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COMPARATIVE BIOGEOGRAPHY OF NORTH AMERICAN PIKA PARASITES: UNRAVELING A HISTORY DRIVEN BY CLIMATE CHANGE

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COMPARATIVE BIOGEOGRAPHY OF NORTH AMERICAN PIKA PARASITES:
UNRAVELING A HISTORY DRIVEN BY CLIMATE CHANGE

By

Heather M. Toman

THESIS

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COMPARATIVE BIOGEOGRAPHY OF PIKA PARASITES: UNRAVELLING A HISTORY DRIVEN BY CLIMATE CHANGE

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ABSTRACT

COMPARATIVE BIOGEOGRAPHY OF NORTH AMERICAN PIKA PARASITES: UNRAVELING A HISTORY DRIVEN BY CLIMATE CHANGE

By
Heather M. Toman

Parasites are an understudied group that can provide important information on ecosystem dynamics and climate change as well as host biogeographic history. I performed a comparative biogeographic study on two endoparasitic helminth lineages associated with pikas (*Ochotona*) - the tapeworm genus *Schizorchis* and the pinworm subgenus *Labiostomum (Eugenuris)*. Colonization history across Beringia was assessed using analyses of historical range estimation and tests for simultaneous divergence. Analysis results allow me reject the hypothesis that these parasites colonized the Nearctic during a single glacial cycle, as evidenced by multiple Nearctic and Palearctic lineage pairs that did not diverge simultaneously. This evidence indicates a pre-Pleistocene (>2.5Mya) history of multiple, independent colonizations of pikas and their parasites across Beringia primarily in an eastward direction. Comparison of these two major parasite lineages indicates semi-independent histories, with trans-Beringian parasite lineage formation likely driven by taxon pulses, with expansion and vicariance cycles reflecting periods of environmental stability and perturbation, leading to complex histories of colonization and host-switching within pikas.
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Deep respect and thanks to the National Science Foundation for granting funding to specimen collection efforts, such as the Beringian Coevolution Project, that has been gathering baseline data for mammals and their parasites across the Beringian region for ten years. This NSF grant, as well as ones awarded to Dr. Kurt Galbreath to collect pikas and their parasites across the American Intermountain West have made research possible for many investigators, including myself (DEB 0196095, DEB 0415668, DEB 1258010, DEB 0506042 and DEB 1256943).
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INTRODUCTION

Over half of all known species can be classified as parasites, and these numbers are undoubtedly underestimated due to the continual discovery of many cryptic species within known groups (Cook et al., 2005; Dobson et al., 2008). Parasites have been understudied despite their potential to provide important information regarding ecosystem dynamics and the effects of historical climate and geological changes (Bermingham & Moritz, 1998). Traditionally, the evolution of parasites has been widely viewed as directly linked to the evolution of their host. This model of cospeciation predicts host and parasite phylogenies to be perfectly congruent (Brooks, 1979; Brooks & McLennan, 1993). However, the accumulation of co-phylogenetic studies partnered with a more detailed understanding of parasite taxonomy has revealed that perfect cospeciation is rare (e.g. Brant & Garder, 2000; Brooks & Ferrao, 2005; Huyse & Volckaert, 2005; Hoberg et al., 2012; Hoberg & Brooks, 2013; Brooks et al., 2015).

Events that lead to differences between host and parasite phylogeny include lineage extinction or duplication, but are primarily driven by host-switching events that correlate with extrinsic historical periods of strong environmental perturbation (such as the episodic glacial cycling of the Quaternary) (Hafner & Page, 1995; Johnson et al., 2002; Zarlenga et al., 2006; Hoberg et al., 2012; Hoberg & Brooks, 2013). During these periods, hosts are most likely to be moving across the landscape in search of suitable habitat, which creates opportunity for contact between species that did not previously overlap. Parasites in this situation are much more likely to successfully switch hosts into species that offer similar resources. Additionally, vicariance events that split or
bottleneck host populations and expose them to different environmental pressures can have discordant phylogenetic outcomes for their parasites (Hoberg and Brooks, 2008; Hoberg et al., 2012). However, when environmental conditions are stable, we may see co-divergence between tightly associated organisms (e.g. Wickström et al., 2003; Haukisalmi et al., 2015).

Studies on parasite biogeography are important in order to gain a more thorough understanding of the processes that lead to parasite diversification. They can also offer insight into future distributions of potential emerging infectious diseases through the use of predictive modeling (Brooks et al., 2014; Hoberg & Brooks, 2015). Another advantage arises from the close association parasites have with their hosts, where a comparative phylogeographic approach can be used to fill in gaps present in host history and illuminate a shared history that may be unavailable by looking at the host alone (Criscione et al., 2005; Nieberding & Olivieri, 2007). In order to distinguish shared historical events from parasite specific processes it is important to include multiple co-distributed, independent lineages of parasites whenever possible (e.g., Galbreath & Hoberg, 2012). In doing this, parasite-specific patterns can also be uncovered, and we can begin to parse out the extrinsic historical factors that could have influenced the evolution of these independent parasite lineages similarly, from differences between parasite and host history that are specific to a single lineage (Galbreath & Hoberg, 2015). In uncovering these patterns of parasite biogeography, and linking them to what is known about the history of the parasite’s environment, we also begin to learn important details about past conditions of a region and how they have influenced assemblages of fauna over time (Cook et al., 2005; Hoberg et al., 2012; Hoberg & Brooks, 2013).
Beringia, which encompasses the area surrounding the Bering Strait from eastern Siberia to northwestern North America (Figure 1), is central to our understanding of Holarctic species distributions and genetic diversity. Since the separation of the continents at the beginning of the Neogene (~25 Myr), Beringia has become an intermittent terrestrial corridor and refugium during glacial maxima, and a barrier to gene flow during warmer periods (Hopkins, 1959; Sher, 1999; Cook et al., 2005; DeChaine 2008). Until the late Pliocene (~3.6 Myr), climate was not a limiting factor for biota during land bridge exposure, as northern conditions were significantly warmer than seen currently. Therefore, major exchanges of land vertebrates were bi-directional and symmetrical. But during the Pleistocene (2.58 Myr – 11.7 Kyr), temperature changes became more extreme and ice sheets advanced and receded with longer periods of more extreme cooling emphasized (Dyke and Prest, 1987; Williams et al., 1998). During this time, Asia and Beringia remained largely ice-free with relatively mild conditions, which allowed Asian species to move into the exposed Beringian land mass. Species from North America were cut off from Beringia due to the Laurentide and Cordilleran ice sheets that covered the majority of Canada and the northern United States (Dyke and Prest, 1987; Roberts, 1991; Williams et al., 1998). As temperatures warmed during interglacials, a corridor between the ice sheets opened, allowing the flora and fauna established in Beringia to move east into North America, thus creating a pattern of mostly west to east colonization (Waltari et al., 2007). However, recent studies are beginning to reveal evidence for multiple colonizations of Holarctic species occurring in both directions across the Bering land bridge during the Pleistocene (e.g. Dawson et al., 2013; Kohli et al., 2015).
The endoparasitic helminths of pikas (genus *Ochotona*) provide an excellent comparative system for investigating colonization history across Beringia and diversification in North America, as they are diverse, widespread, and host-specific to pikas (Grundmann & Lombardi, 1976; Rausch & Smirnova, 1984). Pikas are small lagomorphs with 30 extant species within the single *Ochotona* genus. Most species occur in the Palearctic (Eurasia). The only two that occur in North America are sister species, with *O. collaris* found in Alaska and northern Canada, and *O. princeps* occurring farther south in the American West (Hoffmann & Smith, 2005). The ancestor of the *Ochotona* genus arose in Eurasia, and North American pika species presumably descended from a single ancestral colonization eastward across the Bering land bridge (Rausch & Ritter, 1973; Niu *et al*., 2004; Formozov *et al*., 2006; Lisovsky *et al*., 2007; Lanier & Olson, 2009). Similar to their hosts, the closest relatives to parasites of North American pikas occur in Eurasia. They presumably arrived in the Nearctic with pikas, and diversified after colonization, leading to the species now found in North America (Hoberg *et al*., 2012; Galbreath & Hoberg, 2015). Recent work has hinted that this group likely underwent a more complex history of movement, with some limited evidence for a recent westward movement into the Palearctic (Galbreath & Hoberg, 2012).

Following the simple west-to-east model for Beringian colonization, *O. collaris* was originally thought to be directly descended from Beringian colonizers from Asia, and *O. princeps* originated from individuals who later colonized southward along mountain corridors (Guthrie, 1973). However, phylogenetic evidence from multiple lineages of pika parasites indicates that *O. collaris* likely arose from a southern ancestor (Galbreath and Hoberg, 2012). Parasites from *O. princeps* were consistently found to be ancestral to
parasites found in *O. collaris*, indicating that *O. princeps* is the descendent lineage from Asian pikas that originally came across the Bering land bridge. After moving south into the Intermountain West, pikas subsequently moved back north during a more recent glacial cycle, with glacial vicariance leading to the speciation of *O. collaris*. This revised and more detailed history was inferred based on evidence from a single mitochondrial DNA locus, and suffered from a limited pool of Eurasian parasite specimens. Individual gene genealogies often do not match true evolutionary history due to stochastic processes such as incomplete lineage sorting, and maternally inherited mtDNA may only reflect the history of females (Ballard & Whitlock, 2004; McCormack *et al*., 2009; Leaché & Rannala, 2011). The addition of specimens from a wider geographic area, specifically the Palearctic, as well as sequencing loci from both nuclear and mitochondrial genomic regions, is likely to recover a more complete species history.

Here I provide a multi-locus comparative biogeographical analysis of two major groups of parasites found in pikas, the pinworm subgenus *Labiostomum (Eugenuris)* Schultz, 1948, and the tapeworm genus *Schizorchis* Hansen, 1948. Previous assessments provide a basis to test alternative colonization and diversification hypotheses for this assemblage.

**Hypothesis 1 (H1): Amphi-beringian colonization and diversification history**

**H1a:** Pika parasite lineages colonized the Nearctic via the Bering Land Bridge during a single glacial cycle. Subsequent diversification occurred within North America; therefore all Nearctic pika diversity should be monopyletic with all Nearctic parasite species restricted to the two host species, *O. princeps* and *O. collaris*. Extended sampling of parasites in the Palearctic will only reveal lineages that are highly divergent from
Nearctic parasites. **H1b:** A large single colonization occurred over the Bering land bridge into the Nearctic that brought multiple parasite species for each major lineage. Nearctic pika parasite species could have maintained sister relationships with populations in the Palearctic under this scenario and are therefore not restricted to *O. princeps* and *O. collaris*. Tests should indicate simultaneous divergence between all taxon pairs found in the Palearctic and Nearctic. **H1c:** Multiple colonizations across the Bering land bridge have occurred during independent glacial cycles for one or both major parasite lineages. Nearctic parasites are predicted to be polyphyletic with respect to Palearctic parasites and tests for simultaneous divergence for independent taxon pairs across the Bering Strait will be rejected.

