SPATIAL CONNECTIVITY THROUGH MOUNTAINS AND DESERTS DROVE SOUTH AMERICAN SCORPIONS' DISPERSAL

Jeison M. Barraza[1,2,3], Jorge Avaria-Llautureo[4]✉ & Marcelo M. Rivadeneira[3,5]

1. Doctorado en Ciencias Biológicas. Universidad de La Serena, Chile.
2. Departamento de Biología, Universidad del Atlántico, Puerto Colombia, Colombia.
3. Centro de Estudios Avanzados en Zonas Áridas, CEAZA, Coquimbo, Chile.
4. School of Biological Sciences, University of Reading, UK.
5. Departamento de Biología Marina, Universidad Católica del Norte, Chile.
✉ Corresponding author: j.l.avaria@reading.ac.uk

Abstract

We inferred the geographic dispersal routes and the environmental conditions that shaped the ~30-million-years historical biogeography of *Brachistosternus* scorpions in South America. We evaluated the role that altitude and aridity had on the geographic distance that each species dispersed from the location of the genus common ancestor. Based on previous studies, we evaluated the hypothesis postulating that the species' geographic expansion was promoted by arid conditions in higher altitudes.

To test the hypothesis, we integrated two methodological approaches, the phylogenetic Geographical model and the Conductance model. The Geo model infers the locations of ancestral species in a phylogenetic tree, assuming a spherical space and using samples of georeferenced locations for every species as input data. It allows us to estimate the historical species dispersal routes and distances from the location of the genus common ancestor. The Conductance model is based on circuit theory and infers the geographic routes and distance of least resistance between two points, i.e., an origin and destination. We defined the origin as the location of the genus common ancestor obtained from the Geo model and the destination point as the current geographic location of each species. This model infers the geographic routes with the least cost of resistant for dispersal in a landscape of varying altitude and aridity. Finally, we evaluated the correlation between the two dispersal distances each species has moved from the location of the common ancestor, i.e., the distance inferred from the Geo model and from the Conductance model.

The Geo model shows that *Brachistosternus's* geographical origin was most likely along the coast of south Peru, and central Chile. From this location, extant species dispersed through routes ranging from 873 to 2,800 km on average. The Conductance model that considers the routes with less resistance to elevation and aridity simulated dispersal distances that are highly correlated with the species dispersal distances obtained from the Geo model. We revealed the geographic dispersal routes, with the least resistance to the pressures imposed by changes in altitude and aridity, that 55 species of scorpions have probably followed in the last 30 million years in South America. These geographic routes that went along the Andean Mountains and the arid zones of South America shaped the current spatial distribution radiation of the genus *Brachistosternus*.

Keywords. Aridity, Species Dispersal, Niche Conservatism, Niche Evolution, Geographic Speciation.

Introduction

The geographic distribution of taxa at wide geographic scales is mainly the product of the species geographic movement from the deep-time location of the common ancestor, and the environmental conditions that stimulate or prevent species from dispersing (Caplat et al., 2016; Lester et al., 2007; McDowall, 2004; Santini et al., 2013). In this sense, the present-day distribution of clades can be seen as the product of dispersal ability and the environmental conditions that work as filters on dispersal (Clobert et al., 2009).

Species with low dispersal ability have few opportunities to colonize new places as they cannot extend their range across geographic barriers or harsh environmental conditions (Lester et al., 2007), so global environmental change mediates any change in their local environment (Hulme, 2005). On the other hand, species with high dispersal ability may easily cross geographic barriers and expand their ranges across suitable habitats (species environmental tracking and niche conservatism) or colonize and adapt to places with new environmental conditions (species niche evolution) (Claramunt et al., 2012; Clobert et al., 2004; Kennedy et al., 2018; Straus et al., 2022; Weeks & Claramunt, 2014). Therefore, the present-day geographic distribution of a clade is determined by the geographical origin, dispersal ability, and the environmental selective forces that subsequently act on dispersal ability (Cardillo et al., 2005; Ricklefs, 2006; Sekar, 2012; Weir & Schluter, 2007; Wiens & Donoghue, 2004).

Current methods for reconstructing dispersal routes across wide geographic and temporal scales are mainly based on phylogenetic and conductance models. On one hand, phylogenetic models estimate species ancestral areas and dispersal paths (Ceccarelli et al., 2016; Hackel & Sanmartín, 2021; Sanmartín, 2012). While some methods are based on a discrete categorization of species distribution and their inference into the past (Matzke, 2013), a recent approach, named the Geographical (Geo) model, infers ancestral locations in a three-dimensional space, using georeferenced occurrences combined with phylogenetic trees, creating a much more detailed picture of the ancestral places of origin and geographic dispersal routes (Avaria-Llautureo et al., 2021; 2024; O'Donovan et al., 2018).

On the other hand, Conductance or resistivity models identify the paths with the lowest cost distance among all possible paths linking predefined origins and destinations of species (Etherington, 2016). Conductance models are based on circuit theory and rely on a landscape raster representation commonly known as resistance surface, which usually consists of known or assumed environmental variables that affect species movement (van Etten & Hijmans, 2010). The values of this layer indicate the resistance or difficulty imposed by environmental components on the movement of individuals to predict movement routes (Diniz et al., 2020; Etherington, 2016; Zeller et al., 2012). Phylogenetic and Conductance models rely on different approaches and assumptions. Conductance models ignore ancestral-descendent relationships among species or the history of the landscape, and phylogenetic models are agnostic to landscape heterogeneity. Therefore, the integration of both methods can shed light on the importance of landscape or environmental conditions shaping the historical dispersal and geographic expansion of clades.

South America is an ideal study model to put these ideas to the test. It has undergone significant paleogeographic and paleoclimatic changes during the Cenozoic, including the onset of the Amazonian forests, the uplift of the Andes, the hyper-aridification of the Atacama Desert, and the expansion of open habitats (Almeida et al., 2012; Antoine et al., 2013; Dunai et al., 2005; Hartley, 2003; Hartley et al., 2005; Simon et al., 2009; Veizer & Prokoph, 2015; Zachos et al., 2001). Remarkably, the gradual aridification of South America that began in the late Cretaceous (Garreaud et al., 2010; Hartley et al., 2005) may have played an essential role in shaping species' distribution. Historical aridification could have imposed ecological limitations on dispersal in these bands of high aridity, which encompass *ca.* 1000 km across South America (Abraham et al., 2020; Luebert, 2021; Magalhaes et al., 2019; Roig-Juñent et al., 2006).

Scorpions are a good study model for biogeographical analysis on large spatial and temporal scales because they have adapted to many arid environments by conserving water for an extended period (Ceccarelli et al., 2016; Cloudsley-Thompson, 1975; Lourenço, 1994; Ojanguren-Affilastro et al., 2016; Ojanguren-Affilastro, 2005; Selmane & L'hadj, 2014). In South America, one of the most diverse and abundant clades of scorpions is the genus *Brachistosternus* Pocock, 1893, which is endemic to the region (Ojanguren-Affilastro et al., 2016; Ojanguren-Affilastro et al., 2018). Currently, these species are distributed mainly in the Andean region and the arid zones of the south and east of the continent from extreme southern Patagonia to Ecuador, being exceptionally diverse in the coastal deserts in Chile and Peru (Ochoa, 2002; Ochoa & Ojanguren-

Affilastro, 2007; Ojanguren-Affilastro, 2002; Ojanguren-Affilastro, 2005; Ojanguren-Affilastro, 2007) and at high altitudes in the Andes, up to 4500 m (Ceccarelli et al., 2016; Ochoa & Acosta, 2002; Ojanguren-Affilastro, 2003; Ojanguren-Affilastro & Mattoni, 2006). The last biogeographic study of the genus (Ceccarelli et al., 2016) estimated the location for the most recent common ancestor (MRCA) in the area presently corresponding to the Puna and Coquimbo provinces. It was also suggested that the ancestral location was much lower in altitude, at least 4 km lower in elevation, and probably closer to the coast (Canavan et al., 2014). The study also revealed that the historical process of Andean uplift had a crucial role in accelerating the speciation rates of the Andean clade. It was also suggested that the increase in the diversity of the South American Bothriuridae family and, therefore, of the genus *Brachistosternus*, occurred after the aridification of South America (Ceccarelli et al., 2016; Prendini, 2003). However, it is still unknown how and to what extent the environmental change associated to the Andes uplift and the aridification of South America were associated to the historical geographic expansion of the genus.

