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Evaluating the influence of connectivity and distance on biogeographical patterns in the south-western deserts of North America

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ABSTRACT

Aim To examine the role of geological history, connectivity and distance in shaping the biogeographical structure of North American desert clades that are restricted to habitat islands (sand dunes and relictual aquatic habitats), using statistical model choice on old and new probabilistic biogeographical models.

Location North America, Mojave, Sonoran and Chihuahuan Deserts.

Materials and methods Dated phylogenies were estimated for three field-sampled insect clades (*Trigonoscute*, *Rhaphiomidas* and sand treader crickets), and five other literature-sampled clades (the snails *Assimineia*, *Pyrgulopsis* and *Tryonia*; the desert fringe-toed lizard *Uma*; and the desert pupfish *Cyprinodon*). BioGeoBEARS was used to statistically compare biogeographical models assuming unconstrained or connectivity-constrained dispersal, with or without founder-event speciation (jump dispersal) permitted. Finally, we introduce and test a novel distance-based dispersal model (+x) where dispersal probability is multiplied by distance to the power x .

Results We observed little concordance between biogeographical patterns and timing of geological events. Model comparisons were decidedly in favour of inclusion of founder-event speciation in the models for most taxa, with only a small taxon, *Uma*, showing support for the model favouring vicariance. The inclusion of a constrained-dispersal matrix was favoured by three of the eight taxa examined (*Cyprinodon*, sand treader crickets, and *Trigonoscute*). Surprisingly, tests for distance influencing dispersal probability were mostly negative.

Main conclusions Our results do not show support for any one geological event shaping the biogeographical patterns of these desert taxa. Instead, the histories of desert dune and aquatic taxa are largely products of rare jump dispersal events, and can be considered island-like systems. Although results are negative for the distance-based dispersal model, this in itself demonstrates the superiority of explicit statistical model testing over a *a priori* assumption of fixed models in historical biogeography.

Keywords

BioGeoBEARS, Chihuahuan Desert, deserts, dispersal, historical biogeography, Mojave Desert, Pleistocene, Sonoran Desert, vicariance

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INTRODUCTION

The use of islands as natural laboratories to study evolution dates back to Wallace and Darwin, and island systems have been indispensable for understanding the processes generating biodiversity. Examples from the Galapagos, Caribbean and Hawaiian archipelagos demonstrate the utility of islands

for the study of adaptation, community assembly and speciation (Grant & Grant, 2002; Losos *et al.*, 2003; Gillespie, 2004). In addition to true islands, habitat islands are also of great interest to evolutionary biologists studying many of the same questions (Wake, 1987; Masta, 2000; Knowles & Carstens, 2007). Habitat islands are discrete patches of habitat surrounded by a contrasting habitat (Whittaker &

Fernández-Palacios, 2007). Depending on the habitat and taxon, the area surrounding habitat islands may be totally uninhabitable (much like the ocean for terrestrial taxa), or may be a less stringent constraint. Thus, the rules governing dispersal–vicariance may not be the same between oceanic islands and habitat islands.

Here, we examine the historical biogeography of taxa that occupy sand dune habitat islands in the south-western deserts of North America. These taxa are specialists on sand dunes, and are never found more than 100 m outside dune edges (Norris, 1958; Pierce, 1975; Hardy & Andrews, 1976; Cazier, 1985). This highly specialized habitat preference, combined with the isolated and disjunct distributions of dunes, leads to the question of how these animals came to occupy their current distributions. For example, Norris (1958) first proposed that the fringe-toed lizard genus *Uma* might have used the sandy river corridors and sand transport pathways [the path aeolian (wind blown) sediments follow from source to deposition] as a means of dispersal during Pleistocene climate fluctuations, when sandy sediments would periodically become available. Here we use phylogenetic dating and probabilistic biogeographical inference methods to test this hypothesis for multiple clades.

Background: Geological hypotheses

We aim to test three geological hypotheses for their ability to explain the distributions of dune taxa of south-western deserts: (1) the uplift of the Sierra Madre Occidental, (2) the formation of the Bouse Lakes, and (3) Pleistocene sand transport pathways. The uplift of the Sierra Madre Occidental (c. 34–15 Ma) is postulated to be one of the major factors responsible for dividing the Sonoran and Chihuahuan deserts (Ferrari *et al.*, 1999; Nieto-Samaniego *et al.*, 1999; Riddle & Hafner, 2006). A later-forming geological barrier was the ‘Bouse Embayment’ (Lucchitta, 1979; Lucchitta *et al.*, 2001; Turak, 2000; Spencer *et al.*, 2013), which was created by the proto-Colorado River when high rates of evaporation relative to input formed a series of high-salinity palaeo-lakes (rather than an actual embayment of the Gulf of Mexico) 4.83–4.80 Ma (Spencer & Patchett, 1997; Poulson & John, 2003; House *et al.*, 2005, 2008; Roskowski *et al.*, 2010; Spencer *et al.*, 2013). This will be referred to herein as the Bouse Lakes Formation (BLFs). When the BLFs drained, the Colorado River was connected to the early Pliocene Gulf of California by c. 4.80 Ma (Spencer *et al.*, 2013). Phylogenetic dating can yield some indication of the plausibility of these two pre-Pleistocene geological explanations: if the estimated date ranges of many nodes overlap with the date of a geological event, it is possible that it caused approximately simultaneous speciation events; but if overlap is not observed, the explanation is disconfirmed. If these geological events had an effect on the biogeographical history, then we would expect to see divergence between taxa east–west of the Mojave section of the Colorado River during the formation of the Bouse Lakes and divergence between sister taxa in the

Sonoran and Chihuahuan Deserts during the formation of the Sierra Madre Occidental.

The third major event that might be important is the repeated extension and retreat of lakes and rivers in the desert south-west during Pleistocene glacial-interglacial cycles (Muhs *et al.*, 2003). Under this hypothesis, dune-restricted taxa followed the sandy corridors of Pleistocene lakes and rivers to achieve their current distributions. If the dune-restricted fauna did in fact use river corridors as dispersal pathways, then they should exhibit biogeographical patterns similar to those observed for aquatic organisms of the south-western deserts. This hypothesis is based on the premise that the river corridors initially provided aquatic habitat connections required by fish and other aquatic organisms, and as they began to dry, exposed sandy sediments that were utilized by dune-restricted taxa to traverse the same pathways. If the Pleistocene sand transport pathways hypothesis is correct, then we would expect to see speciation events dating to the Pleistocene, and geographical ranges that are well-explained by dispersal along these pathways.

An alternative to these hypotheses is that geology and connectivity are not important explainers of the geographical range patterns of each clade, and long-distance ‘jump’ dispersal dominates instead. This hypothesis suggests that divergence times will not correlate with geological events, and the geographical range data will be better fit by unconstrained models and those that make use of founder-event speciation.

To test these hypotheses, we estimated dated phylogenies for four sand-dune-restricted clades, and also included four aquatic clades that are found in desert regions adjacent to many of our focal sand dunes. We then conducted maximum likelihood (ML) estimation of biogeographical history under the dispersal-extinction-cladogenesis (DEC) model, and modifications to this model that add founder-event speciation (DEC+J) and distance-dependent dispersal (DEC+x, DEC+J+x). In addition, each model was run with and without connectivity constraints. The ability of the models to explain the data was assessed via standard procedures in statistical model choice.

Background: probabilistic biogeographical methods

Phylogenetic biogeography methods are reviewed in Lawing & Matzke (2014). Although older methods remain popular – such as construction of a historical narrative (Castoe *et al.*, 2009), or construction of total area cladograms from the area cladograms of several taxa (e.g. Brooks *et al.*, 2002) – the field is clearly moving in the direction of statistical inference with probabilistic, parametric models (Ree & Sanmartín, 2009). This tracks the dominant trends in genetics and phylogenetics. Although the term ‘phylogeography’ is sometimes applied to historical biogeography, statistical phylogeography (Knowles & Maddison, 2002) operates at the scale of population genetics (Zink, 2002) and historical biogeography (Ronquist & Sanmartín, 2011) operates at the scale of phylogenetics (Lawing & Matzke, 2014).