**Hypothesis 2 (H2): Nearctic colonization history**

**H2a:** *Ochotona collaris* colonized northward from a southern ancestor, as hypothesized by Galbreath and Hoberg (2012). The diversity of *O. collaris* parasites is predicted to be phylogenetically nested within those of southern *O. princeps* parasites for both parasite lineages. **H2b:** *Ochotona princeps* is derived from a northern Nearctic ancestor. Results supporting this hypothesis will show the diversity of *O. princeps* parasites nested within northern *O. collaris* parasites for both parasite lineages. **H2c:** The two parasite lineages will show conflicting results regarding host ancestry. *Schizorchis* and *L. (Eugenuris)* will differ in their phylogenetic structure concerning their host associations and colonization history, indicating a more complicated history of movement north and south. **H2d:** For both *Schizorchis* and *L. (Eugenuris)*, populations associated with *O. princeps* and *O. collaris* will be reciprocally monophyletic, providing no additional information regarding colonization history within North America.
METHODS

Study System

There are seven major helminth lineages (at the generic to subgeneric level) associated with Nearctic pikas, with a total of ten formally described and eight potentially new species (Galbreath & Hoberg, 2012). In order to test biogeographic hypotheses of pika parasite colonization across the Bering land bridge and species diversification history in North America, I focus on helminths associated with these Nearctic pikas, specifically the pinworm subgenus Labiostomum (Eugenuris) and the tapeworm genus Schizorchis. Both parasite lineages have a total of three described species in North America (L. (E.) talkeetnaeuris, S. ochotonae, S. caballeroi), and they each have three genetically divergent and morphologically distinct clades that may represent additional species-level diversity. Here they are identified as species 1, 2 and 3 for each parasite lineage, as in Galbreath & Hoberg (2012).

Data collection

The majority of the parasites used in this study were from O. princeps collected during a survey of 37 field localities across the full geographic range of the American pika (Galbreath and Hoberg, 2012; 2015), and a smaller proportion from O. collaris hosts (n = 12). In addition, parasite specimens were acquired from several pika species (O. dauurica, O. alpina, O. hyperborea, and O. pallasii) collected in Mongolia during a Beringian Coevolution Project field expedition. Parasites dissected from these pikas were identified to genus level, and those identified as Schizorchis (n=3) and (L.) Eugenuris
(n=4) were added to the few Palearctic specimens (from *O. cansus* and *O. hyperborea*) used by Galbreath and Hoberg (2012). A map of all collection localities is provided in Figure A1.

I extracted or acquired previously extracted DNA from an average of two specimens per locality for each lineage. All DNA was extracted using either a Qiagen DNeasy kit or Epicentre Masterpure DNA extraction kit. For *Schizorchis*, two mitochondrial markers were sequenced, including an 836 base pair (bp) region overlapping sections of the 12s and 16s ribosomal genes (rDNA, n = 154) and a 546 bp section of the cytochrome b (Cytb) gene (n = 82). The *L. (Eugenuris)* dataset included two mitochondrial DNA regions (Cytb [566 bp, n = 111] and cytochrome oxidase I [COI, 369 bp, n = 104]) and one autosomal DNA region, the second internal transcribed spacer between nuclear coded rRNA genes (ITS2 [774 bp, n = 115]). In addition, I acquired sequence data from GenBank for *Schizorchis* (rDNA, n = 150, HQ189777-HQ189840, KP876383-KP876464) and *L. (Eugenuris)* (COI, n = 92 parasite individuals, Genbank #s HQ189933-HQ189987, KP876217-KP876293) from previously published studies (Galbreath & Hoberg, 2012; 2015). Additional parasite sequences were acquired using polymerase chain reaction (PCR) conditions described elsewhere (Galbreath *et al.*, 2009), except for the annealing temperature (AT), which was unique for each primer set. *Schizorchis* sequences were acquired for rDNA using primers Hym16s/Hym12sR (von Nickisch-Rosenegk *et al.*, 2001) (AT = 52°C, n = 7) and for Cytb using primers Hym01/HymLem02 (Makarikov *et al.*, 2013) (AT = 50°C, n = 82). *Labiostomum (Eugenuris)* sequences for *COI* were acquired using primers BPCOX1-F1/BPCOX1-R1 (Sato *et al.*, 2005) (AT = 50°C, n = 18). I designed Cytb (EUCYB-F/EUCYB-R; AT =
42˚C, n = 111) and ITS2 (EUITS2-F/EUITS2-R; AT = 55˚C, n = 115) primers for *L. (Eugenuris)* by importing annotated sequences of *Wellcomia siamensis* and *Enterobius vermicularis* from GenBank into the program Geneious 6.1 (Kearse *et al.*, 2012), performing a global alignment using ClustalW (Thompson *et al.*, 1994), and then using the design primers feature (Primer 3; Untergasser *et al.*, 2012) to find the best sequence locations for optimal primer effectiveness. Primer 3 does this by avoiding repetitive elements and portions of the sequence that could be chimeric. It also uses ratios of base pair richness to determine the optimal primer length for a given melting temperature (a list of all primers provided in Table A1). Vouchers and frozen tissues for parasite specimens and hosts are archived at the United States National Parasite Collection (USNPC), Museum of Southwestern Biology (MSB), and Cornell Museum of Vertebrates (CMV) (Tables B1 & B2).

PCR products were sent to ELIM Biopharmaceuticals for sequencing in both directions. Sequences were then assembled and edited in Geneious 6.1 (Kearse *et al.*, 2012), alignments were performed using the ClustalW algorithm (Thompson *et al.*, 1994) implemented under default parameters. The alignments were checked by eye and indels within ITS2 were manually removed, yielding a final length for this locus of 609 bp.

**Phylogenetic analysis**

To evaluate phylogenetic relationships within and between Palearctic and Nearctic parasite species, I constructed both locus-specific and multi-locus phylogenetic analyses. In order to more accurately parameterize these analyses, statistical selection of the best-fit out of 66 possible substitution models of nucleotide substitution was carried out in jModeltest (Posada, 2008) using the Akaike Information Criterion (AIC) separately
for each locus and species (Table A2). *Hymenolepis diminuta* (GenBank # AF314223) served as an outgroup for *Schizorchis*, and *Labiostomum (Labiostomum) rauschi* (GenBank # HQ189993) for *L. (Eugenuris)* in phylogenetic analyses (Galbreath & Hoberg, 2012). I constructed both maximum likelihood (ML) and Bayesian (BA) trees for each locus to compare results from these two widely used statistical methods. Once constructed, independent gene trees were then compared to assess consistency between markers and determine consistent clades within lineages. I used Garli 2.0 (Zwickl, 2006) to conduct heuristic tree searches and nonparametric bootstrap resampling under the ML criterion. Likelihood searches were run using the default parameters for run optimization, and each bootstrap pseudoreplicate was run until –ln L values converged (changing less than 0.01). PAUP* v. 4.0b10 (Swofford, 2000) was then used to calculate nodal support by computing a consensus tree of 100 bootstrap pseudoreplicates. Gene trees were also constructed under BA methods using MrBayes 3.2 (Ronquist et al., 2012). I performed runs with five chains and 10 million generations, taking samples every 1000 generations, and nodal support was given as posterior probabilities (Figures B1-B5).

Differences can exist between trees generated from a single marker due to stochastic variation and non-neutral evolution. Therefore, multi-locus estimation methods are more useful for resolving true species history (Ballard & Whitlock, 2004). Five individuals were randomly selected from within each major clade and for each genetic marker (when available) for species tree generation in BEAST 2.2 (Drummond et al., 2012). This program employs the coalescent-based *BEAST* (Heled & Drummond, 2010) method of phylogeny estimation which permits multi-locus estimates of species trees. All coding mitochondrial genes (*Cytb* and *CO1*) were tested using PartitionFinder
v1.1.0 (Lanfear *et al.*, 2012) implemented in Python2.7 to select the best-fit codon partitioning scheme and these partitions were implemented in BEAST. In order to determine whether to implement a strict or relaxed molecular clock in BEAST, a likelihood-ratio test of clocklike evolution (Felsenstein, 1988) was performed based on likelihood scores calculated in PAUP* under a clock constraint versus no constraint. In all cases, the null model of a molecular clock could not be rejected (P > 0.1); therefore a strict clock was implemented. The Yule model tree prior was used for species-level coalescent simulation because it is the simplest model with a single parameter, the birth rate. This reduced the number of parameters to be estimated, which minimized bias in the absence of additional parameter information. The specific models of evolution chosen by jModeltest for the locus-specific analyses were applied to the appropriate loci by editing the BEAST XML source code. I fixed the mean substitution rate to a value of 1 so that coalescent times would be calculated in units of substitutions per site. Three independent Markov chain Monte Carlo (MCMC) simulations of 400 million steps were run for each major lineage with different starting seeds, sampling every 4000 steps. Parameter values drawn from the posterior were viewed graphically in Tracer v1.6 (Rambaut *et al.*, 2014) to ensure that parameter estimates reached stationarity, and to confirm that the three independent runs converged on similar parameter estimates. Effective sample size (ESS) values for all parameters were confirmed to exceed 200. Runs were combined using LogCombiner, after discarding the first 10% of each run as burnin, and trees were then summarized using TreeAnnotator (both part of the BEAST package). FigTree v1.4.2 (Rambaut & Drummond, 2009) was used to display the inferred species trees.
**Biogeographic analysis**

Historical biogeographic estimations were reconstructed for both major parasite lineages using statistical model testing with the R package BioGeoBEARS (BioGeography with Bayesian [and likelihood] Evolutionary Analysis in R Scripts) (Matzke, 2013). This package requires a well-supported phylogeny with branch lengths, and branch tips representing entire species, as opposed to individuals. Consensus trees from the multi-locus BEAST analysis provided this input. The BioGeoBEARS program compares six different models using AIC to identify which has the best statistical fit to the data. There are three base models implemented under a maximum likelihood (ML) framework, each with an additional jump dispersal parameter added (+J). The three models are, DEC (dispersal-extinction-cladogenesis), DIVALIKE (dispersal-vicariance analysis under ML), and BayAreaLIKE (Bayesian approach with a large number of areas under ML). Each of these models have different free parameters (such as dispersal, vicariance, or extinction), allowing exploration of the relative roles these biogeographic phenomena might have had in structuring the distribution of lineages over time.

BioGeoBEARS uses current ranges of species to infer biogeographic history. Each species was assigned to one of four geographic regions based on major breaks in extant parasite distributions (Palearctic [P], Alaska/Canada [C], Intermountain West [W], and American southwest [S]). Justification for splitting up regions for *O. princeps* parasites into just W and S, rather than groups representing the five host population phylogroups, is based on species distribution patterns in both lineages (Galbreath & Hoberg, 2015). In both *Schizorchis* and *Eugenuris*, a single species is associated with the southwest portion of the host’s range, and remaining species are widely distributed along
the Cascade Range and Rocky Mountain cordilleras (See Figures A2 & A3 for \textit{O. princeps} parasite distributions). Additionally, species distribution modeling of least-cost corridors has shown that species found primarily in the American southwest have likely been geographically separated from species found widely distributed along the Cascade Range and Rocky Mountain cordilleras since before the Last Glacial Maximum (LGM, \sim 21 thousand years ago) (Galbreath & Hoberg, 2015). BioGeoBEARS allows ancestral ranges to be distributed across multiple regions, and the allowed maximum range size is set by the user. Without additional information to inform restrictions, one less than the total number of regions is recommended, so ancestral range size at a given node was set to a maximum of three (Matzke, 2013). Scripts were run with and without a distance dispersal multiplier, where the probability of dispersal is dependent on the relative distances between range centers. The distance dispersal multiplier matrix I used is provided as Table B3, and an example R script for one parasite lineage is available as Table B4.