In this study, we used the Geo model and Conductance model to infer both the dispersal routes and distances for each species available in the most recent phylogeny of the genus, and the most likely environmental conditions associated to such routes and distances in South America. Specifically, we used the Geo model to infer ancestral species locations in the phylogeny, and we estimated the dispersal routes and distances of all extant species from the MRCA location. Then, using the location of the MRCA as starting point, and the location of extant species as destination points, we estimated the routes and distances with lower cost for dispersal, using Conductance models that considers the independent and combined effect of present-day altitude and aridity as resistance variables to dispersal. We expect to observe a positive correlation between the Geo model dispersal distance and the dispersal distances obtained from the Conductance model that considers the combined effect of altitude and aridity because these are the two geographic and environmental conditions considered to be relevant factors in the radiation of the genus (Ojanguren-Affilastro et al., 2016; Ojanguren-Affilastro, 2005; Ojanguren-Affilastro et al., 2018).

Methods

Study model: The genus *Brachistosternus* currently contains 55 species (Ojanguren-Affilastro et al., 2016; Ojanguren-Affilastro et al., 2023; Ojanguren-Affilastro et al., 2018). They are usually the dominant taxa of scorpions in the areas where they are found (Agusto et al., 2006; Mongiardino-Koch et al., 2017; Nime et al., 2014). Regarding their natural history, the origin of the MRCA has been estimated at *c.* 30 Ma in the Puna and Coquimbo provinces, which include the central Andean Mountains and the central Chile region, respectively. The environmental setting of those locations is predicted to be arid in the past (Ceccarelli et al., 2016), consistent with the origin of the oldest arid regions of western South America (Amundson et al., 2012).

It is important to consider that we are working with all the species that have phylogenetic information to date. We are using the phylogeny that have molecular data provided by Ojanguren et al., (2016), and Ceccarelli et al,. (2016) (with minor posterior taxonomical changes on some species). We are not working with the whole species belonging to the known genus as there remain many species to be discovered and identified.

Occurrence data compilation. We collected all available geographic coordinates, measured in degrees of latitude and longitude, for 55 species of *Brachistosternus*. We searched various sources of information, which include (1) Global Biodiversity Information Facility (GBIF) (Chamberlain et al., 2022), (2) Coleção de História Natural da UFPI - Universidade Federal do Piauí (CHNUFPI), and (3) coordinates extracted in scientific articles about the taxonomy, systematics, and ecological aspects of *Brachistosternus* species.

Data filters. We compiled all geographic information in a single database. Nevertheless, a central challenge to using publicly available species occurrence data in research is problematic geographic coordinates, which are either erroneous or unfit for analyses (Anderson et al., 2016). Problems mainly arise because data aggregators such as GBIF integrate records collected with different methodologies in different places at other times, often without centralized curation and only rudimentary meta-data (Zizka et al., 2020). In addition, problematic coordinates caused by data-entry errors or automated georeferencing from vague locality descriptions are common (Maldonado et al., 2015; Yesson et al., 2007) and produce recurrent problems such as records of terrestrial species in the sea, records with coordinates assigned to the centroids of political entities, and others (Zizka et al., 2020; Zizka et al., 2019). To deal with these issues, we followed the cleaning pipeline outlined in (Führding-Potschkat et al., 2022; Ribeiro et al., 2022; Zizka et al., 2020; Zizka et al., 2019).

During clean and error removal, we focused on spatial mistakes, such as coordinates in the sea and coordinates containing only zeros, duplicated records, equal longitude, and latitude, among others. We used the R package *CoordinateCleaner* v2.0-20 (Zizka et al., 2019) and Biodiversity Data Cleaning "bdc" (Ribeiro et al., 2022) for this cleaning and filtering processes (Appendix S1, Table S1). Then we proceeded to perform additional data filtering according to (Ojanguren-Affilastro et al., 2016); in their species delimitation analysis where some current species of the genus decreased their geographic range (*Brachistosternus angustimanus, B. kamanchaca, B. montanus, B. intermedius, B. pentheri, B. roigalsinai, B. ehrenbergii and B. weijenberghii*). In this case, we perform a second filtering directly on the database to avoid increasing this species' distribution range and coordinates. After cleaning and filtering the species occurrence data, we obtained 290 georeferenced records for 55 *Brachistosternus* species (Appendix S1, Table S2). The number of records for each species ranges from one coordinate in *B. simoneae* to 28 coordinates in *B. ferrugineus*. Therefore, this allows us to have a representation of the geographical range of most species.

Occurrence data from published literature only. To evaluate any potential remaining errors in our compiled geographic database, we used the occurrences available in Ceccarelli et. al., (2016). This database contains the geographic locations of sampled individuals for which the authors extracted molecular data to infer the phylogeny of the genus. We re-ran all the analyses using this geographic database.

Phylogenetic tree. We used a maximum clade credibility (MCC) time-calibrated phylogeny for 55 species (Ceccarelli et al., 2016) that is available as Appendix S2 TreeS1. We named two undescribed species based on a recent study and personal communication with experts on the group's taxonomy (Ojanguren-Affilastro et al. 2023). The named species are the following: *B. sp1* as *B anandrovestigia* and *B. sp6* as *B. misti*. We also rename the species *B. montanus N* as *B. diaguita,* given the study of Ojanguren-Affilastro et al. (2023).

Geographic model. From the compiled geographic database for every *Brachistosternus* species, the posterior distribution of geographical coordinates was inferred across internal phylogenetic nodes. We used the Geographic (Geo) model (O'Donovan et al., 2018) in BayesTraits v4.0 (Meade & Pagel, 2019) to infer geographic location across phylogenetic nodes which represent the ancestral species of the genus and also the speciation events.

The Geo model estimates the posterior distribution of ancestral locations measured in longitude and latitude while sampling all location data (sample of data) within extant species according to their probability. The Geo model considers the spherical nature of the Earth by transforming geographic data into three-dimensional (x, y, and z) coordinates. This natural assumption of the Earth as a spherical object prevents miscalculation of distances between inferred ancestral locations due to the non-continuity of the longitudinal scale (O'Donovan et al., 2018).

We ran three MCMC chains for 500,000,000 iterations, sampled every 100,000, and discarded 400,000,000 as burn-in. These procedures were performed based on the Brownian Motion (BM) model and the Variable Rate (VR) model to test the statistical null hypothesis that species dispersed at constant speed (geographic distance per time unit). The VR model allows the inference of variable speed of species movement without knowing in advance where and when those variations occur in the tree (Venditti et al. 2011). The Geo model output included 1,000 posterior locations for each phylogenetic node. The model that best fits the data (BM vs. VR) was selected using Bayes factors (BF), using the marginal likelihoods estimated by stepping-stone sampling. BF was calculated as double the difference between the log marginal likelihood of the complex and simple models. By convention, BF > 2 indicates positive support for the complex model, BF = 5–10 indicates strong support, and BF > 10 is considered solid support (Meade & Pagel, 2019; Raftery, 1996).

