite phylogenies, there are a variety of other processes that can produce incongruent relationships (Page 1993, 1994). In the case of pikas and their parasites, for example, "missing-the-boat" or local extirpation of parasite populations without associated host extirpation could explain the apparent absence of *Graphidiella* and *Murielus* from many southwestern populations. However, neither these scenarios nor independent parasite differentiation can parsimoniously account for the repeated pattern of geographically widespread parasite species associated with multiple pika lineages. Alternatively, if these species were associated with the ancestor of *O. princeps* before diversification began in the mid-Pleistocene (Galbreath et al. 2010), their widespread occurrence could be explained by a failure to co-diverge (Paterson & Banks 2001). From a micro-evolutionary perspective, this would result if mutation rates are slow and insufficient time has elapsed for lineage sorting to complete (Rannala & Michalakis 2003). Time to lineage sorting is a function of N_e. Unfortunately, rigorous estimates of N_e for parasites are lacking (Criscione et al. 2005), and the mutation rate-scaled estimates calculated here (Table 1, Fig. 3) cannot be translated into absolute values without a robust molecular clock. Thus, it is difficult to assess the relative lineage sorting periods of hosts and parasites.

Incomplete lineage sorting might contribute to the general lack of reciprocal monophyly among parasite clades associated with different host lineages, but it is less convincing as an explanation for the persistence of shallow relationships between parasite haplotypes that span host lineage boundaries. Twelve haplotypes representing six parasite species are shared between well-differentiated host lineages. If they were present in the ancestral population (i.e. before host lineage separation), their antiquity might be reflected in higher frequencies relative to more recently derived haplotypes (Watterson & Guess 1977), yet most shared haplotypes do not occur at higher frequencies than non-shared haplotypes. Older haplotypes are also expected to be widespread, but most of the shared haplotypes are restricted to narrow geographic ranges that overlap boundaries between adjacent host lineages, indicating recent gene flow rather than long-term persistence. Further, the high haplotype diversity apparent in most parasite species, and the occurrence of novel haplotypes in post-glacially colonized populations established within the past 10 thousand years (localities 1 to 6, Fig. 2), demonstrate that new diversity can be acquired rapidly through mutation.

Additional lines of evidence make a strong case for periodic contact between certain host populations, further emphasizing the potential for episodes of parasite dispersal. For example, though pika populations are restricted to high alpine islands under interglacial (e.g. current) climatic conditions, the fossil record shows that past environmental disturbance in the form of climate cooling initiated pika range expansion into low-elevation basins that separate the major mountain ranges of the Intermountain West (Mead 1987, Hafner 1993, Grayson 2005). This presumably explains evidence for nuclear introgression among certain host mtDNA lineages (especially NRM and SRM; Hafner & Sullivan 1995, Galbreath et al. 2010), and undoubtedly created opportunities for parasite gene flow as well. The results of the least-cost corridor analysis also showed that although current conditions do not favor dispersal by pikas and their parasites, movement across the northern and eastern montane corridors during the LGM would have been more likely. The primary pattern of haplotype sharing among parasite populations (i.e. greatest sharing between CR, NRM, and SRM populations) is consistent with this perspective drawn from species distribution modelling and the genetic evidence of historical contact among host populations. Despite a general history of regional isolation that shaped host lineages across the Intermountain West, periodic climate-driven contact created opportunities for parasite dispersal as predicted by the episodic host-switching model of parasite diversification (Hoberg

& Brooks 2008, 2010, 2013). Distribution of genetic diversity thus is shaped by recurrent events driving episodes of expansion, contact, parasite exchange, and isolation – complex processes that contrast with limited models of vicariance (Hoberg & Brooks 2010). Such factors are involved in the assembly of complex faunal mosaics with reticulate histories reflecting chronological and spatial heterogeneity (Thompson 2005, Hoberg & Brooks 2013).