Finally, I tested for simultaneous divergence and colonization of closely related taxon pairs across a common barrier (the Bering Strait) by estimating the number and timing of periods of co-divergence. This was done concurrently for both parasite lineages using coalescent-based hierarchical approximate Bayesian computation methods with multi-locus DNA sequence data through the msBayes software pipeline (Hickerson \textit{et al.} 2007). This method accounts for demographic variation among taxa and stochasticity of the coalescent process by first estimating summary statistics from the observed sequence data. After obtaining these summary statistics I simulated a large number of data sets (1,000,000) using the prior distribution for the demographic sub-
parameters. I set the prior for the maximum number of divergence events possible equal to six, the number of lineage pairs spanning the Bering Strait (pairs listed in Table A3). Lastly, I randomly drew 1000 samples from the simulated data sets and used the acceptance/rejection algorithm to approximate the posterior distribution for the parameters. Due to a lack of robust estimates of mutation rate for either parasite lineage, I calculated relative timing of divergences in units of substitutions per site. I summarized posterior distributions using estimates of Ω [var(τ)/E(τ); Bayesian posterior credible interval] and ψ (number of divergence events) across taxon pairs. I assessed significance for the estimated number of divergences based on 95% confidence intervals of Ω. If the confidence intervals do not encompass 0 for Ω, I can reject simultaneous divergence.
RESULTS

**Taxa and phylogenies**

Individual gene trees built for each locus had similar tree topologies under ML and BA methods but some relationships were inconsistent between loci for both parasite groups (see Figures B1-B5). As shown previously (Galbreath and Hoberg 2012), *S.* species 2 is more closely related to the other Nearctic species than *S. mongoliensis* based on the 12s16s locus. However, addition of Cytb data indicates that *S. mongoliensis* may be more closely related to the Nearctic group, with *S.* species 2 sister to this clade. This was supported in the species tree analysis (Figure A4). For *Labiostomum (Eugeneris)*, incongruent results were evident in the placement of *L. (E.)* species 3 either as separate from and sister to *L. (E.) talkeetnaeuris* (in COI and Cytb) or placed within the diversity of *L. (E.) talkeetnaeuris* (ITS2). In addition, *L. (E.) talkeetnaeuris* itself was consistently found to be paraphyletic, but specimens collected from the same host species were monophyletic. These host-specific clades were treated as separate lineages in the Bayesian multi-locus analysis (Figure A5). Species trees generated via BEAST converged on the same stable tree topology that was consistent between runs and had high ESS values, indicating a well-supported species history was evident from the combined data. Surprisingly, rather than the new Palearctic parasite specimens providing an ancestral backbone to the Nearctic parasite phylogenies, the species-tree topologies revealed multiple clades with mixed Palearctic and Nearctic diversity with high nodal support (Figures A4 & A5).
**Colonization history/Biogeography**

For *Schizorchis*, AIC calculations indicate that the DIVALIKE+J model best fit the data for the BioGeoBEARS biogeographic analyses (weighted AIC: 0.47), which emphasizes the processes of dispersal, extinction and vicariance, as well as founder events with the added jump parameter (as opposed to range-switching and sympatry as in other models). The *L. (Eugenuris)* BioGeoBEARS analysis resulted in AIC calculations supporting the DEC+J model when this was run with no dispersal multipliers compared to models that were run with this added prior (weighted AIC: 0.59). This model is similar to DIVALIKE+J except that it allows for sympatry within a subset of the regions and focuses on small vicariance events instead of widespread vicariance. Ancestral range estimations based on these best-fit models are represented as pie charts on ancestral nodes and corner nodes. Sizes of slices of the pie (color-coded to different geographic regions) show ancestral range probabilities, with >50% indicating a high probability of occurrence (Matzke, 2013).

The *Schizorchis* reconstruction of historical biogeography (Figure A4) indicates a Eurasian origin (although with some ambiguity) with a deep split between two clades that each represent at least one colonization eastward into North America. The first clade includes *S.* species 1 in North America grouped with multiple Eurasian species, which would mean an eastward colonization for *S.* species 1 with eventual movement to the western mountains of the contiguous United States. The second clade includes the rest of the North American species also mixed with Eurasian diversity. Two possible biogeographic histories are possible for this group, due to some ambiguity in ancestral range estimation for the split between *S. mongoliensis* and its sister clade of Nearctic
species. There is a clear eastward colonization into the Nearctic by the ancestor of S. species 2 and its sister clade. Following this, the ancestor to S. mongoliensis possibly returned westward into the Palearctic and then its sister clade colonized eastward back into the Nearctic. Alternatively, S. mongoliensis could have split and independently colonized westward into the Palearctic, leaving its sister clade of current Nearctic diversity in North America with S. species 2, which would mean one less eastward colonization compared to the alternative.

Biogeographic reconstruction for L. (Eugenuris) initially detected four eastward colonizations and one westward colonization (Figure A5). However, none of the Palearctic specimens provided an ancestral backbone to the analysis, and because we have confidence in a Palearctic origin for the lineage, there is reason to scrutinize the range reconstruction for the basal node of the tree. The placement of L. (E.) species 1 at the base of the tree influenced the analysis to place its ancestral range in the Nearctic, along with the rest of the L. (Eugenuris) diversity. However, as we move to the sister clade of L. (E.) species 1, the reconstructions along this branch place these ancestors all in the Palearctic. So instead of invoking a back and forth, eastward then westward, then eastward movement with the subsequent Nearctic species, a more parsimonious explanation is that these ancestors remained in the Palearctic, with separate eastward movements of L. (E.) species 1 and the other Nearctic species across Beringia. In order to test this more directly, I added an outgroup to the L. (Eugenuris) tree by using the same branch length as the L. (E.) species 1 split, added to the base of the tree, and assigned this outgroup to an Asian range. The resulting biogeographic reconstruction is provided in Figure A6, and although there was some ambiguity in the new range reconstructions,
the same DEC+J model was selected and the highest probability of the ancestral ranges for the basal nodes did change to the Palearctic. This alternative scenario eliminates the westward colonization back into the Palearctic, but still indicates four separate eastward colonizations, with the most ancestral colonization of *L. (E.)* species 1 shifted to the node of its direct ancestor. The other three inferred colonizations remain unchanged, one leading to *L. (E.)* species 2, one with the ancestor of *L. (E.)* species 3 and *L. (E.)* *talkeetnaeuris* in *O. princeps*, and a third very recent one with *L. (E.)* *talkeetnaeuris* found in *O. collaris*.

The relative timing of inferred colonizations for both parasite lineages was assessed first by comparing the median node heights (in substitutions per site) estimated through BEAST analyses. The split between *S. yamashitai* and *S.* species 1, and between the unknown lineage from *O. pallasi* and *S.* species 2 have broadly overlapping 95% highest posterior densities (0.0435-0.1135 and 0.0483-0.1058 respectively), indicating that these two eastward colonizations could have occurred during the same glacial cycle. Branch lengths for the *L. (Eugenuris)* phylogeny seem to indicate that all of these colonizations occurred during different time periods; however, 95% confidence intervals on node heights did overlap between all subsequent putative colonizations. The statistical test of simultaneous divergence using MsBayes provided evidence that I can reject simultaneous divergence for all taxon pairs because 95% highest posterior density intervals for $\Omega$ (Var[t]/E[t]) did not include 0. The analysis indicated the strongest support for four discrete divergence times out of the six that were tested (Figure A7). Multiple histories could explain this result, but it provides evidence that at least two of the reconstructed colonizations occurred concurrently.
DISCUSSION

Colonization history/Biogeography

These results provide evidence to reject the hypotheses that these parasites colonized the Nearctic during a single glacial cycle, given complex relationships between multiple Nearctic and Palearctic clades that did not diverge simultaneously. This reveals that a Holarctic perspective is necessary in order to unravel the biogeographic history of pikas and their parasites across Beringia. Biogeographic and divergence time analyses most closely support the hypothesis that North American pikas have a complex history of colonization across Beringia with multiple colonizations over more than one glaciation (H1c).

However, the alternative explanation of a single large pika colonization cannot be fully ruled out. If the rate of mutation across the phylogeny has been inconsistent, then we cannot know if branch lengths across the tree are comparable. Although I could not reject clock-like evolution for either phylogeny using likelihood ratio test, much is still unknown about patterns of parasite evolution (Criscone et al., 2005). Here I provide additional evidence for and against each alternative.

A single colonization across Beringia is a more parsimonious explanation than a complex series of migrations and secondary contact between pikas across Beringia. Under a single colonization scenario, high rates of co-infection would be required in order for pikas to maintain high levels of parasite diversity as they moved across Beringia and became established in the Nearctic. Indeed, infection rates from multiple studies on
Nearctic pikas indicate high parasite loads with multiple species of the same major lineage, as well as multiple lineages in a single host (Hobbs, 1980; Galbreath & Hoberg, 2015). Co-infection rates of *L. (Eugenuris)* and *Schizorchis* in single individuals of *O. princeps* are about 12% (K. Galbreath, unpublished data). However, looking at co-infections within populations (localities) instead of a single individual, the rate goes up to 84%. Also, beyond a simple co-infection of one *L. (Eugenuris)* and one *Schizorchis*, multiple species of each major lineage are often present within a single population.

The single large colonization scenario would not necessitate an extensive history of pikas in the Nearctic (before the Pleistocene), though it would not exclude this hypothesis. Conversely, the multiple colonization hypothesis would require an extensive history for pikas in the Nearctic, allowing them to differentiate and disperse latitudinally on multiple occasions. Estimates for the timing of divergence between *O. princeps* and *O. collaris* are between 3 and 8 Mya (Lanier & Olson, 2009), which is much older than previous Pleistocene estimations. We can apply an approximate divergence estimate of 6 mya for Nearctic pikas to their *Schizorchis* parasites by converting the node age (in substitutions per site) calculated in BEAST for *Schizorchis caballeroi* found only in *O. collaris* and *S. species 3 + S. ochotonae* in *O. princeps*. A very rough estimate of colonization for *S. species 1* and the ancestor of *S. species 2* can then be calculated by using the node ages for their splits from Eurasian species. The diversification of *S. species 1* from *S. yamashitai* is in this way placed at 15.5 Mya, and *S. species 2* from its sister group at 10 Mya. These estimations place both colonizations within the mid-Miocene, when Beringian faunal migrations were thought to be symmetrical between the continents (Williams, 1998).
Fossil evidence also indicates a long and more geographically widespread history of pikas in North America than current distributions imply. Multiple species of pikas that are now extinct inhabited North America, including *O. spanglei* dated to >5.3 Mya from Oregon (Shotwell, 1956) and *O. whartoni* from Alaska assessed to be from 1.9-0.9 Mya (Repenning, 1987). Two morphological forms of *Ochotona* lived in northeastern North America during the late Pleistocene, including a larger species like *O. whartoni* and a smaller *O. collaris* or *O. princeps*-like form. Excavations from nine cave sites in the northern Appalachian Mountains in eastern North America contained *O. princeps*-like pika remains (Guilday, 1979; Churcher & Dods, 1979; Mead & Grady, 1996) that dated from ~850 kya (Repenning & Grady, 1988), and the youngest to ~30 Kya when it is presumed to have been extirpated from that area (Grady & Garton, 1981; 1982). This evidence does not exclude either hypothesis, but it does highlight that this group of hosts has a complex history in North America.

Tests for simultaneous divergence support the multiple colonization hypothesis, with biogeographic analysis providing an outline of how this movement could have proceeded if parasites did diversify within the Nearctic and then establish secondary contact with Palearctic parasites. Additionally, if we look at the genetic structure within these parasite lineages we do not see a pattern we would expect from haplotypes that have been maintained over large times and distances. In order for the genetic structure of these parasites to be unaffected by recent gene flow between populations, as well as lineage sorting, effective population sizes (*N_e*) would need to be extremely large. Methods for reliable estimation of *N_e* have not been developed for parasites (Criscione *et al.*, 2005), but one genetic signal for large *N_e* is haplotypes that are shared at high
frequencies between geographically distant and widespread locations (Watterson & Guess, 1977). \textit{Labiostomum (E.) talkeetnaeuris} in both Nearctic \textit{O. collaris} and Palearctic \textit{O. hyperborea} share a single haplotype, but this haplotype was only found in two individuals, so was therefore not high frequency. In fact, no haplotypes could be considered high frequency. Shared haplotypes are more likely to represent recent gene flow because even though they span host boundaries, they are typically between localities within close geographic proximity. Additionally, novel haplotypes were found in localities that were unavailable for pikas to colonize during the LGM due to the presence of ice sheets (localities above the heavy dashed line in Figures 2 & 3), which is a possible indication that these parasites are able to accumulate new diversity rapidly through mutation (Galbreath & Hoberg, 2015).