Estimating species dispersal distance from the Geo model. To measure the dispersal distance that each extant species in the phylogeny traveled from the location of the genus MRCA, i.e., the Pathwise Distance, we calculated the sum of the distances across all branches – i.e., the branchwise distance - that link the MRCA with each extant species. Each branchwise distance represents the geographic distance between two phylogenetic nodes. The branchwise distances were calculated using the distCosine function in the R package *geosphere* (Hijmans, 2019). The *distCosine* function brings the great circle distance, i.e., shortest distance between two points assuming a spherical space. The distances were calculated according to the law of the cosines, and the method works at both large and small scales (O'Donovan et al., 2018). Therefore, the Pathwise Distance represents the geographic distances of the shortest routes that each extant species has dispersed from the location of the MRCA. Finally, we calculated the branchwise distances and Pathwise Distance using each node geographic centroid across a sample of 100 phylogenetic trees. We also estimated the branchwise distances and Pathwise Distance from each of 100 posterior node-coordinates obtained from a Geo analysis using the MCC tree.

Conductance Models. We constructed the models based on the assumption that animals' ability to disperse successfully varies by landscape features and that this can be modeled as the least-cost of movement across a resistant surface (Diniz et al., 2020; van Etten & Hijmans, 2010). We built three conductance models. The first includes the effect of altitude (Conductance Altitude), the second includes the effect of aridity (Conductance Aridity), and the third one consists of the combined effect of altitude and aridity (Conductance Altitude + Aridity). Raster climatic layers of aridity and altitude were obtained from the library *geodata* in R (Hijmans et al., 2023) at a 0.5º spatial resolution. These raster layers were converted to transition matrices using the reciprocal mean values of 16 possible directors around the focal cell, with a geographic correction, using the library *gdistance* v1.6.4 in R (van Etter 2017).

Estimating species dispersal distance from the Conductance model. For each Conductance model, we estimated the least-cost route-distance between the location of the MRCA estimated with the Geo model, and the location of the present-day distribution of each species. This is the Conductance Distance, i.e., the predicted distance each species has dispersed from the location of the MRCA, through the landscape of less environmental resistance. It is important to note that the Conductance Distance does not consider the location of the ancestral species in the phylogenetic as the Pathwise Distance (obtained from the Geo model analysis) does. To obtain a location the location for the MRCA, we used the geographic centroid from the posterior coordinates inferred with the Geo model. We obtained the MRCA-centroid from each of the 100 phylogenetic trees. To select a representative coordinate for each extant species, we used the coordinate that was sampled with highest probability in the Geo model analyses, in each of the 100 phylogenetic trees. Therefore, we obtained 100 locations for the MRCA and 100 locations for each extant species. As these data is obtained from the Bayesian sample of 100 dated phylogenetic trees, we are considering the phylogenetic uncertainty, in terms of topology and divergence time, and the location uncertainty for the MRCA and extant species, on our estimation of the Conductance Distance.

We also added a shortest distance model (Conductance Euclidian) that does not consider any landscape heterogeneity, so dispersal distances are calculated as simple linear geographic distances, between the location of the MRCA and the location of the present-day distribution, using the *distance* function in the library *terra*, in R (Hijmans, 2023).

Finally, we estimated the Conductance Distance for all conductance models from the Geo model analysis based on the single MCC tree. In this analysis, we estimated the geographic distance from each of the 100 coordinates that represent the posterior distribution of coordinates inferred for the MRCA. This is an additional approach to consider the uncertainty associated with the inference for the location of the MRCA when calculating the Conductance Distance.

C**orrelation between the Pathwise and Conductance Distance.** We evaluated the correlation between the Pathwise Distance obtained from the Geo model and the Conductance Distance using the Pearson correlation coefficient. We evaluated the correlations considering all the geographic distances obtained from each of the 100 phylogenetic trees so that we integrate the phylogenetic uncertainty associated with topology and divergence times. We also evaluated the correlations between the geographic distances obtained from each of the 100 coordinates in the posterior distribution (i.e., from the analysis on the MCC tree). Finally, we evaluated the correlation between the distances obtained from a phylogenetic tree at the specimen level so we can avoid any potential bias associated with the species delimitation process (see below).

Phylogenetic uncertainty. We evaluated whether our main results were affected by multiple aspects of uncertainty associated to the time-calibrated phylogeny of 55 species.

First, we evaluate the uncertainty associated to both the topology and the divergence times in the time-calibrated phylogeny of 55 species. For this, we obtained a sample of 100 time-calibrated phylogenetic trees for the 55 species (Appendix S2 TreeS2). The sample of trees was estimated and provided by Dr. Ceccarelli. We ran the Geo model on each of the 100 trees to estimate species ancestral locations and the Pathwise Distance. Then, we estimated the Conductance Distance from all the conductance models, using the location for the MRCA (geographic centroid) obtained from each of the 100 Geo model analyses as starting points. The destination points for the conductance models were those coordinates sampled with highest frequency in the Geo model analyses across each of the 100 trees.

Second, we evaluated the potential effect of the uncertainty associated with the species delimitation in the time-calibrated phylogeny of 55 species. For this, we used the MCC tree obtained from a Bayesian sample of trees at the individual (specimen) level (Appendix S2 TreeS3). This sample of trees was estimated and provided by Ceccarelli et al. (2016) and contains 120 individuals of *Brachistosternus*. We run the Geo model on the MCC tree using the coordinates of the sampled individuals, available in Ceccarelli et al. (2016), to estimate ancestral locations and the Pathwise Distance. Then, we estimated the Conductance Distance from all the Conductance models, using the location for the MRCA from each coordinate in the posterior distribution of 100 longitudes and latitudes.

Results

The BF comparison support the VR model over the BM model in the Geo model analyses, using the 55 species tree and the compiled occurrence database (BF > 10). This means that ancestral species of *Brachistosternus* dispersed at variable speeds in South America. The mean species Pathwise Distance, obtained from the sample of trees, shows that species dispersed through routes ranging from 873 km (*B. peruvianus*) to 2,807 km (*B. paulae*) (Appendix S1 Table S3). This variability in species dispersal speeds and distances suggests that the changing environmental conditions over time and across space played an essential role in shaping the current geographic distribution of the genus in South America.

Based on the Geo model with variable dispersal speed and the tree with 55 species, the highest posterior density for the geographic distribution of the MRCA of *Brachistosternus* is across the coast of central Chile and the central Andean Mountain of southern Peru, from ~13 to 31 ºS. There is a gap in the distribution, around 20 ºS, identified by a lower density of the posterior distribution of coordinates (Fig. 1).