The clearest signal of parasite biogeographic structure that loosely correlates with host phylogeography is the apparent division between the distinct and relatively depauperate southwestern parasite fauna and the more complex fauna of the north and east. Though boundaries between these two regional faunas are indistinct, the distribution of parasite species suggests that dispersal into the southwestern region by pikas and parasites from the Cascade Range and Rocky Mountains was inhibited even when conditions promoted such dispersal elsewhere. This is consistent with the fact that least-cost corridors generated under LGM conditions depict pathways into the southwestern portion of the pika's range that are no more inviting to dispersal than are those estimated under current conditions (Fig. 4). Given that current isolation among these populations is absolute (Smith & Weston 1990, Hafner 1994), these results suggest that southwestern pikas may have been largely isolated from conspecifics even during glacial periods. Separation between regional faunas due to historical isolation provides a reasonable explanation for species pairs of *L*. (*Eugenuris*) and *L*. (*Labiostomum*) occurring together less frequently than expected by chance. In each pair, one species is widespread within the southwest region and the other represents the northeastern fauna. The overall lack of evidence for competitive exclusion at the population level also corroborates data suggesting that the co-distributed parasites do not exclude one another within individual pika gastrointestinal tracts (Hobbs 1980). However, regional isolation does not fully explain the signal of exclusion observed among *Schizorchis* species, which occurred together in only two populations out of 30. Competitive interactions among tapeworms coupled with population sorting processes may contribute to a complex mosaic of species occurrences across the host landscape.

Demographic growth by pika and parasite populations did not necessarily accompany range expansion, but it seems to have been associated with parasite dispersal among host lineages. Only the two northern pika lineages (NRM and CR) retain the genetic signature of demographic growth as populations expanded during the LGM (Galbreath et al. 2009). Likewise, a clear signal of growth (i.e. corroborated by multiple demographic methods) was detected from only four parasite species. However, demographic growth probably was associated with geographic dispersal given that these are also the majority of species that share haplotypes between multiple host lineages. Thus, range expansion, population growth, and parasite dispersal appear to be linked.

Though not all pika lineages exhibit a signature of demographic growth associated with range expansion during the LGM, all show evidence of population decline during the recent range retraction phase that accompanied post-glacial climate warming (Galbreath et al. 2009). Of the parasite datasets, only two cestode species and no nematodes showed a signal of recent demographic decline. This may reflect a lag in parasite population genetic responses to host demography, or it could indicate an independent parasite response to environmental events. Indeed, the range of demographic responses that were detected in different parasite species (expansion, decline, stability) suggests that parasite population history cannot be assumed to track host history with perfect fidelity.

The episodic host-switching model, and more broadly the integrated components of the Stockholm Paradigm, predict codivergence between host and parasite lineages under stable and persistent environmental conditions (Hoberg & Brooks 2008, 2015). As conditions stabilize, the frequency and magnitude of population range shifts decrease and population isolates, some of which may include newly formed host-parasite associations, embark upon new evolutionary paths. The Holocene, which began roughly 12 thousand years ago and extends to the present, is one such period of environmental stability. The arrival of the Holocene was marked by a period of rapid climate warming that caused pikas to retreat to isolated sky islands (Hafner 1993, Grayson 2005). Since that time, a relatively stable climate has maintained the highly subdivided pika distribution. Isolation among pika populations is clearly evident in the distribution of their mtDNA haplotype variation. In a study on the distribution of genetic variation across 64 populations, no mtDNA haplotypes were shared by multiple populations (Galbreath et al. 2010). Though some parasite haplotypes are shared among populations, providing evidence of recent gene flow, most (82 %) are not shared, reflecting local differentiation. Thus, pikas and parasites are

co-diverging as a consequence of shared isolation in refugial sky islands until another environmental perturbation initiates a new round of population range shifts, faunal mixing, and parasite dispersal.

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Supplementary online materials

Table S1. This table includes the original field ID of each parasite specimen from which sequence data were collected, the museum and catalog number for archived host specimens from which parasites were collected (CUMV = Cornell Museum of Vertebrate Zoology, MSB = Museum of Southwestern Biology, UAM = University of Alaska Museum), the museum and catalog number for archived parasite voucher specimens (USNPC = US National Parasite Collection), Genbank accession numbers, general localities or locality identification numbers (numbers represent locality IDs shown in Fig. 1 of the manuscript), and the latitude and longitude (degrees, minutes, seconds) for each specimen. All specimens represented in the DNA sequence datasets used in this study are included here (Excel file; URL: http://www.ivb.cz/folia/download/galbreath_and_hoberg_table_s1_supplementary_material.xlsx).