\textit{Ochotona princeps/collaris ancestry}

Parasite biogeography has been used as an indicator of host biogeography (Nieberding & Olivieri, 2007; Criscione \textit{et al.}, 2005; Manter, 1966) and the use of multiple parasite lineages allows us to improve our confidence that a given pattern reflects the history of the entire assemblage rather than the parasite independently. Previously, a consistent pattern of \textit{O. collaris} parasite diversity nested within \textit{O. princeps} parasites was detected among five independent parasite lineages, including \textit{Schizorchis} and \textit{L. (Eugenuris)}, providing strong evidence that \textit{O. collaris} is derived from \textit{O. princeps} and moved north into Alaska and northwestern Canada from a southern ancestor (Galbreath & Hoberg, 2012). However, with the currently updated phylogenies of \textit{Schizorchis} and \textit{L. (Eugenuris)}, different biogeographical patterns are revealed. Under the scenario proposed by biogeographical analyses, \textit{L. (Eugenuris) talkeetnaeuris} found
in *O. collaris* may represent a recent colonizer from the Palearctic with no direct link to *O. princeps* parasites, while the origin of *O. collaris* parasite species *S. caballeroi* is more ambiguous. As previously described, *S. caballeroi* could be descendent from a pika recolonization into the Nearctic with subsequent speciation into *S. caballeroi* and sister *O. princeps* species *S. species 3 + S. ochotonae* without any revealed directionality. Alternatively, *S. caballeroi* could be descended from a common ancestor shared by *S. species 2 in O. princeps*, and as their pika hosts moved north, a subset moved across Beringia, their ancestors differentiating into *S. mongoliensis* in Siberia. Either way, with the additional diversity added to the phylogeny, a clear case of *O. princeps* parasite paraphyly is no longer consistently supported. We cannot clearly determine the diversification history of *O. collaris* and *O. princeps* using their parasites. Recent colonization of *O. collaris* parasites could suggest host switching between Eurasian and *O. collaris* pikas after they were established in the Nearctic. However, the alternate explanation of a single large pika colonization into the Nearctic would mean that the phylogenetic associations of these parasites were established before arrival in North America and genetic associations would not provide any evidence for Nearctic pika ancestry.

The geographic ranges of parasite species found in *O. princeps* do not correlate with the pika populations associated with distinct mountain ranges of the Intermountain West (Figure 2 & 3) (Galbreath & Hoberg, 2015) and the results of these biogeographic analyses could imply a different colonization history of parasites into this region than what has been suggested for their host. Lineage divergence times place *O. princeps* in the Intermountain West since the middle Pleistocene (781 – 126 Kya), with diversification
proceeding from the northwest, south and then west. Divergence of the Cascade Range lineage significantly pre-dates the origin of the three eastern lineages (Galbreath et al., 2010; Hafner & Sullivan, 1995). Biogeographic analysis indicates that S. species 1, S. species 2 and L. (E.) species 1 have deep associations with the more southern O. princeps populations. This could reflect extirpation of pikas found in northern ranges or movement between major pika populations during cooler periods when their ranges expanded and connected in some regions. Movement of parasites between mountain ranges after host populations became established was likely, due to evidence of gene flow between pika populations found in nuclear DNA (Galbreath et al. 2009; 2010; Galbreath & Hoberg, 2015).

**Taxonomy and phylogenetics**

The systematics and taxonomy of helminth parasites is incomplete, and there are many challenges associated with this essential base-level work, including misidentifications, and improper documentation, preservation, storage and handling of voucher parasites (Brooks et al., 2014; Hoberg et al., 2009). As an example of this, the current phylogenetic analysis suggests the existence of previously unknown species-level diversity within Schizorchis and L. (Eugeneris). More work needs to be done in identifying many of the Eurasian parasites to species as well as revisiting the species level designations currently in place for Nearctic pinworms. With the additional loci and individuals added to the L. (Eugeneris) phylogeny, it appears that the currently designated L. (Eugeneris) talkeetnaeuris is paraphyletic if L. (E.) species 3 is in fact a distinct species (Figure 3). Current taxonomy of the subgenus Labiostomum (Eugeneris) and the putative monophyletic subfamily Labiostomatinae in lagomorph hosts is
according to Petter and Quentin (1976), but rearrangement of group designations may be
necessary due to the difficulty in distinguishing among closely related genera and species
We rely on catalogued voucher specimens in natural history museums as references for
these morphological determinations. However, a recent examination of type specimens of
Labiostomatinae pinworms revealed that multiple specimens were identified incorrectly
relative to current taxonomy and there is an absence of adequate type series to document
the range of morphological variation as a basis for taxonomic descriptions (Hoberg et al.,
2009).
We are just beginning to understand the taxonomic diversity and host associations of helminths, a group that constitutes multiple branches on the tree of life. It is therefore not surprising that initial hypotheses on how these organisms interact with their environment to evolve and move across the landscape were oversimplifications of a complex process. At its simplest, parasites were thought to be so attached to their hosts that their evolution would exactly track their diversification, similar to the genome of a host organelle (Nieberding & Olivieri, 2007). As evidence has grown that parasites rarely track their hosts with true fidelity, processes such as host switching and independent diversification are used to explain complex host-parasite associations. The concept of ecological fitting has recently been used to explain the patterns of major radiations of host-parasite assemblages as associated with ecological disruptions and breakdowns (Hoberg & Brooks, 2008). It is also not unreasonable to assume some level of co-diversification between hosts and their parasites during periods of ecological stability, but my study has demonstrated that there is much more we need to understand about these understudied organisms before we can clearly draw such connections.

Compared to Europe and North America, the biogeographical history of Asia is poorly understood, even though it must have played a critical role in structuring high-latitude biodiversity (Tarasov et al., 2000; Binney et al., 2009). The addition of more parasite diversity from Asia has shown that many related lineages of these pika parasites are trans-Beringian and may reflect complex colonization patterns that are at least partially
independent from each other and their host, leading us to question the underlying assumptions that allow us to use these parasites as a proxy for understanding host history. This analysis indicates the importance of more in-depth sampling throughout Asia in order to parse out complete species histories.
REFERENCES


Li, M., Shi, S.F., Brown, C.L., & Yang, T.B. (2011) Phylogeographical pattern of Mazocraeoides gonialosae (Monogenea, Mazocraeidae) on the dotted gizzard shad, Konosirus punctatus, along the coast of China. The international Journal for Parasitology 41, 1263-1272.


Figure A1. Range map of *Schizorchis* and *L. (Eugenuris)* collection localities used in this study. Beringia is the area generally within the dashed oval.
Table A1. Primers used for PCR.

<table>
<thead>
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</tr>
<tr>
<td></td>
<td>HYMLEM02</td>
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<td>HYM16SF</td>
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Table A2. Loci sample counts and model selection information for each Nearctic parasite species. N = number of sequenced individuals used and Model (AIC) the nucleotide substitution model chosen by jModelTest under the Akaike information criterion used in phylogenetic analyses. Results from PartitionFinder are given below each coding locus, indicating how they were partitioned in analyses.

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Figure A2. Distribution of *Schizorchis* species within the range of its *O. princeps* host. The red southwestern species (*S. species 2*) corresponds to the southwestern range in BioGeoBEARS, and the other three correspond to the American mountain range.
Figure A3. Distribution of *L. (Eugeneruris)* species within the range of its *O. princeps* host. The red southwestern species (*L. (E.) species 3*) corresponds to the southwestern range in BioGeoBEARS, and the other three correspond to the American mountain range.
Table A3: Taxon pairs used for msBayes analysis. Each pair consists of two monophyletic clades, each containing one or more species, one located only in the Palearctic and the other only in the Nearctic.

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Figure A4. *Schizorchis* BioGeoBEARS biogeographic reconstruction using the BEAST species tree backbone. Open diamonds along branches indicate Bayesian posterior probabilities >.65 and filled diamonds >.95 for subsequent nodal support. Shapes on branch tips indicate host species and color indicates known current geographic ranges. Pie charts on nodes are the probability of ancestral range location/s and directional arrows indicate inferred cross continental colonization across the Bering land bridge either east into North America (orange arrows) or west into Eurasia (pink arrow). The dashed circle surrounding colonization arrows and node indicate uncertainty in range estimation and therefore history of colonization. Individuals from Mongolian pikas identified to genus are indicated as unknown species and S. species 1, 2 and 3 are named as in Galbreath and Hoberg (2012).
Figure A5. *Eugenerus* BioGeoBEARS biogeographic reconstruction using the BEAST species tree backbone. Open diamonds along branches indicate Bayesian posterior probabilities > .80 and filled diamonds > .95 for subsequent nodal support. Shapes on branch tips indicate host species and color indicates known current geographic ranges. Pie charts on nodes are the probability of ancestral range location/s and directional arrows indicate inferred cross continental colonization across the Bering land bridge either east into North America (orange arrows) or west into Eurasia (pink arrow). Individuals from Mongolian pikas identified to genus are indicated as unknown species, and *L. E.* species 1, 2 and 3 are named as in Galbreath and Hoberg (2012).
Figure A6. Same *L. (Eugenuris)* BioGeoBEARS biogeographic reconstruction as in Figure A5 but with an added simulated outgroup from Asia, which reflects the known origin for the lineage. Updated Beringian colonization events are inferred, with directional arrows now all indicating eastward colonization into North America (orange arrows).
Figure A7. Posterior probability comparisons between the number of possible divergence times of taxon pairs using Msbayes.
APPENDIX B

Table B1: *Schizorchis* specimen information list. Museum accession numbers for parasites and associated hosts as well as GenBank numbers for sequenced loci.

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USA, MT, CARBON CO, CUSTER NATL FOR. 5 KM EAST GLACIER LAKE

USA, MT, CARBON CO, CUSTER NATL FOR. 5 KM EAST GLACIER LAKE

USA, MT, CARBON CO, CUSTER NATL FOR. 1 KM EAST EMERALD LAKE

USA, MT, CARBON CO, CUSTER NATL FOR. 1 KM EAST EMERALD LAKE

USA, MT, CUSTER NATL FOR. 1 KM EAST EMERALD LAKE

USA, MT, CUSTER NATL FOR. 1 KM EAST EMERALD LAKE

USA, MT, RAVALLI CO. BITTERROOT NATL. FOR. 9 KM W. OF DARBY

USA, MT, RAVALLI CO. BITTERROOT NATL. FOR. 9 KM W. OF DARBY
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| KG 276 | 20249 | O. princeps | USA, ID, BOISE CO, BOISE NATL. FOR. 14 KM W OF FEATHERVILLE |

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| KG 309 | 20280 | L. (E.) talkeetnaeuris | X | X | X | KP876244.1 | 103552.00 | USA, ID, BOUNDARY CO, PANHANDLE NATL. FOR. ROMAN NOSE LAKES |
| KG 312 | 20283 | L. (E.) talkeetnaeuris | X | X | X | KP876245.1 | 103553.00 | USA, WA, OKANOGON CO, OKANOGAN NATL FOR, 2 KM SE WASH. PASS |
| KG 313 | 20284 | L. (E.) talkeetnaeuris | X | X | X | HQ189970.1 | 103554.00 | USA, WA, OKANOGON CO, OKANOGAN NATL FOR, 2 KM SE WASH. PASS |
| KG 321 | 20291 | L. (E.) talkeetnaeuris | X | X | X | HQ189971.1 | 103731.00 | USA, WA, OKANOGON CO, OKANOGAN NATL FOR, 2 KM SE WASH. PASS |
| KG 322 | 20292 | L. (E.) talkeetnaeuris | X | X | X | KP876249.1 | 103556.00 | USA, WA, OKANOGON CO, OKANOGAN NATL FOR, 2 KM SE WASH. PASS |
| KG 337 | 20306 | L. (E.) talkeetnaeuris | X | X | X | HQ189973.1 | 103733.00 | USA, WA, SKAMANIA CO, GIFFORD-PINCHOT NATL. FOR. |
| KG 342 | 20311 | O. princeps | KG 342 | 20311 | 342p1e | L. (E.) talkeetnaeuris | X | X | X | KP876251.1 | 103558.00 |
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| KG 347 | 20316 | O. princeps | KG 347 | 20316 | 347p4e | L. (E.) sp. 2 | X | X | X | HQ189941.1 | 103856.00 |
| KG 350 | 20319 | O. princeps | KG 350 | 20319 | 350p1e | L. (E.) sp. 3 | X | X | X | KP876281.1 | 103736.00 |
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71
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USA,UT,SUMMIT CO,WASATCH NAT. FOR..22 km E, 5 km N OAKLEY

USA,UT,SUMMIT CO,WASATCH NAT. FOR..24 km E, 6 km N of OAKLEY

USA,UT,SANPETE CO,MANTI-LASAL NAT.FOR. 0.5 km SW ISLAND L.