Parametric biogeography was initiated by the LAGRANGE program (Ree *et al.*, 2005; Ree & Smith, 2008) which used a dispersal-extinction-cladogenesis (DEC) model. DEC has proven widely popular and has been used in hundreds of historical biogeography analyses. In DEC, 'dispersal' means range expansion; and 'extinction' means local extirpation, or range contraction. These processes are Markov processes occurring anagenetically along the branches of a phylogeny, and are controlled by the rate parameters d and e . These parameters are free, and are estimated by ML. In DEC, geographical range can also change during cladogenesis through vicariance or subset sympatry. Whereas d and e are estimated, in DEC the cladogenesis model is fixed, with each allowed event assigned equal probability conditional on the ancestral range. Given the DEC model and an ML estimate of d and e , the likelihood of the geographical range data can be calculated, and the probabilities of ancestral ranges estimated.

Although DEC pioneered the use of maximum likelihood in historical biogeography, the presence of only a single model meant that the full potential of the parametric approach was not exploited. In particular, with only one model available, it was impossible to make use of statistical tools for model comparison and model selection. These tools are ubiquitous in other areas of statistical inference, and include the likelihood ratio test (LRT), Akaike's information criterion (AIC) and sample-size corrected AIC (AICc) (Burnham & Anderson, 2002). Recently, the DEC model was expanded to include founder-event speciation, also known as 'jump dispersal' (Fig. 2), via the DEC+J model (Matzke, 2013, 2014). The j parameter of DEC+J assigns a per-event weight to founder-event speciation, a cladogenetic range-inheritance event where one daughter lineage occupies an area outside of the range of its ancestor. The two-parameter DEC model is nested inside the three-parameter DEC+J model, such that when $j = 0$, DEC+J reduces to DEC. Statistical model comparison often reveals that the data support founder-event speciation as a process important for explanation of the geographical range data at the tips of the phylogeny (Matzke, 2013, 2014; Harris *et al.*, 2014; Voelker *et al.*, 2014), although traditional DEC cladogenesis processes remain important.

The DEC+J model is included in the R package BioGeoBEARS (Matzke, 2013). However, the potential for using statistical model choice to test hypotheses in historical biogeography is far from exhausted. BioGeoBEARS specifies biogeography models as instances of a flexible supermodel. This enables creation of new models with ease, which may then be evaluated against the data via LRT, AIC, or AICc to determine if the addition of free parameters is justified by improvements in data likelihood.

Here we introduce a variant on DEC-type models wherein dispersal probabilities are modified as a function of geographical distance between two areas. LAGRANGE allows inclusion of a user-specified dispersal matrix, which alters the transition matrix between states depending on the

relative probability of dispersal between areas. However, the construction of the dispersal probability matrix was usually somewhat subjective. Recent methods such as SHIBA (Webb & Ree, 2012) and BayArea (Landis *et al.* 2013) allow for dispersal rate to be calculated as a function of distance. However, BayArea contains no model for range evolution at cladogenesis, and SHIBA employs a simulation-based approximate Bayesian approach, which is computationally intensive, restricting analyses to a small number of taxa and areas.

SHIBA and LAGRANGE could also specify constraints on connectivity between areas, setting the probability of dispersal to 0 between unconnected areas. In BioGeoBEARS, both connectivity and/or distance matrices can be included in the biogeographical models, and these can be attached to any cladogenetic models of interest (e.g. DEC or DEC+J). As the likelihood of the geographical range data can be calculated under each model, ML inference and standard model selection can be performed. To the best of our knowledge, this is the first time a study has used formal model selection to test the effects of both connectivity and distance. For a review of the different biogeographical models, see Matzke (2013).

Natural history of focal taxa

Dune taxa

We selected four groups of taxa that are found throughout portions of the North American deserts. All of the sand dune taxa are ecologically restricted to this habitat type. Many dune inhabiting species have specialized morphology for digging into and moving on the sand's surface.

The fly genus *Rhaphiomidas* consists of 23 described species and five subspecies all of which are endemic to the deserts of North America (Van Dam, 2010). The adult flies are active in spring and fall and feed on floral nectar. The larvae are restricted to deep sandy soils and are believed to be generalist predators. Several species are of threatened status, for example, *R. terminatus*, *R. trochilus* and *R. moapa* (Rogers & Van Dam, 2007). *Rhaphiomidas terminatus terminatus* is only known from 20 ha, in the middle of a golf course on the Palos Verdes Peninsula (George & Mattoni, 2006).

The dune weevil *Trigonoscuta* (Coleoptera: Curculionidae), represents 65 species and 90 subspecies (Pierce, 1975). *Trigonoscuta* has a distribution which covers the Californian coastal dunes as well as dunes in the Mojave and Sonoran Deserts. In addition, each of the California Channel Islands has endemic species. *Trigonoscuta* is highly restricted to sand dunes, feeding on a variety of dune plants. All the members of this genus are entirely flightless. Adults bury themselves under the sand during the day and are nocturnally active. *Trigonoscuta* are typically known from only one sand dune system and most species are allopatric (Pierce, 1975). Some authors have questioned the validity of the species that Pierce described, especially the sympatric species as they

show little if any external morphological variation (Anderson, 2002; Evans & Hogue, 2006).

The group commonly known as the sand treader crickets (Rhaphidophoridae: Ceuthophilinae) is comprised of five genera with 13 described species (and many undescribed). All members of this family are entirely flightless. The name 'sand treader' refers to their enlarged tibial spines (sand-basket), which they use to dig into the sand to avoid desiccating during the day. Their burrows are often a meter deep or more in dry years, which requires them to occupy areas of deep aeolian sand. In this study, we focus on a monophyletic clade, all of which are dune-restricted, or are found in association with sandy soils/dunes in the case of *Daihinia*.

The fringe-toed lizards, genus *Uma* (Phrynosomatidae), are entirely restricted to aeolian sand dunes. The genus is adapted to life in sand dunes, possessing a specialized morphology for dealing with this environment (e.g. fringes on their toes which help them to move on sand) (Norris, 1958). Many of these species are also threatened due to habitat loss and other anthropogenic activities such as off-road vehicle use, as are many dune arthropod species (Van Dam & Van Dam, 2008).

Aquatic taxa

Pyrgulopsis (Hydrobiidae) is one of the most diverse aquatic snails in North America, which consists of 134 species (Liu *et al.*, 2013). They have diversified extensively in the desert south-west, and are found primarily in springs. Their specialization on specific water conditions, low dispersal ability and highly restricted ranges (single springs in some cases) are believed to be responsible for their high species diversity (Hershler & Sada, 2002).

The genus *Tryonia* (Cochliopidae) has 32 described species (Hershler *et al.*, 2011). This aquatic snail is found primarily in western North America but has one species in Florida and one in Guatemala. Their young develop inside the female genital duct (Hershler *et al.*, 2011). They are found primarily in springs but a few species occupy brackish water.

The snail genus *Assiminea* (Assimineidae) is found primarily in brackish waters and has a world-wide distribution. The North American species in the *nitida* complex are composed of four described species (Hershler *et al.*, 2007). One is found on the coast of California in brackish waters, and a second along the Gulf of Mexico. The other two are landlocked and are found in Death Valley and the Chihuahuan Desert. They have free-swimming larvae.

The North American pupfish *Cyprinodon* (Cyprinodontidae) are members of a large egg-laying genus with c. 51 species. Here we focus on the western clade exclusively (Echelle, 2008). They are found in waters of varying salinity and are often highly restricted to small desert springs. Several species are threatened due to their restricted ranges, and *C. arcuatus* has been extinct since 1971. This species is morphologically similar to *C. macularius* and *C. eremus* (Minckley *et al.*, 2002) and is not included here.

MATERIALS AND METHODS

Taxon sampling

For the three insect clades (*Trigonoscute*, *Rhaphiomidas* and the sand treader crickets), most specimens were collected from 2006–2011 within the published ranges of these clades, as well as from regions of Baja California and Sonora, Mexico that were well outside the documented ranges for many of these groups. The total number of sampled locations is over 200 (for range maps of sand dune taxa sampled please see Supporting Information). Specimens were preserved in 95% ethanol stored on ice in the field and then transferred to a -20°C freezer. *Trigonoscute* outgroups were selected from the putative sister taxa to *Trigonoscute* (Pierce, 1975), as well as other North American dune-restricted weevils (*Miloderes* Casey, 1888). The ingroup taxa were selected from each of the known populations described in Pierce (1975), as well as localities from museum specimens (CAS, Cdfa, COB, EMEC, LACM, UCD, UCR). For *Rhaphiomidas* flies, outgroups included members of four separate subfamilies of Mydidae, Apioceridae and a single Asilidae. The outgroups for the Ceuthophilinae subfamily of crickets were sampled from the Pistoceuthophilini (*Pistoceuthophilus*), Argytini (*Argyrtes*), and Macropathinae (Macropathini, *Heteromal-laus*). For each location (isolated sand dunes), individual specimens were initially treated as separate taxa in phylogenetic analysis so as not to bias the sampling by imposing previous taxonomic concepts. A maximum of 12 individuals were sampled per population, with an average of four for all but the U.S. coastal species of *Trigonoscute*. This sampling regime was used to assess levels of incomplete lineage sorting between samples, or instances of mitochondrial introgression. Our Supporting Information, Appendix S1 includes: (1) standard molecular lab procedures used for extraction, PCR, sequencing and alignment; (2) references for sequences derived from Genbank for non-insect taxa. For a list of genes used see Table 1.