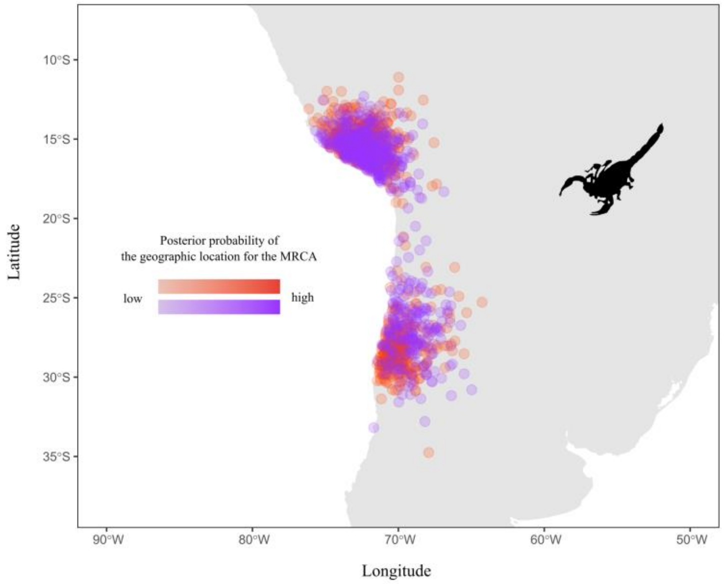

Figure 1. Location for *Brachistosternus* common ancestor estimated from two phylogenetic trees. The most recent common ancestor of *Brachistosternus* (MRCA) was mainly distributed within the arid regions of South America. Specifically, along the central Andean Mountain of southern Peru and central Chile. Red dots: posterior distribution of inferred coordinates using the tree with 55 species. Purple dots: posterior distribution of coordinates using the tree with 120 specimens.

Additionally, most of the internal phylogenetic nodes that represent the ancestral species in the phylogenetic tree of *Brachistosternus* were located along the Andean Mountain and the arid zones of South America, as the highest density of the posterior distribution of coordinates is spread across the Andean Mountain (Fig. 2).

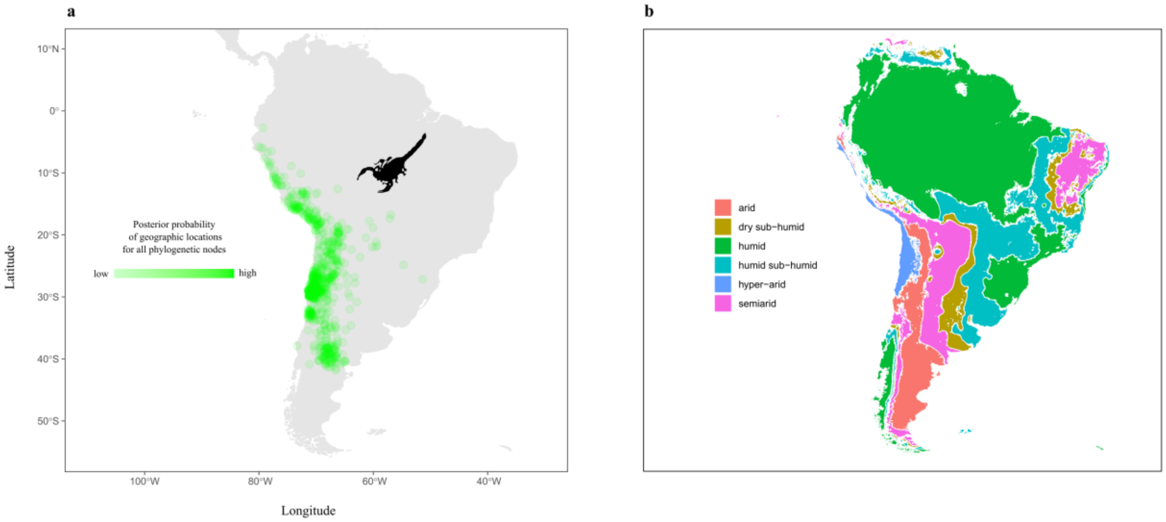

Figure 2. Most of the phylogenetic internal nodes were located along the central Andes and the current arid zones of South America. a: As internal nodes in a phylogenetic tree represent the ancestral species and speciation events of a clade, our results support the idea that the ancestral species of *Brachistosternus* were dispersing and speciating mainly along the Central Andes and the arid zones of South America. Green dots: posterior geographic inferred across the 54 internal nodes of the tree with 55 species. b: Current South American climatic regions.

Conductance models predicted a wide range of Conductance Distances for the genus. The Euclidian conductance model, without environmental restrictions, showed the lowest median value (1,135 km). In contrast, the Conductance Elevation and Conductance Aridity models yielded much longer median distances (>200,000 km). The Geo model and the Conductance Altitude + Aridity models showed intermediate median distances (1,722 and 3,038 km, respectively) (Fig. 3).

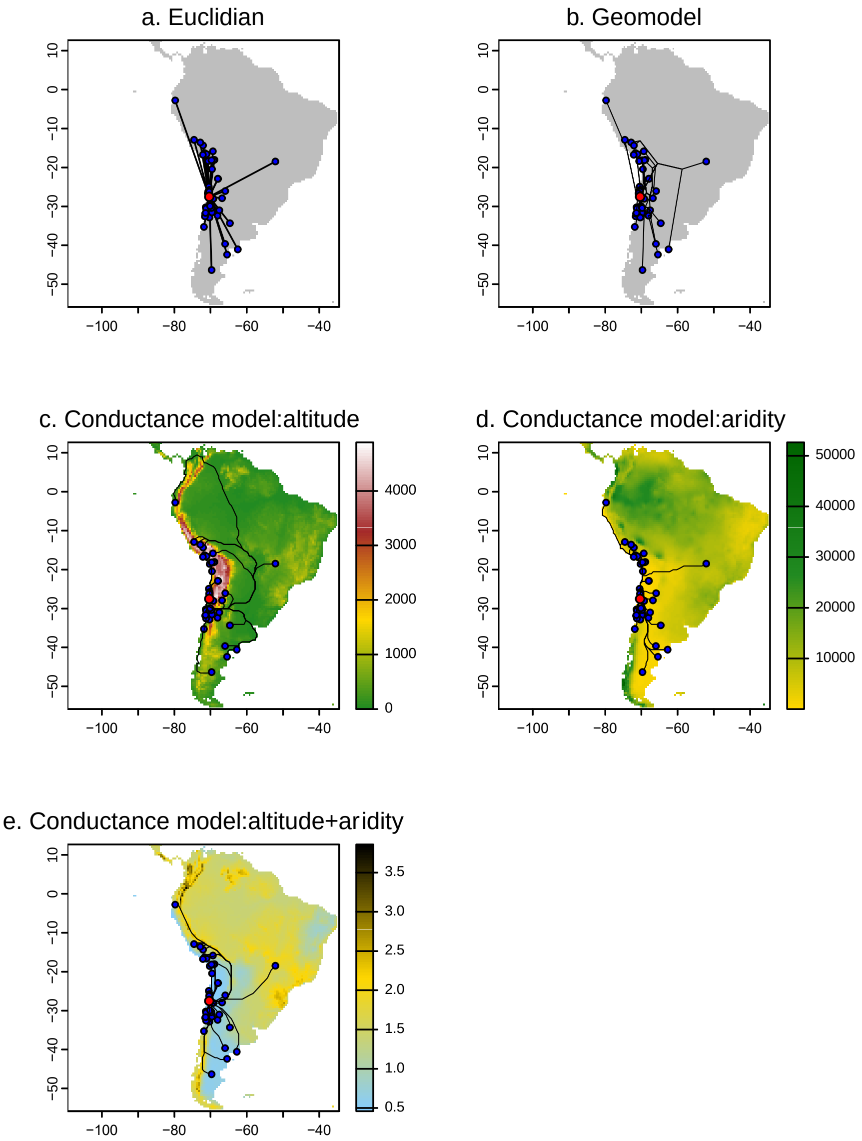

Figure 3. Dispersal routes predicted for *Brachistosternus* according to different models. The red dot represents the location of the common ancestor, and the blue dots are the centroids of the geographic occurrences of each species in the present.