USA,UT,SANPETE CO,MANTI-LASAL NAT.FOR. 0.5 km SW ISLAND L.

USA,UT,WAYNE CO,FISH LAKE NAT.FOR.NW SLOPE FLAT TOP MT.

USA,UT,WAYNE CO,FISH LAKE NAT.FOR. NW slope Flat Top Mt.
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Figure B1: MrBayes gene tree for *Schizorchis* 12S16S using representative haplotypes. Names given as parasite species and region or host name (H_) if parasite species not yet identified. Nodal support provided in posterior probabilities.
Figure B2: MrBayes gene tree for *Schizorchis* Cytb using representative haplotypes. Names given as parasite species and region or host name (H_) if parasite species not yet identified. Nodal support provided in posterior probabilities.
Figure B3: MrBayes gene tree for *L. (Eugenuris)* Cox1 using representative haplotypes. Names given as parasite species and region or host name (H_) if parasite species not yet identified. Nodal support provided in posterior probabilities.
Figure B4: MrBayes gene tree for *L. (Eugenuris)* Cytb using representative haplotypes. Names given as parasite species and region or host name (H_) if parasite species not yet identified. Nodal support provided in posterior probabilities.
Figure B5: MrBayes gene tree for *L. (Eugenuris)* ITS2 using representative haplotypes. Names given as parasite species and region or host name (H_) if parasite species not yet identified. Nodal support provided in posterior probabilities.
Table B3: Dispersal multiplier matrix for BioGeoBEARS. Represents relative ease of access from one region to another on a scale of 0-1. P (Palearctic), C (Canada), M (Intermountain West), S (American southwest).

<table>
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Table B4: R Script for *Schizorchis* BioGeoBEARS Analysis (modified from: http://phylo.wikidot.com/biogeobears)

```r
install.packages("optimx", dependencies=TRUE, repos="http://cran.rstudio.com")

# Install BioGeoBEARS from CRAN 0-cloud:
install.packages("BioGeoBEARS", dependencies=TRUE, repos="http://cran.rstudio.com")

library(optimx)  # (either 2012 or 2013 version, as of January 2014)  
library(parallel)  
library(FD)        # for FD::maxent() (make sure this is up-to-date)  
library(snow)     # (if you want to use multicore functionality; prob. better than library(parallel)) 
library(BioGeoBEARS)

source("http://phylo.wdfiles.com/local--files/biogeobears/cladoRcpp.R") # (needed now that traits model added; source FIRST!)
source("http://phylo.wdfiles.com/local--files/biogeobears/BioGeoBEARS_extract_Qmat_COOMat_v1.R")
source("http://phylo.wdfiles.com/local--files/biogeobears/calc_loglike_sp_v01.R")
source("http://phylo.wdfiles.com/local--files/biogeobears/runBSM_v1.R")
source("http://phylo.wdfiles.com/local--files/biogeobears/stochastic_map_given_inputs.R")
source("http://phylo.wdfiles.com/local--files/biogeobears/summarize_BSM_tables_v1.R")
source("http://phylo.wdfiles.com/local--files/biogeobears/BioGeoBEARS_traits_v1.R") # added traits model
```

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calc_loglike_sp = compiler::cmpfun(calc_loglike_sp_prebyte)  # crucial to fix bug in uppass calculations
calc_independent_likelihoods_on_each_branch = compiler::cmpfun(calc_independent_likelihoods_on_each_branch_prebyte)

setwd("C:\R_BGB\Schiz2.2017")
getwd()
trfn="SchizSpeciesBGB.newick"
geogfn="SchizSp4_geog.data"

moref(geogfn)

# Look at your geographic range data:
tipranges = getranges_from_LagrangePHYLIP(lgdata_fn=geogfn)
tipranges

tr = read.tree(trfn)
tr
plot(tr)
axisPhylo()  # plots timescale
max_range_size = 3

# Run DEC

# Intitialize a default model (DEC model)
BioGeoBEARS_run_object = define_BioGeoBEARS_run()
GeoBEARS_run_object$force_sparse=FALSE  # sparse=TRUE causes pathology & isn't much faster at this scale
GeoBEARS_run_object$speedup=TRUE  # shortcuts to speed ML search; use FALSE if worried (e.g. >3 params)
GeoBEARS_run_object$use_optimx = TRUE
GeoBEARS_run_object$calc_ancprobs=TRUE  # get ancestral states from optim run
GeoBEARS_run_object$include_null_range = TRUE

# Give BioGeoBEARS the location of the phylogeny Newick file
BioGeoBEARS_run_object$trfn = trfn

# Give BioGeoBEARS the location of the geography text file
BioGeoBEARS_run_object$geogfn = geogfn
# Input the maximum range size
BioGeoBEARS_run_object$max_range_size = max_range_size

#BioGeoBEARS_run_object$min_branchlength = 0.000001  # Min to treat tip as a direct ancestor (no speciation event)
BioGeoBEARS_run_object$include_null_range = TRUE  # set to FALSE for e.g. DEC* model, DEC*+J, etc.
# also search script on "include_null_range" for other places to change

# Set up a time-stratified analysis:
# 1. Here, un-comment ONLY the files you want to use.
# 2. Also un-comment "BioGeoBEARS_run_object = section_the_tree(...", below.
# 3. For example files see (a) extdata.dir,
# or (b) http://phylo.wikidot.com/biogeobears#files
# and BioGeoBEARS Google Group posts for further hints)
#
# Uncomment files you wish to use in time-stratified analyses:
BioGeoBEARS_run_object$timesfn = "timeperiods.txt"
BioGeoBEARS_run_object$dispersal_multipliers_fn = "dispersal_multipliers.txt"
#BioGeoBEARS_run_object$areas_allowed_fn = "areas_allowed.txt"
#BioGeoBEARS_run_object$areas_adjacency_fn = "areas_adjacency.txt"
#BioGeoBEARS_run_object$distsfn = "distances_matrix.txt"
# See notes on the distances model on PhyloWiki’s BioGeoBEARS updates page.
#
# Speed options and multicore processing if desired
BioGeoBEARS_run_object$num_cores_to_use = 1
# (use more cores to speed it up; this requires
# library(parallel) and/or library(snow). The package "parallel"
# is now default on Macs in R 3.0+, but apparently still
# has to be typed on some Windows machines. Note: apparently
# parallel works on Mac command-line R, but not R.app.
# BioGeoBEARS checks for this and resets to 1
# core with R.app)

# This function loads the dispersal multiplier matrix etc. from the text files into the model object. Required for these to work!
# (It also runs some checks on these inputs for certain errors.)
BioGeoBEARS_run_object = readfiles_BioGeoBEARS_run(BioGeoBEARS_run_object)

# Divide the tree up by timeperiods/strata (uncomment this for stratified analysis)
BioGeoBEARS_run_object = section_the_tree(inputs=BioGeoBEARS_run_object, make_master_table=TRUE, plot_pieces=FALSE)
# The stratified tree is described in this table:
BioGeoBEARS_run_object$master_table

# Good default settings to get ancestral states
BioGeoBEARS_run_object$return_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_TTL_loglike_from_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_ancprobs = TRUE  # get ancestral states from optim run

# Set up DEC model
# Max values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table$["d","max"] = 400
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table$["e","max"] = 400

# Look at the BioGeoBEARS_run_object; it's just a list of settings etc.
BioGeoBEARS_run_object

# This contains the model object
BioGeoBEARS_run_object$BioGeoBEARS_model_object

# This table contains the parameters of the model
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table

# Run this to check inputs. Read the error messages if you get them!
check_BioGeoBEARS_run(BioGeoBEARS_run_object)

# For a slow analysis, run once, then set runslow=FALSE to just
# load the saved result.
runslow = TRUE
resfn = "Schiz_DEC_2017.Rdata"
if (runslow)
  {
    res = bears_optim_run(BioGeoBEARS_run_object)
    res

    save(res, file=resfn)
    resDEC = res
  } else {
    # Loads to "res"
    load(resfn)
    resDEC = res
  }

#######################################################################
# Run DEC+J
#######################################################################
BioGeoBEARS_run_object = define_BioGeoBEARS_run()
BioGeoBEARS_run_object$trfn = trfn
BioGeoBEARS_run_object$geogfn = geogfn
BioGeoBEARS_run_object$max_range_size = max_range_size
#BioGeoBEARS_run_object$min_branchlength = 0.000001    # Min to treat tip as a direct ancestor (no speciation event)
# also search script on "include_null_range" for other places to change

# Set up a time-stratified analysis:
BioGeoBEARS_run_object$timesfn = "timeperiods.txt"
BioGeoBEARS_run_object$dispersal_multipliers_fn = "dispersal_multipliers.txt"
#BioGeoBEARS_run_object$areas_allowed_fn = "areas_allowed.txt"
#BioGeoBEARS_run_object$areas_adjacency_fn = "areas_adjacency.txt"
#BioGeoBEARS_run_object$distsfn = "distances_matrix.txt"
# See notes on the distances model on PhyloWiki's BioGeoBEARS updates page.

# Speed options and multicore processing if desired
BioGeoBEARS_run_object$speedup=TRUE          # shortcuts to speed ML search; use FALSE if worried (e.g. >3 params)
BioGeoBEARS_run_object$suse_optimx = TRUE
BioGeoBEARS_run_object$num_cores_to_use=1
BioGeoBEARS_run_object$force_sparse=FALSE    # sparse=FALSE causes pathology & isn't much faster at this scale
BioGeoBEARS_run_object$calc_ancprobs=TRUE    # get ancestral states from optim run
BioGeoBEARS_run_object$include_null_range = TRUE

# This function loads the dispersal multiplier matrix etc. from the text files into the model object. Required for these to work!
# (It also runs some checks on these inputs for certain errors.)
BioGeoBEARS_run_object = readfiles_BioGeoBEARS_run(BioGeoBEARS_run_object)

# Divide the tree up by timeperiods/strata (uncomment this for stratified analysis)
BioGeoBEARS_run_object = section_the_tree(inputs=BioGeoBEARS_run_object, make_master_table=TRUE, plot_pieces=FALSE)
# The stratified tree is described in this table:
BioGeoBEARS_run_object$master_table

# Good default settings to get ancestral states
BioGeoBEARS_run_object$return_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_TTL_loglike_from_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_ancprobs = TRUE    # get ancestral states from optim run

# Set up DEC+J model
# Get the ML parameter values from the 2-parameter nested model
# (this will ensure that the 3-parameter model always does at least as good)
dstart = resDECSoutputs@params_table["d","est"]
estart = resDEC$outputs@params_table["e","est"]
jstart = 0.0001

# Input starting values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","init"] = dstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","est"] = dstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","init"] = estart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","est"] = estart

# Max values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","max"] = 400
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","max"] = 400