Phylogenetic dating analyses

We chose to partition sequences by codon position because it has been demonstrated repeatedly that incorporating different rates of DNA evolution for each codon position outperforms single-partition strategies (Brandley *et al.*, 2005; Fyler *et al.*, 2005; Seago *et al.*, 2011). Model selection was performed in MrMODELTEST2 (Nylander, 2002). The models for different partitions were selected using AIC and AICc. For phylogenetic reconstruction, BEAST 1.7.5 (Drummond *et al.*, 2012) was used. Phylogenetic trees were dated using a lognormally distributed relaxed clock model using the birth-death tree prior (Drummond *et al.*, 2006; see Table 1 for calibration priors). Each of the Markov chain Monte Carlo (MCMC) analyses was run for sufficient generations to reach stationarity, with trees and model parameters sampled from the stationary posterior distribution. Stationarity was assessed

using the program TRACER 1.5.3 (Drummond, 2007). The most challenging part of the analysis was derivation of dating priors; we used (admittedly approximate) fossil and biogeographical calibration points; if none were available then an informative prior on the relaxed clock rate was used (Table 1). We decided against performing a gene-tree/species tree analysis (Pamilo & Nei, 1988) mainly because of the available data for our clades (Table 1). For 6/8 clades, mtDNA (a single locus) was all that was available. For the sand treader crickets there were two available loci, COI (mtDNA) and H3 (nuclear DNA). H3 is slowly evolving and was sequenced only to provide improved resolution deep in the tree. More loci are available for *Rhaphiomidas* flies, but the nuclear genes chosen are slow-evolving and have sparse sampling.

Biogeographical analyses

Biogeographical model fitting and ancestral range estimation

For biogeographical analyses, we used the R package BioGEOBEARS (Matzke, 2013). BioGEOBEARS requires as inputs (1) a dated phylogeny, (2) a file of geographical ranges indicating presence/absence of each species or coalescing population in each discrete area in the analysis and (3) constraint matrices indicating connectivity and/or distance between the discrete areas. The sampling localities were grouped into the following discrete areas: Mojave River watershed, Owens Valley River, Bristol Trough and Clarks Path sand transport pathway, Parker Dunes, Colorado River Dunes, Sonoran Desert, Chihuahuan Desert, Great Basin Desert, Great Plains and Coastal Dunes (Fig. 1). We did not have any species that occupied more than four areas, so we allowed for a maximum of four areas at each node, therefore a total of 562 possible states (geographical ranges) in the state space. We could not include larger numbers of areas due to computational limitations. Areas and distances between the areas were defined in ArcGIS software (Fig. 1), with distance measured in kilometres along the most likely path of dispersal (for Pleistocene river connections) or closest distance between the borders of two areas (for disconnected areas). These distances were used in the constrained-distance-dependent dispersal matrix. The boundaries between the sand transport pathways (Clarks, Bristol, Parker and Mojave River) were set as defined by Muhs *et al.* (2003). The Colorado River pathway was traced as the area adjacent to the river, as this was one of the hypothesized dispersal corridors of Norris (1958). For the distances and shapes of the Great Basin, Sonoran and Chihuahuan deserts, we set the perimeters of these areas to encompass the most peripheral dunes of each region. The specimen-level phylogenies were pruned so that a single operational taxonomic unit (OTU) was left per species/coalescing monophyletic population. As the branches are very short within the coalescing populations of the trees, it would make very little difference which

specimen was used, so we randomly selected one tip from each population and used it as a representative of the population. Pruning was done because DEC-type models, including the DEC+J model (Fig. 2), assume that a lineage can possibly inhabit more than one area. If a specimen-level tree is used in a DEC analysis, biased results will be obtained if the individual specimens themselves are used as OTUs, because a specimen can only inhabit a single area. When all OTUs inhabit single areas, the data will tend to prefer '+J' models (Matzke, 2013, 2014). This is acceptable if each species/monophyletic population really is restricted to a single area, but not if this is due to the OTUs being specimens. The geographical structure of gene trees *within* species/coalescing populations also is interesting, but is not the topic of this study. We implemented eight models in BioGEOBEARS. The eight models are: (1) the DEC model, unconstrained, (2) DEC+J unconstrained, (3) DEC model with dispersal constrained to adjacent areas, (4) the DEC+J model with dispersal constrained to adjacent areas, (5) the DEC+x model, where dispersal is limited to adjacent areas and modified by distance taken to the power x , (6) the DEC+J+x model, which adds jump dispersal, also modified by distance to the power x , (7) DEC+x without adjacent area constraints and (8) DEC+J+x without adjacent area constraints.

A common misconception about constraints in DEC/DEC+J-type analyses is that constrained analyses will always yield a lower maximum log-likelihood than unconstrained analyses. Dispersal constraints can actually increase or decrease the likelihood of the data, keeping in mind that the ML estimates of d and e can be different between constrained and unconstrained models. In essence, a model would confer the highest likelihood if it gave high probability to just the dispersal events needed to explain the observed tip ranges, and low probability to all of the events that would produce unobserved ranges. When a constraints matrix rules out unnecessary dispersal events, d can be optimized to explain just the 'right' events to explain the data. This is the case if the data and the constraints match. For example, if many sister species in a large phylogeny are (A, B), and none are (A, C), then a model that allows $A \leftrightarrow B$ dispersal but disallows $A \leftrightarrow C$ dispersal might be favoured.

Modifying dispersal probability as a function of distance

The '+x' models in BioGEOBEARS take the base dispersal rates specified by the rest of the model, and modify them as follows:

$$R_{\text{mod.}} = R_{\text{orig.}} \times \text{distance}^x \quad (1)$$

$$W_{\text{mod.}} = W_{\text{orig.}} \times \text{distance}^x \quad (2)$$

where $R_{\text{orig.}}$ is the original dispersal rate (for anagenetic range expansion dispersal), $R_{\text{mod.}}$ the modified dispersal rate, and the distance is in kilometres. $W_{\text{orig.}}$ and $W_{\text{mod.}}$ are the original and modified per-event weights for founder-event jump dispersal at cladogenesis (under DEC-type models, for range-change events at cladogenesis, each possible event is

Table 1 Summary of sequence data used in the analysis. Loci count and type are given. Number of specimens sampled per species, plus specimen totals and number of species, are provided. If species were pre-defined in the literature, they are listed as 'predefined'. If they were discovered through examination in this study they are listed as 'discovered'. The node/clock prior column lists the node or clock priors set in BEAST used to calibrate the tree, followed by the references for each.

