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Spatial Connectivity Through Mountains and Deserts Drove South American Scorpions Dispersal

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ABSTRACT

Aim: The aim of this study is to infer the geographic dispersal paths and the environmental conditions that shaped the 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 the previous studies, we evaluated the hypothesis postulating that species geographic expansion was promoted by arid conditions in high altitudes.

Location: South America.

Taxon: *Brachistosternus* genus.

Methods: We integrated two methodological approaches in this study, the phylogenetic Geographical model and the Conductance model, considering the uncertainty associated with the phylogenetic relationship and the species classification. 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 species dispersal routes and distances from the location of the genus common ancestor. The Conductance model is based on the circuit theory and infers the geographic route and distance of least resistance between an origin and destination point. We defined the origin as the location of the genus common ancestor obtained from the Geo model and a destination point as the current geographic location of each species. This model infers the geographic routes with the least cost of resistance for dispersal in a landscape of varying altitude and aridity. Finally, we evaluated the correlation between the two dispersal distances each species have moved from the location of the common ancestor, that is, the distance inferred from the Geo model and from the Conductance model.

Results: 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 thorough routes ranging from 873 to 2800km in average. The Conductance model that considers the routes with least resistance to elevation and aridity simulated dispersal distances that are highly correlated with the species dispersal distances obtained from the Geo model.

Main Conclusions: 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 of the genus *Brachistosternus*.

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1 | Introduction

The geographic distribution of taxa is mainly the product of species geographic dispersal 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 colonise 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 colonise and adapt to places with new environmental conditions (species niche evolution) (Claramunt et al. 2012; Clobert, Ims, and Rousset 2004; Kennedy et al. 2018; Straus et al. 2022; Weeks and 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, Orme, and Owens 2005; Ricklefs 2006; Sekar 2012; Weir and Schluter 2007; Wiens and Donoghue 2004).

Current methods for reconstructing dispersal routes across wide geographic and temporal scales are mainly based on phylogenetic and conductance models. On the one hand, phylogenetic models estimate species ancestral areas and dispersal paths (Ceccarelli et al. 2016; Hackel and Sanmartín 2021; Sanmartín 2012). Although some methods are based on a discrete categorisation 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. 2024, 2021; O'Donovan, Meade, and Venditti 2018).

On the other hand, Conductance or resistivity models identify the paths with the lowest cost distance among all possible paths linking predefined origin 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 and 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, McGarigal, and Whiteley 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 may 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, López, and Juez-Larré 2005; Hartley 2003; Hartley et al. 2005; Simon et al. 2009; Veizer and Prokoph 2015; Zachos et al. 2001). Remarkably, the gradual aridification of South America that began in the late Cretaceous (Garreaud, Molina, and Farias 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-Affilastró et al. 2016; Ojanguren-Affilastró 2005; Selmane and 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-Affilastró et al. 2016; Ojanguren-Affilastró, Pizarro-Araya, and Ochoa 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 and Ojanguren-Affilastró 2007; Ojanguren-Affilastró 2002, 2005; Ojanguren-Affilastró et al. 2007) and at high altitudes in the Andes, up to 4500 m (Ceccarelli et al. 2016; Ochoa and Acosta 2002; Ojanguren-Affilastró 2003; Ojanguren-Affilastró and 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 with the Andes uplift and the aridification of South America were associated with the historical geographic expansion of the genus.

In this study, we used the Geo model and Conductance model to infer the dispersal routes and distances for each species available in the most recent phylogeny of the genus, and the most likely environmental conditions associated with 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 least cost for dispersal, using Conductance models that consider 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, Pizarro-Araya, and Ochoa 2018).

2 | Materials and Methods

2.1 | Study Model

The genus *Brachistosternus* currently contains 51 described species, being two of them nomina dubia (Ojanguren-Affilastro et al. 2016, 2023; Ojanguren-Affilastro, Pizarro-Araya, and Ochoa 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, Casanoves, and Mattoni 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).

We used the most updated phylogenetic tree for the genus to date from Ceccarelli et al. (2016), which contains 55 phylogenetic species. We are using the phylogeny that has molecular data provided by Ojanguren-Affilastro 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 many species remain to be discovered and identified.