# Add j as a free parameter
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","type"] = "free"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","init"] = jstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","est"] = jstart

check_BioGeoBEARS_run(BioGeoBEARS_run_object)
resfn = "Schiz_DEC+J_2017.Rdata"
runslow = TRUE
if (runslow)
{
  #sourceAll("/Dropbox/_njm/__packages/BioGeoBEARS_setup")

  res = bears_optim_run(BioGeoBEARS_run_object)
  res

  save(res, file=resfn)

  resDECj = res
} else {
  # Loads to "res"
  load(resfn)
  resDECj = res
}

# PDF plots

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from BioGeoBEARS import plot_BioGeoBEARS_results

# Plot ancestral states - DEC
analysis_titletxt = "BioGeoBEARS DEC on Schiz"
results_object = resDEC
scriptdir = np(system.file("extdata/a_scripts", package="BioGeoBEARS"))
res2 = plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="text", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)

# Pie chart
plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="pie", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)

dev.off()  # Turn off PDF

# Plot ancestral states - DECJ
analysis_titletxt = "BioGeoBEARS DEC+J on Schiz"
results_object = resDECj
scriptdir = np(system.file("extdata/a_scripts", package="BioGeoBEARS"))
res1 = plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="text", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)

# Pie chart
plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="pie", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)

dev.off()  # Turn off PDF

system(cmdstr)  # Plot it
# Run DEC w/o Dispersal Multipliers

BioGeoBEARS_run_object = define_BioGeoBEARS_run()

BioGeoBEARS_run_object$force_sparse=FALSE  # sparse=FALSE causes pathology & isn't much faster at this scale
BioGeoBEARS_run_object$speedup=TRUE          # shorcuts to speed ML search; use FALSE if worried (e.g. >3 params)
BioGeoBEARS_run_object$use_optimx = TRUE
BioGeoBEARS_run_object$calc_ancprobs=TRUE    # get ancestral states from optim run
BioGeoBEARS_run_object$include_null_range = TRUE

# Set up a time-stratified analysis
# (un-comment to use; see example files in extdata_dir,
# and BioGeoBEARS google group posts for further hints)
#BioGeoBEARS_run_object$timesfn = "timeperiods.txt"
#BioGeoBEARS_run_object$dispersal_multipliers_fn = "dispersal_multipliers.txt"
#BioGeoBEARS_run_object$areas_allowed_fn = "areas_allowed_aros5g.txt"
#BioGeoBEARS_run_object$areas_adjacency_fn = "areas_adjacency.txt"
#BioGeoBEARS_run_object$distsfn = "distances_matrix.txt"
# See notes on the distances model on PhyloWiki's BioGeoBEARS updates page.

# Input the maximum range size
BioGeoBEARS_run_object$max_range_size = max_range_size

# Multicore processing if desired
BioGeoBEARS_run_object$num_cores_to_use=1
# (use more cores to speed it up; this requires
# library(parallel) and/or library(snow). The package "parallel"
# is now default on Macs in R 3.0+, but apparently still
# has to be typed on some Windows machines. Note: apparently
# parallel works on Mac command-line R, but not R.app.
# BioGeoBEARS checks for this and resets to 1
# core with R.app)

# Sparse matrix exponentiation is an option for huge numbers of ranges/states (600+)
BioGeoBEARS_run_object$force_sparse=FALSE

# Give BioGeoBEARS the location of the geography text file
BioGeoBEARS_run_object$geogfn = geogfn

# Give BioGeoBEARS the location of the phylogeny Newick file
BioGeoBEARS_run_object$trfn = trfn

# This function loads the dispersal multiplier matrix etc. from the text files into the model object. Required for these to work!
# (It also runs some checks on these inputs for certain errors.)
BioGeoBEARS_run_object = readfiles_BioGeoBEARS_run(BioGeoBEARS_run_object)

# Divide the tree up by timeperiods/strata (uncomment this for stratified analysis)
#BioGeoBEARS_run_object = section_the_tree(inputs=BioGeoBEARS_run_object, make_master_table=TRUE, plot_pieces=FALSE)
# The stratified tree is described in this table:
#BioGeoBEARS_run_object$master_table

# Good default settings to get ancestral states
BioGeoBEARS_run_object$return_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_TTL_loglike_from_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_ancprobs = TRUE

# Set up DEC model
# Max values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table$["d","max"] = 400
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table$["e","max"] = 400

# Look at the BioGeoBEARS_run_object; it's just a list of settings etc.
BioGeoBEARS_run_object

# This contains the model object
BioGeoBEARS_run_object$BioGeoBEARS_model_object

# This table contains the parameters of the model
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table

# Run this to check inputs. Read the error messages if you get them!
check_BioGeoBEARS_run(BioGeoBEARS_run_object)

# For a slow analysis, run once, then set runslow=FALSE to just
# load the saved result.
runslow = TRUE
resfn = "Schiz_DEC_2017_DECnoDisMult.Rdata"
if (runslow)
{
  res = bears_optim_run(BioGeoBEARS_run_object)
res

save(res, file=resfn)
resDECnoMult = res
} else {
  # Loads to "res"
  load(resfn)
  resDECnoMult = res

# Run DEC+J W/o dispersal multipliers
BioGeoBEARS_run_object = define_BioGeoBEARS_run()
BioGeoBEARS_run_object$trfn = trfn
BioGeoBEARS_run_object$geogfn = geogfn
BioGeoBEARS_run_object$max_range_size = max_range_size

# Set up the stratified part
#BioGeoBEARS_run_object$timesfn = "timeperiods.txt"
#BioGeoBEARS_run_object$dispersal_multipliers_fn = "dispersal_multipliers.txt"
#BioGeoBEARS_run_object$areas_allowed_fn = "areas_allowed_aros5g.txt"
#BioGeoBEARS_run_object$areas_adjacency_fn = "areas_adjacency.txt"
#BioGeoBEARS_run_object$distsfn = "distances_matrix.txt"
# See notes on the distances model on PhyloWiki's BioGeoBEARS updates page.

BioGeoBEARS_run_object$speedup=TRUE          # shorcuts to speed ML search; use FALSE if worried (e.g. >3 params)
BioGeoBEARS_run_object$suse_optimx = TRUE
BioGeoBEARS_run_object$num_cores_to_use=1
BioGeoBEARS_run_object$sforce_sparse=FALSE  # sparse=FALSE causes pathology & isn't much faster at this scale
BioGeoBEARS_run_object$calc_ancprobs=TRUE    # get ancestral states from optim run
BioGeoBEARS_run_object$include_null_range = TRUE

# This function loads the dispersal multiplier matrix etc. from the text files into the model object. Required for these to work!
# (It also runs some checks on these inputs for certain errors.)
BioGeoBEARS_run_object = readfiles_BioGeoBEARS_run(BioGeoBEARS_run_object)

# Divide the tree up by timeperiods/strata (uncomment this for stratified analysis)
#BioGeoBEARS_run_object = section_the_tree(inputs=BioGeoBEARS_run_object, make_master_table=TRUE, plot_pieces=FALSE)
# The stratified tree is described in this table:
#BioGeoBEARS_run_object$master_table
# Good default settings to get ancestral states
BioGeoBEARS_run_object$return_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_TTL_loglike_from_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_ancprobs = TRUE

# Set up DEC+J model
# Get the ML parameter values from the 2-parameter nested model
# (this will ensure that the 3-parameter model always does at least as good)
dstart = resDECnoMult$outputs@params_table["d","est"]
estart = resDECnoMult$outputs@params_table["e","est"]
jstart = 0.0001

# Input starting values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","init"] = dstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","est"] = dstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","init"] = estart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","est"] = estart

# Max values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","max"] = 400
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","max"] = 400

# Add j as a free parameter
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","type"] = "free"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","init"] = jstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","est"] = jstart

check_BioGeoBEARS_run(BioGeoBEARS_run_object)

resfn = "Schiz_DEC+J_2017_DEC+JnoDisMult.Rdata"
runslow = TRUE
if (runslow)
{
  #sourceall("/Dropbox/_njm/_packages/BioGeoBEARS_setup/")

  res = bears_optim_run(BioGeoBEARS_run_object)

  res

  save(res, file=resfn)
# PDF plots

```
# Plot ancestral states - DEC
analysis_titletxt = "BioGeoBEARS DEC No Dispersal Multipliers Schiz"

# Setup
results_object = resDECnoMult
scriptdir = np(system.file("extdata/a-scripts", package="BioGeoBEARS"))

# States
res2 = plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="text", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)

# Pie chart
plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="pie", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)
```

# Plot ancestral states - DECJ

```
# Setup
results_object = resDECjnoMult
scriptdir = np(system.file("extdata/a-scripts", package="BioGeoBEARS"))

# States
```
res1 = plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="text", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)

# Pie chart
plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="pie", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)

dev.off()  # Turn off PDF

system(cmdstr)  # Plot it

# DIVALIKE AND DIVALIKE+J ANALYSIS
# NOTE: The BioGeoBEARS "DIVALIKE" model is not identical with
# Ronquist (1997)'s parsimony DIVA. It is a likelihood
# interpretation of DIVA, constructed by modelling DIVA's
# processes the way DEC does, but only allowing the
# processes DIVA allows (widespread vicariance: yes; subset
# sympathy: no; see Ronquist & Sanmartin 2011, Figure 4).
#
# DIVALIKE is a likelihood interpretation of parsimony
# DIVA, and it is "like DIVA" -- similar to, but not
# identical to, parsimony DIVA.
#
# I thus now call the model "DIVALIKE", and you should also. ;-)  

# Run DIVALIKE

BioGeoBEARS_run_object = define_BioGeoBEARS_run()
BioGeoBEARS_run_object$strfn = trfn
BioGeoBEARS_run_object$geogfn = geogfn
BioGeoBEARS_run_object$max_range_size = max_range_size
BioGeoBEARS_run_object$min_branchlength = 0.000001  # Min to treat tip as a direct ancestor (no speciation event)
BioGeoBEARS_run_object$include_null_range = TRUE  # set to FALSE for e.g. DEC* model, DEC*+J, etc.

# also search script on "include_null_range" for other places to change

# Set up a time-stratified analysis:
BioGeoBEARS_run_object$timesfn = "timeperiods.txt"
BioGeoBEARS_run_object$dispersal_multipliers_fn = "dispersal_multipliers.txt"
#BioGeoBEARS_run_object$areas_allowed_fn = "areas_allowed.txt"
#BioGeoBEARS_run_object$areas_adjacency_fn = "areas_adjacency.txt"
#BioGeoBEARS_run_object$distsfn = "distances_matrix.txt"
# See notes on the distances model on PhyloWiki's BioGeoBEARS updates page.