The Pathwise Distance inferred from the Geo model showed a significant and positive correlation with the Conductance Distance predicted from all the conductance models, and when including the phylogenetic uncertainty associated to the phylogeny of 55 species (Pearson correlation coefficient = 0.73, p = 0, Fig. 4b; Table 1).

When running the Geo model on the tree at the individual level and using the published coordinates of Ceccarelli et al. (2016), we can see that most of the posterior distribution for the location of the MRCA overlaps with the most likely location obtained from the sample of trees with 55 species (Fig. 1). Additionally, the phylogenetic correlation between the Geo model Pathwise Distance and the distances obtained from all the conductance models were positive and significant (Pearson correlation coefficient = 0.49, p = 0, Appendix S1 Table S4, Fig. 4c).

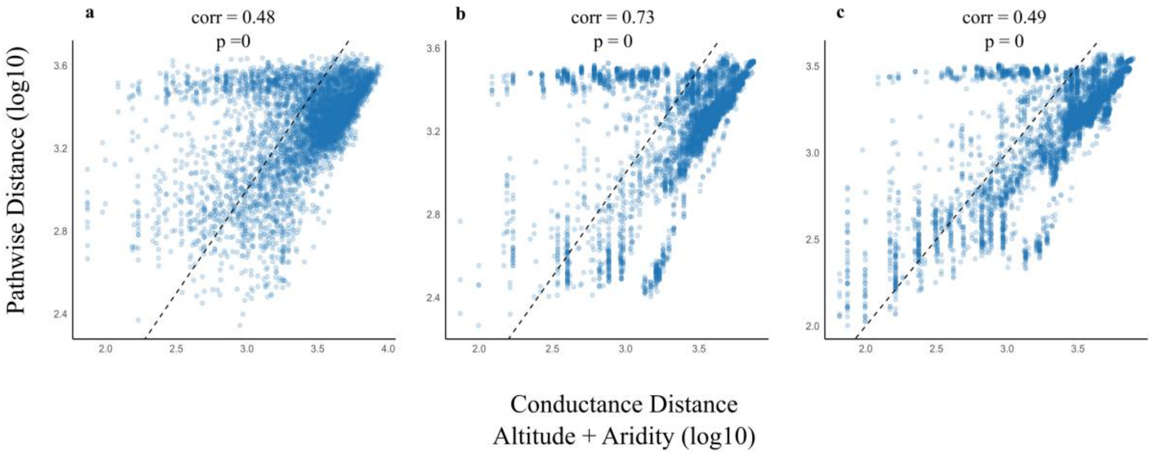

Figure 4. Relationship between the Pathwise Distance and the Conductance Distance. a: Distances obtained from each coordinate in the posterior distribution, based on the analyses of the MCC tree with 55 species. b: Distances obtained from each centroid of the posterior distribution of coordinates, based on the analyses of the sample of 100 phylogenetic trees with 55 species. c: Distances obtained from each coordinate in the posterior distribution, based on the analyses of the MCC tree of 120 specimens. The segment line in each figure represents the 1:1 relationship.

Discussion

Our results provide the first evaluation of the potential environmental factors that shaped the historical dispersal pattern of *Brachistosternus* in South America, using a novel methodological framework that combines the Geo model and Conductance models. Our results show that the geographical origin of the MRCA of *Brachistosternus* was primarily concentrated in the arid regions of South America, from (approx.) 13 to 31 ºS and from 63 to 71 ºW. This result partially agrees with inferences made by other research on the genus (Ceccarelli et al., 2016), who estimated the MRCA location in the area corresponding to the Puna and Coquimbo Provinces in the South American transition zone. Our results aggress in that the most likely distribution of the MRCA was along the Coquimbo province. However, our results exclude the Puna province identified as "G province" by Ceccarelli et al. (2016). Additionally, our results show that the MRCA was also likely distributed in the central Andean Mountains of southern Peru, which is away of the Puna "G province".

The Pathwise Distance was correlated with the distances obtained from all the conductance models, including the Euclidian model, when using the MCC tree of 55 species, the sample of 100 trees, and MCC tree at the specimen level. This can be understood if we consider that all the models estimate the routes with shortest distances but in different ways. The Geo model is a phylogenetic model that does not consider explicitly the environment, and estimates the great circle distance, i.e., the shortest distance, between each pair of phylogenetic nodes that connect a branch while considering the variation in species dispersal ability. Those distances are then summed across all the branches that link the MRCA with each extant species. On the other hand, the conductance model is a non-phylogenetic model that considers the environments and estimates the distances of the routes with less resistance in environmental change, but between two points only, the location of the MRCA and the location of each extant species. The correlation between the predicted distances obtained from those two different approaches then give support for the idea that the species of the genus *Brachistosternus* have, historically, dispersed through routes with less resistance in terms of changes in altitude and aridity. As the ancestral species of this genus probably started the dispersal process from an arid location at low altitudes, our results imply that species were dispersing through the routes with the less change in altitude, and with less change in the degree of aridity, to finally colonise mainly arid environments located at high altitudes. A theoretical implication of this result is that there should be a tendency to conserve both the arid niche over the evolutionary history of *Branchistosternus* and the biological traits adapted to such arid conditions, and we should observe more change in the elevation of the places that the species have inhabited.

Additionally, the Geo model results from all the phylogenetic trees used in this study show that most of the ancestral species, or phylogenetic internal nodes, were located along the central Andean Mountain and the arid zones of South America. This result implies that the dispersal process was partially associated to the Andean uplift, which supports the idea suggested by Ceccarelli et al. (2016) that the group's dispersal process and speciation pattern have been historically connected to the uplift of the Andean Mountain range. Furthermore, as the internal phylogenetic nodes also represent the speciation events of the clade, our estimated locations for all the phylogenetic nodes expand our understanding about the geography of speciation in *Branchistosternus*. This last idea is based on, first, the fact that most of the phylogenetic nodes were in the Central Andes, which agrees with the increase in speciation rates for the Andean clade obtained by Ceccarelli et al. (2016). Second, all the other phylogenetic nodes are likely located along the main arid zones of South America. This means that, in addition to elevation associated to the Andean uplift, aridity could have promoted the divergence into new species of *Brachistosternus*. If this idea is true, there should be a positive relationship between aridity and the speciation rates patterns of *Branchistosternus*.

Considering that species dispersed through the routes with less cost in changes of altitude and aridity, our study suggests that dispersal through more arid conditions as the Andean mountains were uplifting drove the overall dispersal and radiation of *Brachistosternus* during the last 30 Ma, and that the evolution of both the Andes and the Arid Diagonal could have co-molded this evolutionary pattern. Consequently, the gradual aridification of South America with the hyper-aridification of the Atacama Desert and the expansion of open arid habitats (Dunai et al., 2005; Hartley, 2003; Hartley et al., 2005; Luebert, 2021) may have played an essential role in shaping species distribution by generating new arid habitats and corridors for species that could move and adapt to arid conditions.

Acknowledgements

We thank to F. Sara Ceccarelli for her help in sharing the phylogeny of the genus *Brachistosternus*. We also thank Andres Ojanguren-Affilastro, Jose Ochoa, Leonardo Sousa Carvalho, Ricardo Pinto da Rocha, Mauro Cardoso Júnior, Patricio Tapia and Alvaro Salazar, who shared part of the geographical and biological data of *Brachistosternus*, and maps used in this publication. This work is part of the Ph.D. thesis of J.M.B., supported by the National Agency of Investigation and Development from Chile (ANID) Doctoral Fellowship 21221382. The research of J.A.-L. was supported by ANID FONDECYT postdoctoral grant no. 320065, ANID/ FONDECYT regular grant no. 1201506 and 1170815, ANID-ATE BiodUCCT grant no. 220044, and The Leverhulme Trust Research Leadership Award (RL-2019-012). The research of M.M.R. was supported by ANID/FONDECYT regular grant no. 1200843 and ANID-CENTROS REGIONALES R20F0008 (CLAP).