Taxon	mtDNA loci	Nuclear loci	Range no. samples per species (average) and total no. samples (tips)	No. species	Species pre-defined or discovered	MCMC no. gens. in BEAST	Calibration node/clock prior	Type and Reference
<i>Rhaphiomidas</i>	CO1, CO2, 16S	EF1-alpha, PGD, SNF, WG, CAD	1–34 (8.4) (219 total)	26	Discovered	20,000,000	Higher Mydidae stem, Normal (mean = 120.0 SD = 10.0)	Fossil from the Crato Formation, Brazil (Albian) (Grimaldi, 1990)
Sand treater crickets	CO1	H3	2–37 (9.5) (227 ingroup, 420 total)	24	Discovered	40,000,000	Caelifera and Ensifera divergence Normal(mean = 250.0 SD = 10.0); (<i>Troglophilus</i> , <i>Dolichopoda</i> , <i>Euhadenocetus</i> , <i>Hadenocetus</i>) Lognormal(mean = 1.0 SD = 1.0 offset = 34.0), Gryllidae Lognormal(mean = 1.0 SD = 1.0 offset = 107.0). includeStem = 'true' for all groups Gulf of California split parent node, Normal(mean = 6.0 SD = 2.0)	Fossil, Permo-Triassic boundary (Grimaldi & Engel, 2005). Fossil, Baltic amber (Chopard, 1936; Allegrucci <i>et al.</i> , 2005). Fossil (Hedges & Leuzinger, 2011)
<i>Trigonoscuta</i>	CO1		1–23 (5.5) (138 reduced to help MCMC, 411 total)	25	Discovered	40,000,000		Geological vicariance (Murphy & Aguirre-Léon, 2002; Oskin & Stock, 2003)
<i>Uma</i>	CytB, ATPase		19–81 (36.8) (184 total)	5	Pre-defined, only five species	40,000,000	<i>Uma</i> stem Normal(mean = 33.6 SD = 5.0)	Fossil <i>Phrynosoma</i> from Split Rock Formation, clade origin earlier (Robinson & Van Devender, 1973). Split Rock Formation overlies White River formation of Oligocene age (Love, 1961)
<i>Cyprinodon</i>	CytB, NDI		1–10 (3.8) (87 total)	23	Pre-defined	40,000,000	<i>Cyprinodon rubrofluvialis</i> Red river-Pecos split parent node Normal(mean = 4.5 SD = 0.5); <i>Cyprinodon macularius-Cyprinodon eremus</i> parent node(Pinacate volcanic field eruptions diverted the Río Sonoyta from the Lower Colorado River) Normal(mean = 1.3 SD = 0.5) (see Echelle, 2008)	Geological vicariance (Echelle, 2008)

Table 1 Continued

Taxon	mtDNA loci	Nuclear loci	Range no. samples per species (average) and total no. samples (tips)	No. species	Species pre-defined or discovered	MCMC no. gens. in BEAST	Calibration node/clock prior	Type and Reference
<i>Assimineia</i>	CO1, 16S		1–13 (3.5) (42 total)	12	Pre-defined	20,000,000	Lognormal prior on clockrate (mean = 0.0183 SD = 1.0)	Clock rate (Wilke, 2003)
<i>Pyrgulopsis</i>	CO1, ND1		1–37 (2) (208 total)	100	Pre-defined	10,000,000	<i>Pyrgulopsis owensensis</i> , <i>Pyrgulopsis perturbata</i> , parent node Normal(mean = 0.819, SD = 0.015); <i>Pyrgulopsis</i> stem Lognormal(mean = 5.0 SD = 1.0 offset = 15.0)	Geological, Bishop Tuff formation (Hershler & Liu, 2008). Fossil <i>Pyrgulopsis truckeeensis</i> (Firby, 1993; Stewart & Perkins, 1999; Hershler & Liu, 2004)
<i>Tryonia</i>	CO1		1–14 (2.8) (108 total)	38	Pre-defined	20,000,000	<i>Tryonia</i> stem Lognormal(mean = 10.85 SD = 1.0 offset = 10)	Fossil (Hershler <i>et al.</i> , 1999)

assigned a per-event weight, and the probability of the event is this weight divided by the sum of the weights of all events; (Matzke, 2014). When $x = 0$, as in non-‘+x’ models, distance has no effect on dispersal, and these models are nested within distance-dependent models. When x is negative, dispersal probability drops off as distance increases. In the unlikely event that x were positive, dispersal probability would increase with distance. If $x = -2$ (Fig. 3), the inverse square law is being followed (often considered in studies of dispersal in ecological studies; see Darlington, 1938 for a review and critique of the law in dispersalist historical biogeography). It should be noted that it is entirely possible that range expansion and jump dispersal could follow different dispersal kernels, and that dispersal kernels could have a shape more complex than an exponential function. However, testing these possibilities would require a more complex model, with more free parameters, and possibly more data to estimate them, and thus should be reserved for a future study. As it is conceivable that the units on distance might be important for successful search of the parameter space, we repeated the ML analyses with the distances rescaled by dividing by the maximum distance; likelihoods were identical so these results are not shown.

Statistical model choice

As DEC-type models are nested within DEC+J-type models, these models can be compared in pairwise fashion using the LRT, a chi-squared test with one degree of freedom. For comparing all of the models on a particular data set, nested or not, AIC and AICc were used. AIC- and AICc-based weights were calculated and used to calculate relative model probabilities as percentages (Burnham & Anderson, 2002; see Supporting Information for the full calculations), in order to assess the support that geographical range data lend to each model.

RESULTS

Sampling effort and missing taxa

The study area includes over 200 localities and encompasses sand dune taxa from the Pacific Coast to the Great Plains of North America. For *Uma*, *Trigonoscutea* and *Assimineia*, we had complete sampling of species. For *Rhaphiomidas* we sampled all but one of the described species, *R. hoguei*, which is only known from one specimen occurring near Laredo, Texas. Repeated attempts to sample this species in the field were unsuccessful. This species is most similar to *R. brevisrostris* and could be another Sonoran-Chihuahuan Desert divergence in *Rhaphiomidas*.

For the sand treater crickets we sampled all of the described species except for two species of *Daihiniodes* from the Chihuahuan Desert. This genus is most likely para- or polyphyletic with *Daihinibaenetes*, and this group in general is in need of revision. For all the other genera of sand

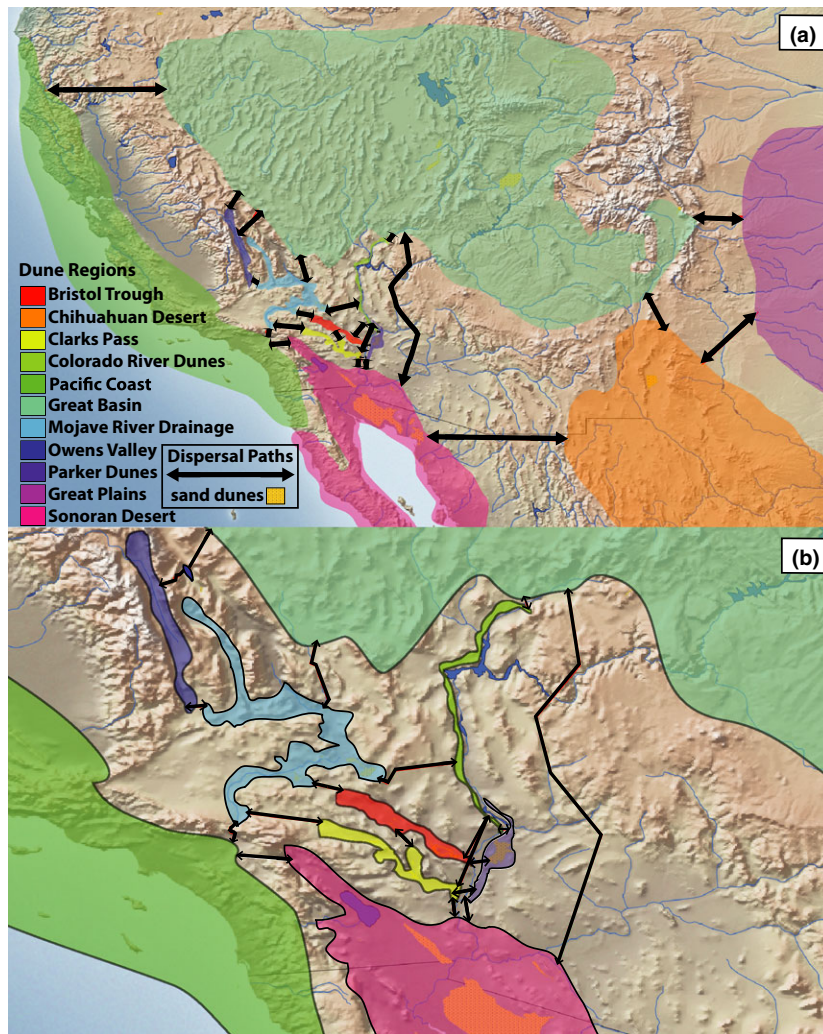


Figure 1 (a) The geographical areas used in BioGeoBEARS analyses are shaded. Arrows denote proposed dispersal paths and distances. The connectivity shown by the arrows was used to make the constraint matrices. The distances are implemented in the multiplier of dispersal probability matrices. (b) Close-up of dispersal paths.

treader crickets we had complete sampling. In the course of this study many undescribed species from this group were collected.