# Speed options and multicore processing if desired
BioGeoBEARS_run_object$use_optimx = TRUE
BioGeoBEARS_run_object$num_cores_to_use=1

BioGeoBEARS_run_object$force_sparse=FALSE  # sparse=FALSE causes pathology & isn't much faster at this scale
BioGeoBEARS_run_object$speedup=TRUE       # shortcuts to speed ML search; use FALSE if worried (e.g. >3 params)
BioGeoBEARS_run_object$calc_ancprobs=TRUE  # get ancestral states from optim run

# This function loads the dispersal multiplier matrix etc. from the text files into the model object. Required for these to work!
# (It also runs some checks on these inputs for certain errors.)
BioGeoBEARS_run_object = readfiles_BioGeoBEARS_run(BioGeoBEARS_run_object)

# Divide the tree up by timeperiods/strata (uncomment this for stratified analysis)
BioGeoBEARS_run_object = section_the_tree(inputs=BioGeoBEARS_run_object, make_master_table=TRUE, plot_pieces=FALSE)

# The stratified tree is described in this table:
BioGeoBEARS_run_object$master_table

# Good default settings to get ancestral states
BioGeoBEARS_run_object$return_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_TTL_loglike_from_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_ancprobs = TRUE  # get ancestral states from optim run

# Set up DIVALIKE model
# Remove subset-sympatry
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["s","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["s","init"] = 0.0
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["s","est"] = 0.0
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["ysv","type"] = "2-j"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["ys","type"] = "ysv*1/2"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["y","type"] = "ysv*1/2"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["v","type"] = "ysv*1/2"

# Allow classic, widespread vicariance; all events equiprobable
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["mx01v","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["mx01v","init"] = 0.5
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["mx01v","est"] = 0.5

# No jump dispersal/founder-event speciation
# BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","type"] = "free"
# BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","init"] = 0.01
# BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","est"] = 0.01

# Max values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","max"] = 400
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","max"] = 400

check_BioGeoBEARS_run(BioGeoBEARS_run_object)

runslow = TRUE
resfn = "Schiz_DIVALIKE_2017.Rdata"
if (runslow) {
  res = bears_optim_run(BioGeoBEARS_run_object)
  save(res, file=resfn)
  resDIVALIKE = res
} else {
  # Loads to "res"
  load(resfn)
  resDIVALIKE = res
}

# Run DIVALIKE+J
BioGeoBEARS_run_object = define_BioGeoBEARS_run()
BioGeoBEARS_run_object$trfn = trfn
BioGeoBEARS_run_object$geogfn = geogfn
BioGeoBEARS_run_object$max_range_size = max_range_size
#BioGeoBEARS_run_object$min_branchlength = 0.000001  # Min to treat tip as a direct ancestor (no speciation event)
BioGeoBEARS_run_object$include_null_range = TRUE    # set to FALSE for e.g. DEC* model, DEC*+J, etc.
# also search script on "include_null_range" for other places to change

# Set up a time-stratified analysis:
#BioGeoBEARS_run_object$timesfn = "timeperiods.txt"
#BioGeoBEARS_run_object$dispersal_multipliers_fn = "manual_dispersal_multipliers.txt"
#BioGeoBEARS_run_object$areas_allowed_fn = "areas_allowed.txt"
#BioGeoBEARS_run_object$areas_adjacency_fn = "areas_adjacency.txt"
#BioGeoBEARS_run_object$distsfn = "distances_matrix.txt"
# See notes on the distances model on PhyloWiki's BioGeoBEARS updates page.

# Speed options and multicore processing if desired
BioGeoBEARS_run_object$use_optimx = TRUE
BioGeoBEARS_run_object$num_cores_to_use=1

# This function loads the dispersal multiplier matrix etc. from the text files into the model object. Required for these to work!
# (It also runs some checks on these inputs for certain errors.)
BioGeoBEARS_run_object = readfiles_BioGeoBEARS_run(BioGeoBEARS_run_object)

# Divide the tree up by timeperiods/strata (uncomment this for stratified analysis)
BioGeoBEARS_run_object = section_the_tree(inputs=BioGeoBEARS_run_object, make_master_table=TRUE, plot_pieces=FALSE)
# The stratified tree is described in this table:
BioGeoBEARS_run_object$master_table

# Good default settings to get ancestral states
BioGeoBEARS_run_object$return_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_TTL_loglike_from_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_ancprobs = TRUE    # get ancestral states from optim run

# Set up DIVALIKE+J model
# Get the ML parameter values from the 2-parameter nested model
# (this will ensure that the 3-parameter model always does at least as good)
dstart = resDIVALIKE$outputs@params_table["d","est"]
estart = resDIVALIKE$outputs@params_table["e","est"]
jstart = 0.0001

# Input starting values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","init"] = dstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","est"] = dstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","init"] = estart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","est"] = estart

# Max values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","max"] = 400
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","max"] = 400

# Remove subset-sympatry
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["s","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["s","init"] = 0.0
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["s","est"] = 0.0

BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["ysv","type"] = "2-j"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["ys","type"] = "ysv*1/2"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["y","type"] = "ysv*1/2"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["v","type"] = "ysv*1/2"

# Allow classic, widespread vicariance; all events equiprobable
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["mx01v","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["mx01v","init"] = 0.5
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["mx01v","est"] = 0.5

# Add jump dispersal/founder-event speciation
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","type"] = "free"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","init"] = jstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","est"] = jstart

# Under DIVALIKE+J, the max of "j" should be 2, not 3 (as is default in DEC+J)
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","min"] = 0.00001
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","max"] = 1.99999

check_BioGeoBEARS_run(BioGeoBEARS_run_object)
resfn = "Schiz_DIVALIKE+J_2017.Rdata"
runslow = TRUE
if (runslow)
{
    #sourceall("/Dropbox/_njm/_packages/BioGeoBEARS_setup/"
    res = bears_optim_run(BioGeoBEARS_run_object)
    res
    save(res, file=resfn)
    resDIVALIKEj = res
} else {
    # Loads to "res"
    load(resfn)
    resDIVALIKEj = res
}

pdffn = "Schiz_DIVALIKE_vs_DIVALIKE+J_2017.pdf"
pdf(pdffn, width=6, height=6)

# Plot ancestral states - DIVALIKE
analysis_titletxt = "BioGeoBEARS DIVALIKE on Schizorchis"

# Setup
results_object = resDIVALIKE
scriptdir = np(system.file("extdata/a_scripts", package="BioGeoBEARS"))

# States
res2 = plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="text", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)

# Pie chart
plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="pie", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)

# Plot ancestral states - DIVALIKE+J
analysis_titletxt = "BioGeoBEARS DIVALIKE+J on Schizorchis"
# Setup
def ABBER(sim_obj):
    # Setup
    results_object = resDIValIKEj
    scriptdir = np(system.file("extdata/a_scripts", package="BioGeoBEARS"))
    
    # States
    res1 = plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="text", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)
    
    # Pie chart
    plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="pie", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)

    dev.off()
    cmdstr = paste("open ", pdffn, sep="")
    system(cmdstr)

    #######################################################
    # BAYAREALIKE AND BAYAREALIKE+J ANALYSIS
    #######################################################
    # NOTE: As with DIVA, the BioGeoBEARS BayArea-like model is
    # not identical with the full Bayesian model implemented
    # in the "BayArea" program of Landis et al. (2013).
    #
    # Instead, this is a simplified likelihood interpretation
    # of the model. Basically, in BayArea and BioGeoBEARS-BAYAREALIKE,
    # "d" and "e" work like they do in the DEC model of Lagrange
    # (and BioGeoBEARS), and then BayArea's cladogenesis assumption
    # (which is that nothing in particular happens at cladogenesis) is
    # replicated by BioGeoBEARS.
    #
    # This leaves out 3 important things that are in BayArea:
    # 1. Distance dependence (you can add this with a distances
    #    matrix + the "x" parameter in BioGeoBEARS, however)
    # 2. A correction for disallowing "e" events that drive
    #    a species extinct (a null geographic range)
    # 3. The neat Bayesian sampling of histories, which allows
    #    analyses on large numbers of areas.
    #
    # The main purpose of having a "BAYAREALIKE" model is
# to test the importance of the cladogenesis model on particular datasets. Does it help or hurt the data likelihood if there is no special cladogenesis process?
#
# BAYAREALIKE is a likelihood interpretation of BayArea, and it is "like BayArea" -- similar to, but not identical to, Bayesian BayArea. I thus now call the model "BAYAREALIKE", and you should also. :-) 
# Run BAYAREALIKE

BioGeoBEARS_run_object = define_BioGeoBEARS_run()
BioGeoBEARS_run_object$trfn = trfn
BioGeoBEARS_run_object$geogfn = geogfn
BioGeoBEARS_run_object$max_range_size = max_range_size
# BioGeoBEARS_run_object$min_branchlength = 0.000001    # Min to treat tip as a direct ancestor (no speciation event)
BioGeoBEARS_run_object$include_null_range = TRUE    # set to FALSE for e.g. DEC* model, DEC**+J, etc.
# also search script on "include_null_range" for other places to change

# Set up a time-stratified analysis:
BioGeoBEARS_run_object$timesfn = "timeperiods.txt"
BioGeoBEARS_run_object$dispersal_multipliers_fn = "dispersal_multipliers.txt"
#BioGeoBEARS_run_object$areas_allowed_fn = "areas_allowed.txt"
#BioGeoBEARS_run_object$areas_adjacency_fn = "areas_adjacency.txt"
#BioGeoBEARS_run_object$distsfn = "distances_matrix.txt"
# See notes on the distances model on PhyloWiki’s BioGeoBEARS updates page.

# Speed options and multicore processing if desired
BioGeoBEARS_run_object$suse_optimx = TRUE
BioGeoBEARS_run_object$num_cores_to_use=1

BioGeoBEARS_run_object$force_sparse=FALSE    # sparse=FALSE causes pathology & isn't much faster at this scale
BioGeoBEARS_run_object$speedup=TRUE          # shortcuts to speed ML search; use FALSE if worried (e.g. >3 params)
BioGeoBEARS_run_object$calc_ancprobs=TRUE    # get ancestral states from optim run

# This function loads the dispersal multiplier matrix etc. from the text files into the model object. Required for these to work!
# (It also runs some checks on these inputs for certain errors.)
BioGeoBEARS_run_object = readfiles_BioGeoBEARS_run(BioGeoBEARS_run_object)

# Divide the tree up by timeperiods/strata (uncomment this for stratified analysis)
BioGeoBEARS_run_object = section_the_tree(inputs=BioGeoBEARS_run_object, make_master_table=TRUE, plot_pieces=FALSE)
# The stratified tree is described in this table:
BioGeoBEARS_run_object$master_table

# Good default settings to get ancestral states
BioGeoBEARS_run_object$return_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_TTL_loglike_from_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_ancprobs = TRUE  # get ancestral states from optim run

# Set up BAYAREALIKE model
# No subset sympaty
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["s","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["s","init"] = 0.0
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["s","est"] = 0.0

# No vicariance
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["v","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["v","init"] = 0.0
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["v","est"] = 0.0

# No jump dispersal/founder-event speciation
# BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","type"] = "free"
# BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","init"] = 0.01
# BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","est"] = 0.01

# Max values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","max"] = 400
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","max"] = 400

# Adjust linkage between parameters
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["ysv","type"] = "1-j"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["ys","type"] = "ysv*1/1"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["y","type"] = "1-j"

# Only sympatric/range-copying (y) events allowed, and with
# exact copying (both descendants always the same size as the ancestor)
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["mx01y","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["mx01y","init"] = 0.9999
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["mx01y","est"] = 0.9999

# Check the inputs
check_BioGeoBEARS_run(BioGeoBEARS_run_object)

runslow = TRUE
resfn = "Schiz_BAYAREALIKE_2017.Rdata"
if (runslow)
  {
    res = bears_optim_run(BioGeoBEARS_run_object)
    res

    save(res, file=resfn)
    resBAYAREALIKE = res
  }
else {
  # Loads to "res"
  load(resfn)
  resBAYAREALIKE = res
}

#######################################################
# Run BAYAREALIKE+J
#######################################################
BioGeoBEARS_run_object = define_BioGeoBEARS_run()
BioGeoBEARS_run_object$trfn = trfn
BioGeoBEARS_run_object$geogfn = geogfn
BioGeoBEARS_run_object$max_range_size = max_range_size
#BioGeoBEARS_run_object$min_branchlength = 0.000001  # Min to treat tip as a direct ancestor (no speciation event)
BioGeoBEARS_run_object$include_null_range = TRUE  # set to FALSE for e.g. DEC* model, DEC*+J, etc.
# also search script on "include_null_range" for other places to change

# Set up a time-stratified analysis:
BioGeoBEARS_run_object$timesfn = "timeperiods.txt"
BioGeoBEARS_run_object$dispersal_multipliers_fn = "dispersal_multipliers.txt"
#BioGeoBEARS_run_object$areas_allowed_fn = "areas_allowed.txt"
#BioGeoBEARS_run_object$areas_adjacency_fn = "areas_adjacency.txt"
#BioGeoBEARS_run_object$distsfn = "distances_matrix.txt"
# See notes on the distances model on PhyloWiki's BioGeoBEARS updates page.
# Speed options and multicore processing if desired
BioGeoBEARS_run_object$use_optimx = TRUE
BioGeoBEARS_run_object$num_cores_to_use=1