Data availability statement

All the data used in this study will be available as supplementary information upon publication in a peer-review journal.

References

Abraham, E. M., Rodríguez, M. D., Rubio, M. C., Guida-Johnson, B., Gomez, L., & Rubio, C. (2020). Disentangling the concept of "South American Arid Diagonal". *Journal of Arid environments*, *175*, 104089. https://doi.org/https://doi.org/10.1016/j.jaridenv.2019.104089

Agusto, P., Mattoni, C. I., Pizarro-Araya, J., Cepeda-Pizarro, J., & Lopez-Cortes, F. (2006). Communities of scorpions (Arachnida: Scorpiones) of the transitional coastal desert of Chile. *Revista Chilena de Historia Natural*, *79*(4), 407-421. https://doi.org/http://rchn.biologiachile.cl/pdfs/2006/4/Agusto_et_al_2006.pdf

Almeida, E. A. B., Pie, M. R., Brady, S. G., & Danforth, B. N. (2012). Biogeography and diversification of colletid bees (Hymenoptera: Colletidae): emerging patterns from the southern end of the world. *Journal of biogeography*, *39*(3), 526-544. https://doi.org/https://doi.org/10.1111/j.1365-2699.2011.02624.x

Amundson, R., Dietrich, W., Bellugi, D., Ewing, S., Nishiizumi, K., Chong, G., Owen, J., Finkel, R., Heimsath, A., & Stewart, B. (2012). Geomorphologic evidence for the late Pliocene onset of hyperaridity in the Atacama Desert. *Bulletin*, *124*(7-8), 1048-1070.

Anderson, R. P., Araújo, M., Guisan, A., Lobo, J. M., Martínez-Meyer, E., Peterson, A. T., & Soberón, J. (2016). Final report of the task group on GBIF data fitness for use in distribution modelling. *Global Biodiversity Information Facility*, 1-27. https://doi.org/https://assets.ctfassets.net/uo17ejk9rkwj/4T60zRVRHGoyQ6sYIImmoy/ec98d2a617c4bc5324158579929e613e/Final_report_of_the_task_group_on_GBIF_data_fitness_for_use_in_distribution_modelling_ver1.1.pdf

Antoine, P.-O., Roddaz, M., Brichau, S., Tejada-Lara, J., Salas-Gismondi, R., Altamirano, A., Louterbach, M., Lambs, L., Otto, T., & Brusset, S. (2013). Middle Miocene vertebrates from the Amazonian Madre de Dios Subandean Zone, Perú. *Journal of South American Earth Sciences*, *42*, 91-102. https://doi.org/https://doi.org/10.1016/j.jsames.2012.07.008

Avaria-Llautureo, J., Venditti, C., Rivadeneira, M. M., Inostroza-Michael, O., Rivera, R. J., Hernández, C. E., & Canales-Aguirre, C. B. (2021). Historical warming consistently decreased size, dispersal and speciation rate of fish. *Nature Climate Change*, *11*(9), 787-793. https://doi.org/https://doi.org/10.1038/s41558-021-01123-5

Avaria-Llautureo, J., Püschel, T., A., Meade, A., Baker, J., Nicholson, S., L., Chris Venditti. (2024). The radiation and geographic expansion of euprimates through diverse climates. EcoEvoRxiv. https://doi.org/10.32942/X2FS77

Canavan, R. R., Carrapa, B., Clementz, M. T., Quade, J., DeCelles, P. G., & Schoenbohm, L. M. (2014). Early Cenozoic uplift of the Puna Plateau, Central Andes, based on stable isotope paleoaltimetry of hydrated volcanic glass. *Geology*, *42*(5), 447-450. https://doi.org/10.1130/g35239.1

Caplat, P., Edelaar, P., Dudaniec, R. Y., Green, A. J., Okamura, B., Cote, J., Ekroos, J., Jonsson, P. R., Löndahl, J., Tesson, S. V., & Petit, E. J. (2016). Looking beyond the mountain: dispersal barriers in a changing world. *Frontiers in Ecology and the Environment*, *14*(5), 261-268. https://doi.org/https://doi.org/10.1002/fee.1280

Cardillo, M., Orme, C. D. L., & Owens, I. P. F. (2005). Testing for latitudinal bias in diversification rates: an example using new world birds. *Ecology*, *86*(9), 2278-2287. https://doi.org/https://doi.org/10.1890/05-0112

Ceccarelli, F. S., Ojanguren-Affilastro, A. A., Ramírez, M. J., Ochoa, J. A., Mattoni, C. I., & Prendini, L. (2016). Andean uplift drives diversification of the bothriurid scorpion genus Brachistosternus. *Journal of biogeography*, *43*(10), 1942-1954. https://doi.org/https://doi.org/10.1111/jbi.12760

Chamberlain, S., Oldoni, D., & Waller, J. (2022). rgbif: interface to the global biodiversity information facility API. https://doi.org/https://doi.org/10.5281/zenodo.6023735

Claramunt, S., Derryberry, E. P., Remsen, J. V., & Brumfield, R. T. (2012). High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1733), 1567-1574. https://doi.org/https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2011.1922

Clobert, J., Ims, R. A., & Rousset, F. (2004). Causes, Mechanisms and Consequences of Dispersal. In I. Hanski & O. E. Gaggiotti (Eds.), *Ecology, Genetics and Evolution of Metapopulations* (pp. 307-335). Academic Press. https://doi.org/https://doi.org/10.1016/B978-012323448-3/50015-5

Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S., & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology letters*, *12*(3), 197-209. https://doi.org/https://doi.org/10.1111/j.1461-0248.2008.01267.x

Cloudsley-Thompson, J. (1975). Adaptations of Arthropoda to Arid Environments. *Annual Review of Entomology*, *20*(1), 261-283. https://doi.org/https://www.annualreviews.org/doi/abs/10.1146/annurev.en.20.010175.001401

Diniz, M. F., Cushman, S. A., Machado, R. B., & De Marco Júnior, P. (2020). Landscape connectivity modeling from the perspective of animal dispersal. *Landscape Ecology*, *35*(1), 41-58. https://doi.org/10.1007/s10980-019-00935-3

Dunai, T. J., López, G. A. G. l., & Juez-Larré, J. (2005). Oligocene–Miocene age of aridity in the Atacama Desert revealed by exposure dating of erosion-sensitive landforms. *Geology*, *33*(4), 321-324. https://doi.org/https://doi.org/10.1130/G21184.1

Etherington, T. R. (2016). Least-Cost Modelling and Landscape Ecology: Concepts, Applications, and Opportunities. *Current Landscape Ecology Reports*, *1*(1), 40-53. https://doi.org/10.1007/s40823-016-0006-9

Führding-Potschkat, P., Kreft, H., & Ickert-Bond, S. M. (2022). Influence of different data cleaning solutions of point-occurrence records on downstream macroecological diversity models. *Ecology and Evolution*, *12*(8), e9168. https://doi.org/https://doi.org/10.1002/ece3.9168

Garreaud, R. D., Molina, A., & Farias, M. (2010). Andean uplift, ocean cooling and Atacama hyperaridity: A climate modeling perspective. *Earth and Planetary Science Letters*, *292*(1), 39-50. https://doi.org/https://doi.org/10.1016/j.epsl.2010.01.017