For species of the western *Cyprinodon* clade, previous authors (Echelle, 2008) sampled all but one species, *C. arcuatus*, which is believed to be extinct. For *Pyrgulopsis* we included 100 of the 134 described species, drawing on sequences from the literature, with almost complete representation of the western species. In the Death Valley system we lacked *P. aardahli* and *P. nevadensis* which have not been collected since the late 1800s and are likely extinct (Hershler, 1994). For *Tryonia* we have representatives from 29 of the 32 described species, as well as undescribed species from the Chihuahuan desert region (Hershler *et al.*, 2011).

Molecular Data

Sequence data were obtained for total of 411 *Trigonoscute* individuals (855 bp mtDNA COI), 227 sand treader cricket individuals [(1536 bp mtDNA COI), (353 bp nDNA H3)], and 219 *Rhaphiomidas* individuals [(2904 bp mtDNA; COI,

COII, 16S), (3720 bp nDNA; EF1alpha, PGD, snf, Wg, CAD)].

Phylogenetic dating analyses

The estimated ages of the study clades varied greatly. For example, *Rhaphiomidas* diverged from the rest of the Mydidae during the early Cretaceous (see Supporting Information for trees). Other genera were much younger, such as *Assiminea*, which is < 10 million years old, with many divergences dated to the Pleistocene. Graphics of the dated phylogenies are available in Supporting Information.

Statistical comparison of biogeographical models

The results of ML inference on each data set and biogeographical model are given in Supporting Information, along with the ML parameter estimates of d , e and where applicable, j and x (in models that do not include j or x , these parameters are fixed to 0). The data usually reject the null hypothesis that the DEC-type model explained the data as well as the DEC+J-type model. The exceptions were *Uma*,

Anagenetic range-change events

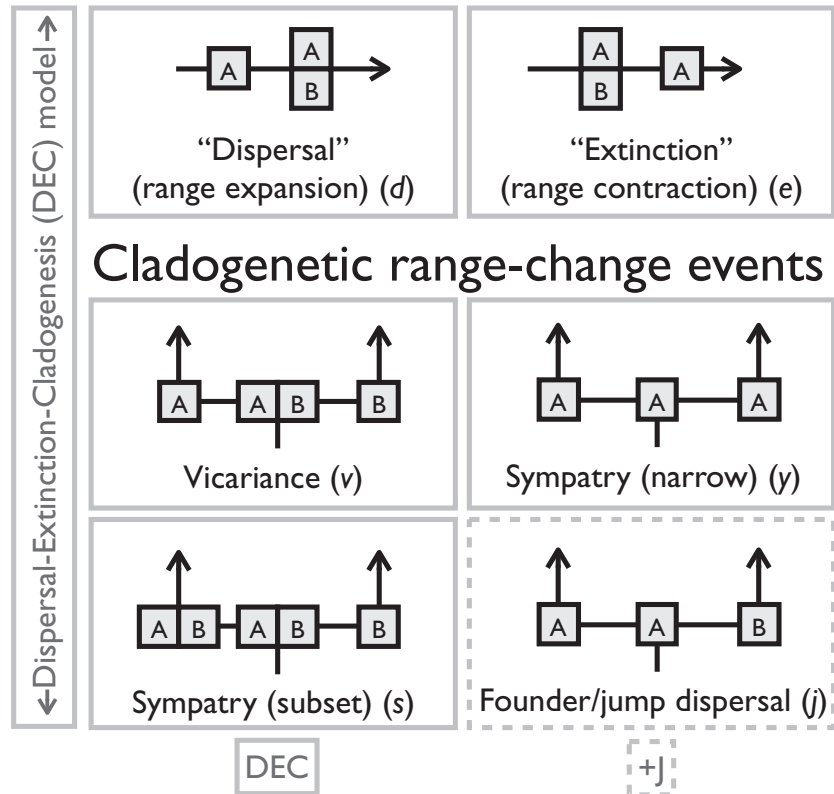


Figure 2 Cladogenetic and anagenetic processes allowed in DEC and DEC+J models.

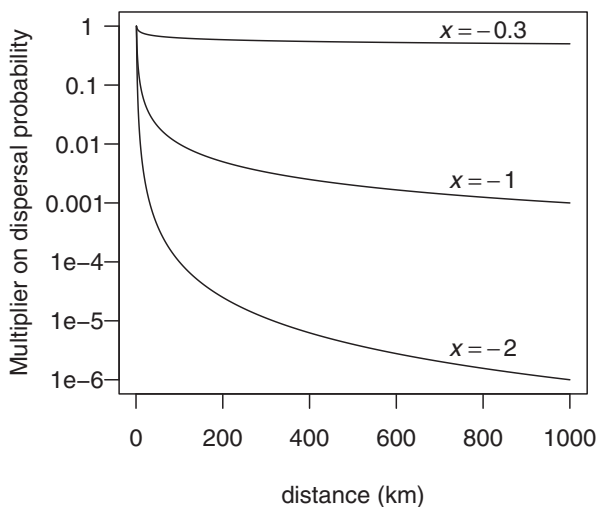


Figure 3 Relationship between the value of x and multiplier on dispersal probability, given distance.

and constrained-dispersal analyses of *Assimineae* and *Trigonoscute*. With *Assimineae* and *Trigonoscute*, addition of the adjacency matrix dramatically reduced the log-likelihood advantage of the DEC+J model over the DEC model, such that DEC could not be statistically rejected. However, these constrained models were much poorer explanations of the data than the unconstrained models (see below), so failure to distinguish the models may simply be a side-effect of the

general poor fit of the constrained models. In the case of *Uma*, the data were so few that no power existed to distinguish the different models, and ML optimization failed in one case, probably due to an extremely flat likelihood surface.

Comparing all of the models with AIC and AICc (Table 2) revealed that the constrained-dispersal matrix was preferred over the unconstrained-dispersal matrix in two of the eight groups, the *Cyprinodon* pupfish and the *Ceuthophilinae* crickets. In one of the groups (*Trigonoscute*), the constrained and unconstrained matrices produced similar likelihoods, separated only by 0.2 log-likelihood units. In *Trigonoscute*, the DEC+ x +J model was a slight improvement (by 1.1 log-likelihood units) relative to the DEC+J unconstrained model. This means that DEC+ x +J was the favoured model for *Trigonoscute* with AIC, but only ranks third under AICc, which more strongly penalizes extra free parameters in small datasets.

Four of the clades overwhelmingly favoured unconstrained DEC+J models. These were *Rhaphiomidas* flies and the three aquatic snail clades (*Assimineae*, *Pyrgulopsis* and *Tryonia*). Unconstrained DEC was the poorest-performing model overall, never achieving even 1% relative model probability under any data set, under AIC or AICc (except *Uma*, which had the aforementioned power problems).

For the individual taxon-specific biogeographical reconstructions, see Supporting Information.

Table 2 Summary of data likelihoods under each model, and results of statistical model choice. Note *Uma* was had too few taxa to calculate AICc, indicated by N/A. Unconstrained models allowed dispersal between any of the areas and adjacent-only implemented the dispersal constraints, as seen in Fig. 1. The DEC+x models used distance between areas to implement dispersal constraints.