BioGeoBEARS_run_object$force_sparse=FALSE  # sparse=FALSE causes pathology & isn't much faster at this scale
BioGeoBEARS_run_object$speedup=TRUE         # shortcuts to speed ML search; use FALSE if worried (e.g. >3 params)
BioGeoBEARS_run_object$calc_ancprobs=TRUE   # get ancestral states from optim run

# This function loads the dispersal multiplier matrix etc. from the text files into the model object. Required for these to work!
# (It also runs some checks on these inputs for certain errors.)
BioGeoBEARS_run_object = readfiles_BioGeoBEARS_run(BioGeoBEARS_run_object)

# Divide the tree up by timeperiods/strata (uncomment this for stratified analysis)
BioGeoBEARS_run_object = section_the_tree(inputs=BioGeoBEARS_run_object, make_master_table=TRUE, plot_pieces=FALSE)
# The stratified tree is described in this table:
BioGeoBEARS_run_object$master_table

# Good default settings to get ancestral states
BioGeoBEARS_run_object$return_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_TTL_loglike_from_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_ancprobs = TRUE    # get ancestral states from optim run

# Set up BAYAREALIKE+J model
# Get the ML parameter values from the 2-parameter nested model
# (this will ensure that the 3-parameter model always does at least as good)
dstart = 4.89
estart = 4.89
jstart = 0.0001

# Input starting values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","init"] = dstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","est"] = dstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","init"] = estart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","est"] = estart

# Max values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","max"] = 400
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","max"] = 400
# No subset sympatry
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["s","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["s","init"] = 0.0
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["s","est"] = 0.0

# No vicariance
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["v","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["v","init"] = 0.0
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["v","est"] = 0.0

# *DO* allow jump dispersal/founder-event speciation (set the starting value close to 0)
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","type"] = "free"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","init"] = jstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","est"] = jstart

# Under BAYAREALIKE+J, the max of "j" should be 1, not 3 (as is default in DEC+J) or 2 (as in DIVALIKE+J)
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","max"] = 0.99999

# Adjust linkage between parameters
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["ysv","type"] = "1-j"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["ys","type"] = "ysv*1/1"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["y","type"] = "1-j"

# Only sympatric/range-copying (y) events allowed, and with
# exact copying (both descendants always the same size as the ancestor)
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["mx01y","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["mx01y","init"] = 0.9999
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["mx01y","est"] = 0.9999

# NOTE (NJM, 2014-04): BAYAREALIKE+J seems to crash on some computers, usually Windows
# machines. I can't replicate this on my Mac machines, but it is almost certainly
# just some precision under-run issue, when optim/optimx tries some parameter value
# just below zero. The "min" and "max" options on each parameter are supposed to
# prevent this, but apparently optim/optimx sometimes go slightly beyond
# these limits. Anyway, if you get a crash, try raising "min" and lowering "max"
# slightly for each parameter:
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","min"] = 0.0000001
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["d","max"] = 4.9999999
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","min"] = 0.0000001
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["e","max"] = 4.9999999
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","min"] = 0.00001
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table["j","max"] = 0.99999

check_BioGeoBEARS_run(BioGeoBEARS_run_object)
resfn = "Schiz_BAYAREALIKE+J_2017.Rdata"
runslow = TRUE
if (runslow)
{
  res = bears_optim_run(BioGeoBEARS_run_object)
  res
  save(res, file=resfn)
  resBAYAREALIKEj = res
}
else {
  # Loads to "res"
  load(resfn)
  resBAYAREALIKEj = res
}

pdffn = "Schiz_BAYAREALIKE_vs_BAYAREALIKE+J_2017.pdf"
pdf(pdffn, width=6, height=6)

# Plot ancestral states - BAYAREALIKE

# Setup
results_object = resBAYAREALIKE
scriptdir = np(system.file("extdata/a_scripts", package="BioGeoBEARS"))

# States
res2 = plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="text", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)

# Pie chart
plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="pie", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)

# Plot ancestral states - BAYAREALIKE+J
# States
res1 = plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="text", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)

# Pie chart
plot_BioGeoBEARS_results(results_object, analysis_titletxt, addl_params=list("j"), plotwhat="pie", label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8, plotsplits=TRUE, cornercoords_loc=scriptdir, include_null_range=TRUE, tr=tr, tipranges=tipranges)

dev.off()
cmdstr = paste("open ", pdfn, sep="")
system(cmdstr)

# CALCULATE SUMMARY STATISTICS TO COMPARE
# DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE, BAYAREALIKE+J
#

# REQUIRED READING:
#
# Practical advice / notes / basic principles on statistical model
# comparison in general, and in BioGeoBEARS:
# http://phylo.wikidot.com/advice-on-statistical-model-comparison-in-biogeobears
#******************************************************************************
#******************************************************************************
# Set up empty tables to hold the statistical results
restable = NULL
teststable = NULL
#******************************************************************************
# Statistics -- DEC vs. DEC+J
#******************************************************************************
# We have to extract the log-likelihood differently, depending on the
# version of optim/optimx
LnL_2 = get_LnL_from_BioGeoBEARS_results_object(resDEC)
LnL_1 = get_LnL_from_BioGeoBEARS_results_object(resDECj)
numparams1 = 3
numparams2 = 2
stats = AICstats_2models(LnL_1, LnL_2, numparams1, numparams2)
stats
# DEC, null model for Likelihood Ratio Test (LRT)
res2 = extract_params_from_BioGeoBEARS_results_object(results_object=resDEC, returnwhat="table", addl_params=c("j"), paramsstr_digits=4)
# DEC+J, alternative model for Likelihood Ratio Test (LRT)
res1 = extract_params_from_BioGeoBEARS_results_object(results_object=resDECj, returnwhat="table", addl_params=c("j"), paramsstr_digits=4)
# The null hypothesis for a Likelihood Ratio Test (LRT) is that two models
# confer the same likelihood on the data. See: Brian O'Meara's webpage:
# http://www.brianomeara.info/tutorials/aic
# ...for an intro to LRT, AIC, and AICc
rbind(res2, res1)
tmp_tests = conditional_format_table(stats)
restable = rbind(restable, res2, res1)
teststable = rbind(teststable, tmp_tests)
#******************************************************************************
# Statistics -- DEC vs. DEC+J w/o multipliers
We have to extract the log-likelihood differently, depending on the version of optim/optimx

LnL_2 = get_LnL_from_BioGeoBEARS_results_object(resDECnoMult)
LnL_1 = get_LnL_from_BioGeoBEARS_results_object(resDECjnoMult)

numparams1 = 3
numparams2 = 2
stats = AICstats_2models(LnL_1, LnL_2, numparams1, numparams2)
stats

# DEC, null model for Likelihood Ratio Test (LRT)
res2 = extract_params_from_BioGeoBEARS_results_object(results_object=resDECnoMult, returnwhat="table", addl_params=c("j"), paramsstr_digits=4)
# DEC+J, alternative model for Likelihood Ratio Test (LRT)
res1 = extract_params_from_BioGeoBEARS_results_object(results_object=resDECjnoMult, returnwhat="table", addl_params=c("j"), paramsstr_digits=4)

# The null hypothesis for a Likelihood Ratio Test (LRT) is that two models confer the same likelihood on the data. See: Brian O'Meara's webpage:
# http://www.brianomeara.info/tutorials/aic
# ...for an intro to LRT, AIC, and AICc

rbind(res2, res1)
tmp_tests = conditional_format_table(stats)
restable = rbind(restable, res2, res1)
teststable = rbind(teststable, tmp_tests)

# Statistics -- DIVALIKE vs. DIVALIKE+J
# We have to extract the log-likelihood differently, depending on the version of optim/optimx
LnL_2 = get_LnL_from_BioGeoBEARS_results_object(resDIVALIKE)
LnL_1 = get_LnL_from_BioGeoBEARS_results_object(resDIVALIKEj)

numparams1 = 3
numparams2 = 2
stats = AICstats_2models(LnL_1, LnL_2, numparams1, numparams2)
stats

# DIVALIKE, null model for Likelihood Ratio Test (LRT)
res2 = extract_params_from_BioGeoBEARS_results_object(results_object=resDIVALIKE, returnwhat="table", addl_params=c("j"), paramsstr_digits=4)  
# DIVALIKE+J, alternative model for Likelihood Ratio Test (LRT)
res1 = extract_params_from_BioGeoBEARS_results_object(results_object=resDIVALIKEj, returnwhat="table", addl_params=c("j"), paramsstr_digits=4)

rbind(res2, res1)
conditional_format_table(stats)

tmp_tests = conditional_format_table(stats)

restable = rbind(restable, res2, res1)
teststable = rbind(teststable, tmp_tests)

#########################################################################  
# RESULTS: DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE, BAYAREALIKE+J"DECnoMult", "DEC+JnoMult"
#########################################################################  

numparams1 = 3
numparams2 = 2
stats = AICstats_2models(LnL_1, LnL_2, numparams1, numparams2)
stats

tmp_tests = conditional_format_table(stats)

restable = rbind(restable, res2, res1)
teststable = rbind(teststable, tmp_tests)
teststable$salt = c("DEC+J", "DEC+JnoMult", "DIVALIKE+J", "BAYAREALIKE+J")
teststable$null = c("DEC", "DEC noMult", "DIVALIKE", "BAYAREALIKE")
row.names(restable) = c("DEC", "DEC+J", "DECnoMult", "DEC+JnoMult", "DIVALIKE", "DIVALIKE+J", "BAYAREALIKE", "BAYAREALIKE+J")

# Look at the results!!
restable
testtable

#############################################################################
# Save the results tables for later -- check for e.g. # convergence issues
# Save the results tables for later -- check for e.g. # convergence issues
#############################################################################

# Loads to "restable"
save(restable, file="restable_v1.Rdata")
load(file="restable_v1.Rdata")

# Loads to "testtable"
save(teststable, file="teststable_v1.Rdata")
load(file="teststable_v1.Rdata")

# Also save to text files
write.table(restable, file="restable.txt", quote=FALSE, sep="\t")
write.table(unlist_df(teststable), file="teststable.txt", quote=FALSE, sep="\t")

#############################################################################
# Model weights of all six models
#############################################################################
restable2 = restable

# With AICs:
AICtable = calc_AIC_column(LnL_vals=restable$LnL, nparam_vals=restable$numparams)
restable = cbind(restable, AICtable)
restable_AIC_rellike = AkaikeWeights_on_summary_table(restable=restable, colname_to_use="AIC")
restable_AIC_rellike

# With AICcs -- factors in sample size
samplesize = length(tr$tip.label)
AICtable = calc_AICc_column(LnL_vals=restable$LnL, nparam_vals=restable$numparams, samplesize=samplesize)
restable2 = cbind(restable2, AICtable)
restable_AICc_rellike = AkaikeWeights_on_summary_table(restable=restable2, colname_to_use="AIC")

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restable_AICc_rellike
free_params = row.names(resDECj$output@params_table[resDECj$output@params_table$type=="free",])
names(restable_AICc_rellike) = c("LnL", "numparams", free_params, "AICc", "AICc_wt")

# Also save to text files
write.table(restable_AIC_rellike, file="restable_AIC_rellike.txt", quote=FALSE, sep="\t")
write.table(restable_AICc_rellike, file="restable_AICc_rellike.txt", quote=FALSE, sep="\t")

# Save with nice conditional formatting
write.table(conditional_format_table(restable_AIC_rellike), file="restable_AIC_rellike_formatted.txt", quote=FALSE, sep="\t")
write.table(conditional_format_table(restable_AICc_rellike), file="restable_AICc_rellike_formatted.txt", quote=FALSE, sep="\t")