Hackel, J., & Sanmartín, I. (2021). Modelling the tempo and mode of lineage dispersal. *Trends in ecology & evolution*, *36*(12), 1102-1112. https://doi.org/https://doi.org/10.1016/j.tree.2021.07.007

Hartley, A. J. (2003). Andean uplift and climate change. *Journal of the Geological Society*, *160*(1), 7-10. https://doi.org/https://doi.org/10.1144/0016-764902-083

Hartley, A. J., Chong, G., Houston, J., & Mather Anne, E. (2005). 150 million years of climatic stability: evidence from the Atacama Desert, northern Chile. *Journal of the Geological Society*, *162*(3), 421-424. https://doi.org/https://doi.org/10.1144/0016-764904-071

Hijmans, R. J. (2019). Introduction to the” geosphere” package (Version 1.5-10). https://doi.org/https://cran.r-project.org/web/packages/geosphere/vignettes/geosphere.pdf

Hijmans, R. J. (2023). terra: Spatial Data Analysis. R package version 1.7-39. *The R Foundation for Statistical Computing*. https://CRAN.R-project.org/package=terra

Hijmans, R. J., Barbosa, M., Ghosh, A., & Mandel, A. (2023). geodata: download Geographic Data. *R package version 0.5–8*. https://CRAN.R-project.org/package=geodata

Hulme, P. E. (2005). Adapting to climate change: is there scope for ecological management in the face of a global threat? *Journal of Applied Ecology*, *42*(5), 784-794. https://doi.org/https://doi.org/10.1111/j.1365-2664.2005.01082.x

Kennedy, J. D., Borregaard, M. K., Marki, P. Z., Machac, A., Fjeldså, J., & Rahbek, C. (2018). Expansion in geographical and morphological space drives continued lineage diversification in a global passerine radiation. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1893), 20182181. https://doi.org/https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2018.2181

Lester, S. E., Ruttenberg, B. I., Gaines, S. D., & Kinlan, B. P. (2007). The relationship between dispersal ability and geographic range size. *Ecology letters*, *10*(8), 745-758. https://doi.org/https://dx.doi.org/10.1111/j.1461-0248.2007.01070.x

Lourenço, W. (1994). Diversity and endemism in tropical versus temperate scorpion communities. *Compte rendu des séances de la société de biogéographie*, *70*(3), 155-160.

Luebert, F. (2021). The two South American dry diagonals. *Frontiers of Biogeography*, *13*(4). https://doi.org/https://dx.doi.org/10.21425/f5fbg51267

Magalhaes, I., Neves, D., Santos, F., Vidigal, T., Brescovit, A. D., & Santos, A. (2019). Phylogeny of Neotropical Sicarius sand spiders suggests frequent transitions from deserts to dry forests despite antique, broad-scale niche conservatism. *Molecular phylogenetics and evolution*, *140*, 106569.

Maldonado, C., Molina, C. I., Zizka, A., Persson, C., Taylor, C. M., Albán, J., Chilquillo, E., Rønsted, N., & Antonelli, A. (2015). Estimating species diversity and distribution in the era of Big Data: to what extent can we trust public databases? *Global Ecology and Biogeography*, *24*(8), 973-984. https://doi.org/https://doi.org/10.1111/geb.12326

Matzke, N. (2013). *BioGeoBEARS: BioGeography with Bayesian (and Likelihood) Evolutionary Analysis in R Scripts.* . In *University of California, Berkeley, CA*

McDowall, R. M. (2004). What biogeography is: a place for process. *Journal of biogeography*, *31*(3), 345-351. https://doi.org/https://doi.org/10.1046/j.0305-0270.2003.01020.x

Meade, A., & Pagel, M. (2019). BayesTraits V3. 0.2: a computer package for analyses of trait evolution. *Website: http://www.evolution.rdg.ac.uk/BayesTraitsV3.0.2/BayesTraitsV3.0.2.html*.

Mongiardino-Koch, N., Ceccarelli, F. S., Ojanguren-Affilastro, A. A., & Ramirez, M. J. (2017). Discrete and morphometric traits reveal contrasting patterns and processes in the macroevolutionary history of a clade of scorpions. *Journal of Evolutionary Biology*, *30*(4), 814-825. https://doi.org/https://doi.org/10.1111/jeb.13050

Nime, M. F., Casanoves, F., & Mattoni, C. I. (2014). Scorpion diversity in two different habitats in the Arid Chaco, Argentina. *Journal of insect conservation*, *18*, 373-384. https://doi.org/https://doi.org/10.1007/s10841-014-9646-4

O’Donovan, C., Meade, A., & Venditti, C. (2018). Dinosaurs reveal the geographical signature of an evolutionary radiation. *Nature Ecology & Evolution*, *2*(3), 452-458. https://doi.org/https://doi.org/10.1038/s41559-017-0454-6

Ochoa, J. A. (2002). Nueva especie de Brachistosternus Pocock (Scorpiones: Bothriuridae) del sur del Perú. *Revista Peruana de Biología*, *9*(2), 55-63. https://doi.org/http://research.amnh.org/users/lorenzo/PDF/Ochoa.2003.RPB.turpuq.pdf

Ochoa, J. A., & Acosta, L. E. (2002). Two new Andean species of Brachistosternus Pocock (Scorpiones: Bothriuridae). *Euscorpius*, *2002*(2), 1-13. https://doi.org/https://dx.doi.org/10.18590/10.18590/issn.1536-9307/2002v.2002.issue2

Ochoa, J. A., & Ojanguren-Affilastro, A. A. (2007). Systematics and distribution of Brachistosternus (Brachistosternus) ehrenbergii (Gervais,), with the first record of stridulation in this genus Brachistosternus (Scorpiones: Bothriuridae). *Studies on Neotropical Fauna and Environment*, *42*(1), 61-69. https://doi.org/https://doi.org/10.1080/01650520600800310

Ojanguren-Affilastro, A. (2002). Nuevos aportes al conocimiento del género Brachistosternus en Chile, con la descripción de dos nuevas especies (Scorpiones, Bothriuridae). *Boletín de la Sociedad de Biología de Concepción (Chile)*, *73*, 37-46.

Ojanguren-Affilastro, A., Mattoni, C. I., Ochoa, J. A., Ramírez, M. J., Ceccarelli, F. S., & Prendini, L. (2016). Phylogeny, species delimitation and convergence in the South American bothriurid scorpion genus Brachistosternus Pocock 1893: Integrating morphology, nuclear and mitochondrial DNA. *Molecular phylogenetics and evolution*, *94*, 159-170. https://doi.org/https://doi.org/10.1016/j.ympev.2015.08.007

Ojanguren-Affilastro, A. A. (2003). Las especies andinas de Brachistoternus (Leotosternus), con la descripción de tres nuevas especies (Scorpiones, Bothriuridae). *Revista Ibérica de Aracnología*(8), 23-36. https://doi.org/http://sea-entomologia.org/PDF/RIA_8/R08-005-023.pdf

Ojanguren-Affilastro, A. A. (2005). Notes on the genus Brachistosternus (Scorpiones, Bothriuridae) in Chile, with the description of two new species. *The Journal of Arachnology*, *33*(1), 175-192. https://doi.org/https://doi.org/10.1636/H03-20