No. free parameters (K)	n	DEC		DEC+J		DEC+x		DEC+x+J		DEC+x		DEC+x+J	
		unconstrained	adjacent-only	unconstrained	adjacent-only	unconstrained	adjacent-only	unconstrained	adjacent-only	unconstrained	adjacent-only	unconstrained	adjacent-only
Log-likelihoods (LnL)		2	2	3	3	2	3	4	4	3	3	4	4
<i>Assiminea</i>	12	-26.5	-26.7	-19.8	-25.9	-26.7	-26.7	-25.9	-25.9	-24.7	-24.7	-18.9	-18.9
Sand treachers	24	-76.2	-75.2	-62.9	-62.8	-75.2	-75.2	-63.1	-63.1	-76.2	-76.2	-63.0	-63.0
<i>Cyprinodon</i>	23	-34.3	-32.3	-29.8	-28.5	-32.3	-32.2	-28.5	-28.5	-33.9	-33.9	-29.8	-29.8
<i>Pyrgulopsis</i>	100	-210.7	-204.3	-171.1	-187.7	-204.3	-203.4	-187.7	-187.7	-210.7	-210.7	-171.1	-171.1
<i>Rhaphiomidas</i>	26	-106.9	-110.5	-96.5	-101.5	-110.5	-108.6	-100.8	-100.8	-103.0	-103.0	-95.3	-95.3
<i>Trigonoscuta</i>	25	-59	-56.1	-54.1	-54.3	-56.1	-54.9	-53	-53	-58.5	-58.5	-52.5	-52.5
<i>Tryonia</i>	38	-104.5	-105	-88.7	-95.5	-105	-104.7	-95.5	-95.5	-104.4	-104.4	-87.6	-87.6
<i>Uma</i>	5	-9.2	-9.3	-9.2	-9.3	-9.3	-8.1	-9.3	-9.3	-8.5	-8.5	-9.1	-9.1
AIC													
<i>Assiminea</i>	57	57.4	57.4	45.6	57.8	57.4	59.4	59.8	59.8	55.4	55.4	45.8	45.8
Sand treachers	156.4	156.4	154.4	131.8	131.6	154.4	156.4	134.2	134.2	158.3	158.3	133.9	133.9
<i>Cyprinodon</i>	72.6	72.6	68.6	65.6	63	68.6	70.4	65	65	73.8	73.8	67.7	67.7
<i>Pyrgulopsis</i>	425.4	425.4	412.6	348.2	381.4	412.6	412.8	383.4	383.4	427.3	427.3	350.1	350.1
<i>Rhaphiomidas</i>	217.8	217.8	225	199	209	225	223.2	209.6	209.6	212.1	212.1	198.6	198.6
<i>Trigonoscuta</i>	122	122	116.2	114.2	114.6	116.2	115.8	114	114	123.0	123.0	113.0	113.0
<i>Tryonia</i>	213	213	214	183.4	197	214	215.4	199	199	214.8	214.8	183.2	183.2
<i>Uma</i>	22.4	22.4	22.6	24.4	24.6	22.6	22.2	26.6	26.6	23.0	23.0	26.1	26.1
Relative model probability (AIC)													
<i>Assiminea</i>	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	47%	47%
Sand treachers	0%	0%	0%	40%	40%	0%	0%	11%	11%	0%	0%	13%	13%
<i>Cyprinodon</i>	0%	0%	3%	54%	54%	3%	1%	20%	20%	0%	0%	5%	5%
<i>Pyrgulopsis</i>	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	27%	27%
<i>Rhaphiomidas</i>	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	55%	55%
<i>Trigonoscuta</i>	0%	0%	7%	15%	15%	7%	8%	20%	20%	0%	0%	33%	33%
<i>Tryonia</i>	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	53%	53%
<i>Uma</i>	21%	21%	19%	7%	7%	19%	23%	3%	3%	16%	16%	3%	3%
AICc													
<i>Assiminea</i>	58.3	58.3	58.7	60.8	60.8	58.7	62.4	65.5	65.5	58.4	58.4	51.5	51.5
Sand treachers	157.0	157.0	155.0	132.8	132.8	155.0	157.6	136.3	136.3	159.5	159.5	136.0	136.0
<i>Cyprinodon</i>	73.2	73.2	69.2	64.3	64.3	69.2	71.7	67.2	67.2	75.1	75.1	69.9	69.9
<i>Pyrgulopsis</i>	425.5	425.5	412.7	381.7	381.7	412.7	413.1	383.8	383.8	427.6	427.6	350.6	350.6
<i>Rhaphiomidas</i>	218.3	218.3	225.5	210.1	210.1	225.5	224.3	211.5	211.5	213.2	213.2	200.5	200.5
<i>Trigonoscuta</i>	122.5	122.5	116.7	115.7	115.7	116.7	116.9	116.0	116.0	124.1	124.1	115.0	115.0
<i>Tryonia</i>	213.3	213.3	214.3	197.7	197.7	214.3	216.1	200.2	200.2	215.5	215.5	184.4	184.4
<i>Uma</i>	28.4	28.4	28.6	48.6	48.6	28.6	46.2	N/A	N/A	47.0	47.0	N/A	N/A

Table 2 Continued

Relative model probabilities (AICc)	DEC		DEC+J		DEC		DEC+J		DEC+x		DEC+x+J	
	unconstrained	adjacent-only	unconstrained	adjacent-only	unconstrained	adjacent-only	unconstrained	adjacent-only	unconstrained	adjacent-only	unconstrained	adjacent-only
<i>Assiminea</i>	1%	1%	80%	0%	1%	0%	0%	0%	1%	0%	18%	0%
<i>Sand treader</i>	0%	0%	40%	44%	0%	44%	0%	0%	0%	8%	9%	0%
<i>Cyprinodon</i>	1%	5%	16%	59%	5%	59%	1%	14%	0%	14%	4%	0%
<i>Pyrgulopsis</i>	0%	0%	74%	0%	0%	0%	0%	0%	0%	0%	26%	0%
<i>Rhaphiomidas</i>	0%	0%	55%	0%	0%	0%	0%	0%	0%	0%	45%	0%
<i>Trigonoscuta</i>	1%	11%	21%	17%	11%	17%	10%	15%	0%	15%	25%	0%
<i>Tryonia</i>	0%	0%	54%	0%	0%	0%	0%	0%	0%	0%	46%	0%
<i>Uma</i>	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

DISCUSSION

Statistical model comparison reveals that our study clades fall into three groups: (1) clades where the unconstrained DEC+J model overwhelmingly dominates (*Assiminea*, *Pyrgulopsis*, *Tryonia* and *Rhaphiomidas*), (2) clades with majority support for models that constrain dispersal to occur only between adjacent areas (*Trigonoscuta*, and *Cyprinodon* pupfish, Fig. 4) and (3) a clade with too few data to confidently prefer any model (*Uma*). If data were to be collected that allowed *Uma* to be broken into a series of localized, monophyletic populations, it is possible that a model including jump dispersal would be preferred, as *Uma* populations seem to have a biogeographical pattern similar to *Trigonoscuta* populations. However, such data are not available at present.

Leaving *Uma* aside, all of the clades show support for models that include founder-event speciation as a process. This support is either moderate (*Trigonoscuta*) or very strong (the rest). This confirms the results of Matzke (2014), which showed that founder-event speciation is important in oceanic island systems, and extends these results to habitat islands of the desert south-west.

The fact that the inferred dating of speciation and biogeographical events shows little correlation with ancient geological events (uplift of the Sierra Madre Occidental *c.* 34–15 Ma, or BLF *c.* 4.80 Ma, see Table 3) accords with the importance of founder-event speciation. If jump dispersal is the primary means by which allopatric speciation happens, there is not likely to be a strong geological correlation to such events. While major geological events are the easiest ones to detect in the rock record (e.g. tectonic, mountain uplift and major flooding events), and thus have played an important role as explanations in the vicariance biogeography tradition, our data show little support for the role of ancient geological events in the diversification of the desert biota under study. However, due to uncertainty in dating analyses the assessment of the three major geological hypotheses is put forward as a preliminary consideration. The biogeographical statistical model choice results presented here do not depend on the absolute dates, as none of the models employ time-stratified constraints.

The young ages and very strong support for the unconstrained DEC+J model in snail taxa may be an indication of the importance of bird-mediated dispersal. Other authors have hypothesized this for snails (Hershler & Liu, 2008), and there is some evidence for birds distributing snail larvae (van Leeuwen *et al.*, 2012). *Tryonia* have larvae that develop inside the snail female's genital tract (Hershler, 2001) unlike the other genera of snails in this study, and this may help explain why, with one exception, each species is confined to a single locality, a pattern which strongly favours DEC+J over DEC (Matzke, 2014). *Tryonia porrecta* is the only member of this genus that is parthenogenic, which may explain why this species has a relatively broad distribution (Hershler *et al.*, 2005). Mathematically, the low likelihood of the data under the constrained-dispersal matrix is due to the fact that

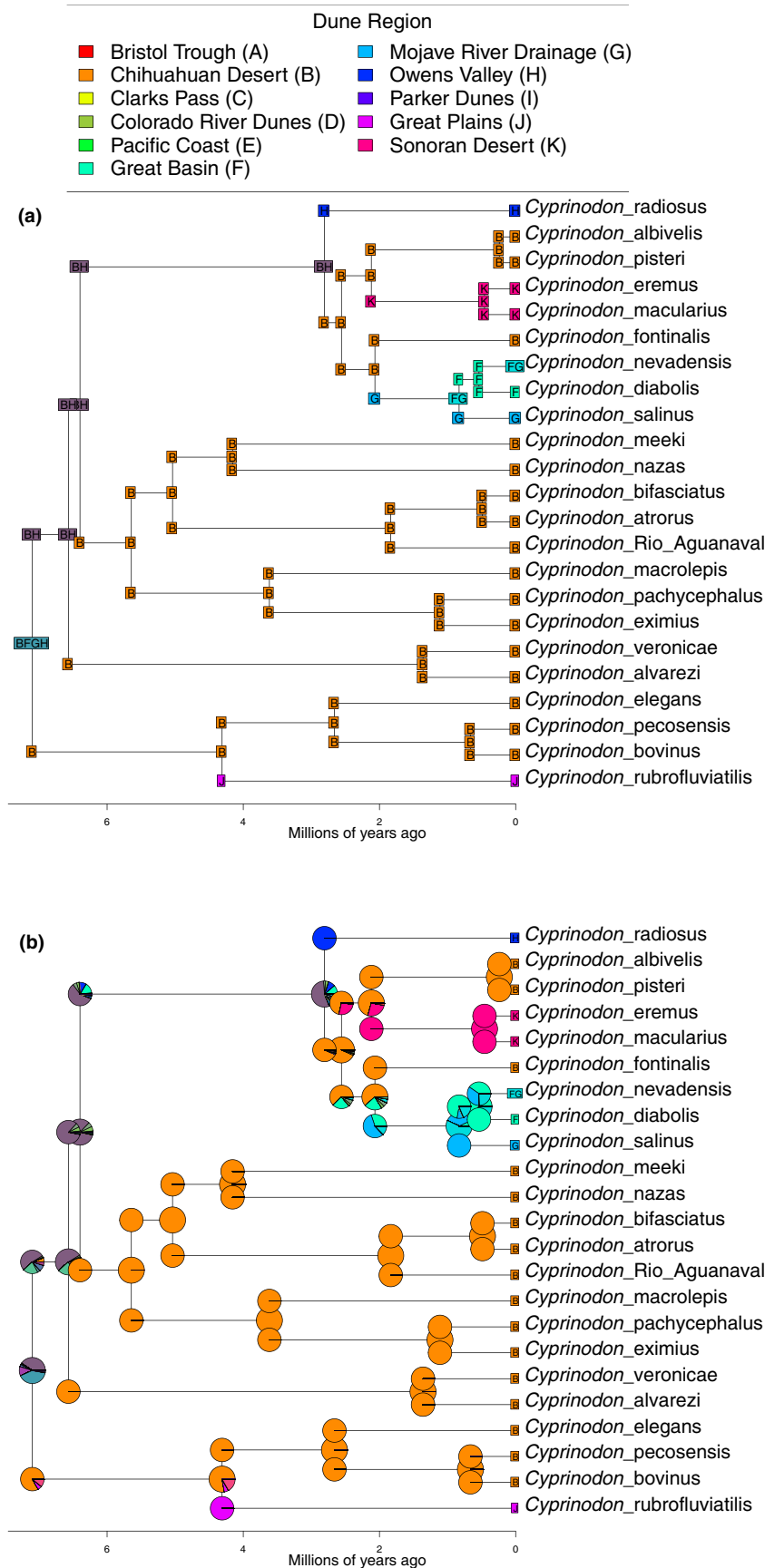


Figure 4 Ancestral state estimation for *Cyprinodon* pupfish in BioGeoBEARS, using the favoured DEC+J model, with connectivity constraints. (a) Plot of the single-most-probable state (geographical range) at each node (just before speciation) and post-split (just after speciation). (b) Pie charts represent the probabilities of each possible geographical range just before and after each speciation event.

Table 3 Assessment of whether or not any dated biogeographical events match well with geological hypotheses. Columns list taxa, habitat type and hypothesized geological events. The geological hypotheses were tested by seeing if speciation events occurred between specific areas, hypothesized to be influenced by the geology, during the time frame of the event. If estimated dates were consistent with one of the geological hypotheses, the nodes and their ages are listed. If the expected biogeographical pattern between areas was not seen, then 'no speciation between areas' is indicated. If the biogeographical pattern matched, but speciation did not occur in the correct time frame, then 'no speciation between areas during time period' is indicated.

Taxa	Habitat type	Sierra Madre Occidental uplift [c. 34–15 Ma Sonoran-Chihuahuan Deserts (areas K and B) (median, 95% credible interval)]	Bouse Lakes formation [4.83–4.80 Ma East and West sides of the lower Colorado River (areas I and A,C,D) (median, 95% credible interval)]	2.58 Ma Quaternary glaciation sand transport river corridors [(speciation between adjacent areas and within area between adjacent dunes/springs) (median, 95% credible interval)]
<i>Rhaphionidas</i>	Dune	<i>R. episcopus</i> and <i>R. pachyrhynchus</i> (12.3, 4.0–22.8) <i>R. xanthos</i> and <i>R. painteri</i> (12.8, 6.3–22.6) No speciation between areas	No speciation between areas	No speciation between areas during time period
Sand treaders	Dune	No speciation between areas	No speciation between areas	<i>M. sp.</i> Ibez Dunes and <i>M. sp.</i> Dumont Dunes (2.5, 0.9–3.9); <i>A. sp.</i> Cadiz/Rice Dunes and <i>A. sp.</i> Palen Dunes (2.9, 1.7–4.6) <i>T. sp.</i> Ludlow Dunes and <i>T. sp.</i> Rice Dunes group (0.9, 0.5–1.6) <i>U. inornata</i> and <i>U. notata</i> (0.5, 0.2–0.7)
<i>Trigonoscuta</i>	Dune	No speciation between areas	No speciation between areas during time period	
<i>Uma</i>	Dune	<i>U. scoparia</i> , <i>U. notata</i> , <i>U. inornata</i> and <i>U. exsul</i> , <i>U. paraphygas</i> (14.7, 7.6–22.4) No speciation between areas during time period	No speciation between areas	<i>C. albivolis</i> and <i>C. pisteri</i> (0.2, 0.1–0.4); <i>C. eremus</i> and <i>C. macularius</i> (0.5, 0.2–0.8); <i>C. salinus</i> and <i>C. nevadensis</i> , <i>C. diabolis</i> (0.8, 0.5–1.2); <i>C. nevadensis</i> and <i>C. diabolis</i> (0.5, 0.3–0.7); <i>C. radiosus</i> and rest of Western pupfish clade (2.8, 1.9–3.7); <i>C. sp.</i> Rio Aguanava and <i>C. bifasciatus</i> , <i>C. atrorius</i> (1.8, 1.1–2.6); <i>C. pachycephalus</i> and <i>C. eximius</i> (0.4, 0.2–0.6); <i>C. elegans</i> and <i>C. pecosensis</i> , <i>C. bovinus</i> (2.7, 1.8–3.6); <i>C. pecosensis</i> and <i>C. bovinus</i> (0.7, 0.4–1.0) Many (45 speciation events between adjacent or within areas) <i>A. cienegensis</i> and <i>A. pecos</i> (0.3, 0.005–1.9); <i>A. sp.</i> 20A and <i>A. infima</i> clade (0.3, 0.005–1.4); <i>A. infima</i> and <i>A. sp.</i> A25B Inyo clade (0.1, 0.003–0.8); <i>A. sp.</i> A25B and <i>A. sp.</i> 27A clade (0.08, 0.002–0.5); <i>A. sp.</i> 30B and <i>A. sp.</i> 26A clade (0.1, 0.002–0.6) Many (20 speciation events between adjacent or within areas)
<i>Cyprinodon</i>	Aquatic			
<i>Pyrgulopsis</i>	Aquatic	No speciation between areas during time period	No speciation between areas	
<i>Assimineae</i>	Aquatic	No speciation between areas	No speciation between areas	
<i>Tryonia</i>	Aquatic	No speciation between areas during time period	No speciation between areas	