Ojanguren-Affilastro, A. A., Ceccarelli, F. S., Mattoni, C. I., Salas, L., Iuri, H., Ochoa, J. A., & Barrios, A. (2023). On the southernmost high Andean scorpion species, with the identification of a cryptic new species of Brachistosternus (Bothriuridae) through morphology, molecular data and species distribution models. *Zoologischer Anzeiger*, *302*, 248-259. https://doi.org/https://doi.org/10.1016/j.jcz.2023.01.001

Ojanguren-Affilastro, A. A., & Mattoni, C. I. (2006). A new species of Brachistosternus from Chilean central Andes (Scorpiones: Bothriuridae). *Studies on Neotropical Fauna and Environment*, *41*(1), 79-85. https://doi.org/https://doi.org/10.1080/01650520500243595

Ojanguren-Affilastro, A. A., Pizarro-Araya, J., & Ochoa, J. A. (2018). Five new scorpion species of genus Brachistosternus (Scorpiones: Bothriuridae) from the deserts of Chile and Peru, with comments about some poorly studied diagnostic characters of the genus. *Zootaxa*, *4531*(2), 151-194. https://doi.org/https://www.mapress.com/zt/article/view/zootaxa.4531.2.1

Ojanguren-Affilastro, A. A. A., Pablo Pizarro-Araya, Jaime Mattoni, Camilo I. (2007). Two new scorpion species of genus Brachistosternus (Scorpiones: Bothriuridae) from northern Chile. *Zootaxa*, *1623*(1), 55–68. https://doi.org/https://doi.org/10.11646/zootaxa.1623.1.4

Prendini, L. (2003). A new genus and species of bothriurid scorpion from the Brandberg Massif, Namibia, with a reanalysis of bothriurid phylogeny and a discussion of the phylogenetic position of Lisposoma Lawrence. *Systematic Entomology*, *28*(2), 149-172. https://doi.org/https://doi.org/10.1046/j.1365-3113.2003.00207.x

Raftery, A. E. (1996). *Markov chain Monte Carlo in practice*, 163–187

Ribeiro, B. R., Velazco, S. J. E., Guidoni-Martins, K., Tessarolo, G., Jardim, L., Bachman, S. P., & Loyola, R. (2022). bdc: A toolkit for standardizing, integrating and cleaning biodiversity data. *Methods in Ecology and Evolution*, *13*(7), 1421-1428. https://doi.org/https://doi.org/10.1111/2041-210X.13868

Ricklefs, R. E. (2006). Global variation in the diversification rate of passerine birds. *Ecology*, *87*(10), 2468-2478. https://doi.org/https://doi.org/10.1890/0012-9658(2006)87[2468:GVITDR]2.0.CO;2

Roig-Juñent, S., Domínguez, M., Flores, G., & Mattoni, C. (2006). Biogeographic history of South American arid lands: A view from its arthropods using TASS analysis. *Journal of Arid environments*, *66*(3), 404-420.

Sanmartín, I. (2012). Historical Biogeography: Evolution in Time and Space. *Evolution: Education and Outreach*, *5*(4), 555-568. https://doi.org/10.1007/s12052-012-0421-2

Santini, L., Di Marco, M., Visconti, P., Baisero, D., Boitani, L., & Rondinini, C. (2013). Ecological correlates of dispersal distance in terrestrial mammals [journal article]. *Hystrix, the Italian Journal of Mammalogy*, *24*(2), 181-186. https://doi.org/https://doi.org/10.4404/hystrix-24.2-8746

Sekar, S. (2012). A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy? *Journal of Animal Ecology*, *81*(1), 174-184. https://doi.org/https://doi.org/10.1111/j.1365-2656.2011.01909.x

Selmane, S., & L'hadj, M. (2014). Regression analysis on scorpion envenomation and climate variables in M'Sila province, Algeria from 2001 to 2010. *Int J Math Trends Technol*, *13*(1), 1-9. https://doi.org/https://ijmttjournal.org/archive/ijmtt-v13p501

Simon, M. F., Grether, R., de Queiroz, L. P., Skema, C., Pennington, R. T., & Hughes, C. E. (2009). Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Sciences*, *106*(48), 20359-20364. https://doi.org/https://www.pnas.org/doi/abs/10.1073/pnas.0903410106

Straus, S., Forbes, C., Little, C. J., Germain, R. M., Main, D. A., O'Connor, M. I., Thompson, P. L., Ford, A. T., Gravel, D., & Guzman, L. M. (2022). Macroecological variation in movement profiles: body size does not explain it all. *bioRxiv*, 2022.2004.2021.489049. https://doi.org/https://www.biorxiv.org/content/biorxiv/early/2022/04/22/2022.04.21.489049.full.pdf

van Etten, J., & Hijmans, R. J. (2010). A Geospatial Modelling Approach Integrating Archaeobotany and Genetics to Trace the Origin and Dispersal of Domesticated Plants. *PLoS One*, *5*(8), e12060. https://doi.org/10.1371/journal.pone.0012060

Veizer, J., & Prokoph, A. (2015). Temperatures and oxygen isotopic composition of Phanerozoic oceans. *Earth-Science Reviews*, *146*, 92-104. https://doi.org/https://doi.org/10.1016/j.earscirev.2015.03.008

Weeks, B. C., & Claramunt, S. (2014). Dispersal has inhibited avian diversification in Australasian archipelagoes. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1791), 20141257. https://doi.org/https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2014.1257

Weir, J. T., & Schluter, D. (2007). The Latitudinal Gradient in Recent Speciation and Extinction Rates of Birds and Mammals. *Science*, *315*(5818), 1574-1576. https://doi.org/10.1126/science.1135590

Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in ecology & evolution*, *19*(12), 639-644. https://doi.org/https://doi.org/10.1016/j.tree.2004.09.011

Yesson, C., Brewer, P. W., Sutton, T., Caithness, N., Pahwa, J. S., Burgess, M., Gray, W. A., White, R. J., Jones, A. C., & Bisby, F. A. (2007). How global is the global biodiversity information facility? *PLoS One*, *2*(11), e1124. https://doi.org/https://doi.org/10.1371/journal.pone.0001124

Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present. *Science*, *292*(5517), 686-693. https://doi.org/https://www.science.org/doi/abs/10.1126/science.1059412

Zeller, K. A., McGarigal, K., & Whiteley, A. R. (2012). Estimating landscape resistance to movement: a review. *Landscape Ecology*, *27*(6), 777-797. https://doi.org/10.1007/s10980-012-9737-0

Zizka, A., Carvalho, F. A., Calvente, A., Baez-Lizarazo, M. R., Cabral, A., Coelho, J. F. R., Colli-Silva, M., Fantinati, M. R., Fernandes, M. F., & Ferreira-Araújo, T. (2020). No one-size-fits-all solution to clean GBIF. *PeerJ*, *8*, e9916. https://doi.org/https://doi.org/10.7717/peerj.9916

Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., & Scharn, R. (2019). CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution*, *10*(5), 744-751. https://doi.org/https://doi.org/10.1111/2041-210X.13152

Table 1. Pearson correlation coefficient for the relationship between the Pathwise Distance and Conductance Distance based a sample of 100 time-calibrated phylogenetic trees for 55 species. The table lower off-diagonals shows the correlation values. Upper off-diagonals show the p-values.

	Pearson correlation coefficient				
Model	Geomodel	Conductance Euclidian	Conductance Altitude	Conductance Aridity	Conductance Altitude+ Aridity
Geomodel	-	0	0	0	0
Conductance Euclidian	0.68	-	0	0	0
Conductance Altitude	0.59	0.62	-	0	0
Conductance Aridity	0.33	0.60	0.40	-	0
Conductance Altitude+Aridity	0.73	0.94	0.80	0.62	-