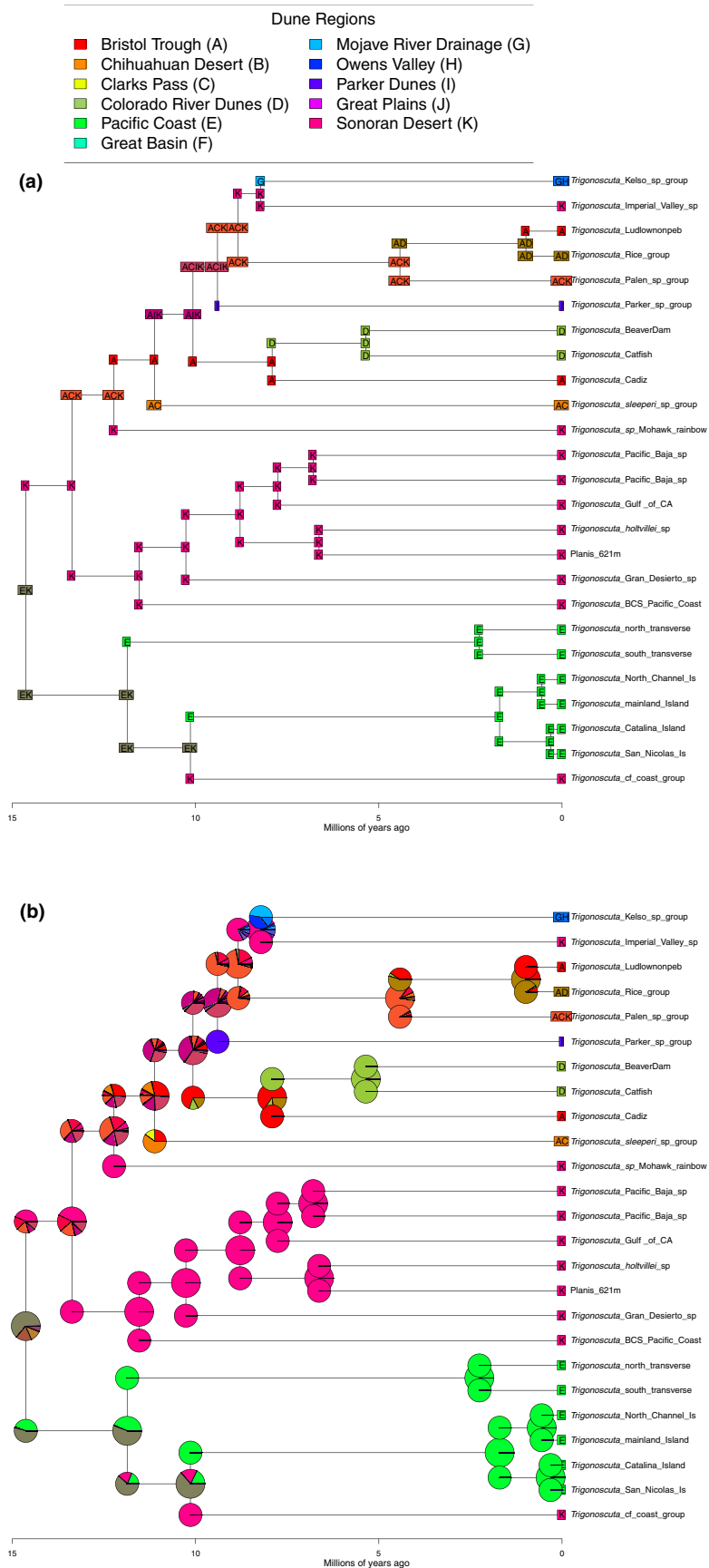


Figure 5 Ancestral state estimation for *Trigonoscute* weevils in BioGeoBEARS, using the favoured DEC+X+J model with no connectivity constraints. (a) Plot of the single-most-probable state (geographical range) at each node (just before speciation) and post-split (just after speciation). (b) Pie charts represent the probabilities of each possible geographical range just before and after each speciation event.

snail clades often have sister taxa in areas that are not allowed in the connectivity matrix, such as between the Mojave River Drainage and Sonoran Desert. *Pyrgulopsis* also has several sister taxa with distributions not allowed by the connectivity matrix. The fact that *Rhaphiomidas* flies are also well fit by unconstrained DEC+J suggests that dispersal through flight is also important in this group.

In the case of *Cyprinodon* (pupfish), models including the constrained-dispersal matrix gathered 79% of the total probability based on AICc weights, with the DEC+J constrained model having 59% probability. This finding is consistent with hypothesized riverine transport between areas. The strong support for DEC+J as opposed to DEC in the constrained models suggests that while new populations were founded by dispersal during periods of river connectivity, these were nevertheless rare events correlated with cladogenesis. It must be admitted, however, that the vicariance model available in DEC (and thus DEC+J) is actually a quite crude equal-weights model, and thus does not include anything increasing the probability of vicariance events after a widespread habitat has been broken up; thus future, more sophisticated probabilistic models of vicariance might yield stronger statistical support for vicariance in *Cyprinodon*.

Cyprinodon and *Trigonoscutea* species occupy Death Valley and other northern extensions of the Mojave River Drainage Basin, and they share pattern and timing in these basins. Both taxa seem to have undergone local dispersal in the Mojave River Basin during the Pleistocene, with long periods of isolation indicated by deeper nodes. In addition, *Trigonoscutea* was the only lineage where the DEC+J+x model was one of the best-fitting models (Fig. 5). This is likely due to their poor dispersal ability (flightless with small slow moving legs), which is reflected in biogeographical distributions where close phylogenetic relatives tend to occupy nearby geographical areas. The fact that *Cyprinodon* shows little support for a distance effect might indicate that rare, stochastic events – perhaps major floods – were the main avenue of dispersal, rather than slow, progressive colonization of a series of intermediate locations.

It seems highly probable that dispersal probability and distance must be correlated to some extent in historical biogeography, so we were surprised that distance-based models were often not supported in our study groups. There are several possible explanations for this. Firstly, it might be the case that distances may be too small to be a strong predictor of dispersal in this sub-continental study region. Secondly, connectivity of sandy washes during or after flooding may be more important in some study groups, at which point distance becomes irrelevant. Thirdly, it is possible that the heterogeneous nature of the intervening habitat plays a large role in blocking dispersal, for example, mountain ranges preventing dispersal even over short linear distances.

Extinction could be a partial explanation for some of the observed disjunct distributions. However, this is very difficult to test, due to the limitations of the fossil record for most of

these taxa. Extinction is a possible explanation particularly in *Cyprinodon*, for example, if intermediate populations existed between the Sonoran Desert and Owens Valley, became extinct when ancient drainages such as those hypothesized to link the Bristol Trough to the Colorado River dried up (Crews & Gillespie, 2014), then extinction could help to explain some of the disjunct distributions in this group.

CONCLUSIONS

Our results demonstrate that constructing new biogeographical models, and assessing their fit to the geographical range data of different clades, can give insight into the biogeographical processes that are important in each group, and also what life history traits may be influencing these distributions. Statistical model choice tools also indicate when certain predictors are not useful. In the case of these data and models, the x parameter was rarely useful. This may be due to the design of the study, which was focused on testing previously popular hypotheses for desert biogeography, based on vicariance concepts, and was also focused within one region of a continent. Distance is extremely likely to be an important factor influencing dispersal probability, at least at the coarsest geographical scales (dispersal between continents and between remote oceanic islands). We believe that this method has broad applicability to many biogeographical regions other than just islands or habitat islands. For example, defining biogeographical regions on a contiguous landscape often results in adjacent areas touching each other in geographical space. Here, researchers could use various metrics for environmental distance between regions, and test which have the strongest explanatory value.

Two main conclusions can be drawn from this study. First, the construction of spatially explicit models of connectivity and distance is feasible using GIS, and the usefulness of these models can be assessed with likelihood-based statistics. This strategy is less problematic than past efforts which used subjectively chosen dispersal rate modifiers to represent these factors, which are then fixed in subsequent analysis, although at the time it was the best option available (Clayton *et al.*, 2009; Condamine *et al.*, 2013). Second, there is some biogeographical evidence supporting the sand/river transport pathways for flightless dune taxa and the desert pupfish. The other, more vagile taxa largely disperse through founder-event speciation, with sand dune and aquatic habitats in the deserts playing a role similar to oceanic islands.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 (1) Maps of sampling locations and dunes (2) standard molecular lab procedures used for extraction, PCR, sequencing, alignment and a table of primers used; (3) references for sequences derived from Genbank of non-insect taxa; (4) dispersal constraint matrices and BioGeoBEARS results table; (5) results of BEAST analyses.

DATA ACCESSIBILITY

The outputs of all BioGeoBEARS analyses make for a massive PDF (> 100 pages) not suitable for Supporting Information. However, as the details of the range data and ancestral range inferences may be of interest to some, we have permanently uploaded the PDF to figshare: <http://figshare.com/s/53e25a28691511e5b8e906ec4bbcf141>

BIOSKETCHES

Matthew H. Van Dam is interested in interaction of geological processes and natural history of an organism shaping its biogeographical pattern; he is also interested in weevil systematics.

Nicholas J. Matzke is a Discovery Early Career Research Award (DECRA) Fellow at The Australian National University, in the lab of Craig Moritz. He works on likelihood and Bayesian methods in biogeography. He is also the author of the R package BioGeoBEARS.

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