2.2 | 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, Oldoni, and Waller 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.

2.3 | 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 centralised 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, 2019). To deal with these issues, we followed the cleaning pipeline outlined in (Führding-Potschkat, Kreft, and Ickert-Bond 2022; Ribeiro et al. 2022; Zizka et al. 2020, 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 and 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 and 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.

2.4 | 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.

2.5 | 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 and Tree S1. This MCC tree includes 12 undescribed species. 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).

2.6 | 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, Meade, and Venditti 2018) in BayesTraits v4.0 (Meade and 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 (Avaria-Llautureo et al. 2021; O'Donovan, Meade, and Venditti 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 1000 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 and Pagel 2019; Raftery 1996).

2.7 | Estimating Species Dispersal Distance From the Geo Model

To measure the dispersal distance that each extant species in the phylogeny travelled from the location of the genus MRCA, i.e., the Pathwise Distance, we calculated the sum of the distances across all branches (branchwise distance) that link the MRCA with each extant species. The branchwise distances were calculated using the *distCosine* function in the R package *geosphere* (Hijmans 2019). The *distCosine* function brings the great circle distance, that is, 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, Meade, and Venditti 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's geographic centroid across a sample of 100 phylogenetic trees. We also estimated the branchwise distances and Pathwise Distance from each of 100 coordinates obtained from an analysis using the MCC tree.

2.8 | 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 modelled as the least-cost of movement across a resistant surface (Diniz et al. 2020; van Etten and 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). Rasters climatic layers of aridity and altitude were obtained from the library *geodata* in R (Hijmans et al. 2023) at a 0.5° spatial resolution. These rasters 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 Etten 2017).

2.9 | 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 the location for the MRCA, we used the geographic MRCA-centroid from the posterior coordinates inferred with the Geo model. We also 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 from all conductance models, using each of the 100 coordinates in the posterior distribution that represents the location of the MRCA. These coordinates were obtained from the Geo model analysis on the MCC tree.

2.10 | Correlation Between Species Dispersal Distances

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 the each of the 100 phylogenetic trees so that we integrate the phylogenetic uncertainty, associated with the topology and divergence times, into our results. We also evaluated the correlations using 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 evaluate in our results the potential bias associated with the species delimitation process (see below).

2.11 | Phylogenetic Uncertainty

We evaluate the uncertainty associated with 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 and Tree S2). The sample of trees was estimated and provided by Ceccarelli et al. (2016). 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.

2.12 | Species Delimitation Uncertainty

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 a Bayesian sample of trees at the individual-specimen-level (Appendix S2 and Tree S3). This sample of trees was estimated and provided by Ceccarelli et al. (2016) and contains 120 individuals of *Brachistosternus*. By running our analyses on this phylogenetic tree at the specimen level, we ensure to exclude any error associated with the species delimitation process. Additionally, we used the coordinates for each sampled individual, available in Ceccarelli et al. (2016), so that we are also excluding any error associated with the geographic distribution at the species level. We run the Geo model on the MCC tree of individuals 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 as origin points, and using the coordinate of each specimen as the destination points.

3 | Results

The BF comparison supports 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 2807 km (*B. paulae*) (Appendix S1 and 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 MCC 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 $\sim 13^\circ$ to 31° S. There is a gap in the distribution, around 20° S, identified by a lower density of the posterior distribution of coordinates (Figure 1).

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 those areas (Figure 2).

Conductance models predicted a wide range of Conductance Distance for the genus (Table 1). The Euclidian conductance model, without environmental restrictions, showed the lowest median value (1135 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 (1722 and 3038 km, respectively) (Figure 3).

The Pathwise Distance inferred from the Geo model showed a significant and positive correlation with the Conductance Distance predicted from all the conductance models, when using the distances obtained from the MCC tree (Pearson correlation coefficient = 0.48, $p = 0$, Figure 4a) and from the 100 phylogenetic trees of 55 species (Pearson correlation coefficient = 0.73, $p = 0$, Figure 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 MCC tree with 55 species (Figure 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 and Table S4, Figure 4c).

4 | 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° S and from 63° to 71° W. This result partially agrees with inferences made by previous research on the genus (Ceccarelli et al. 2016),

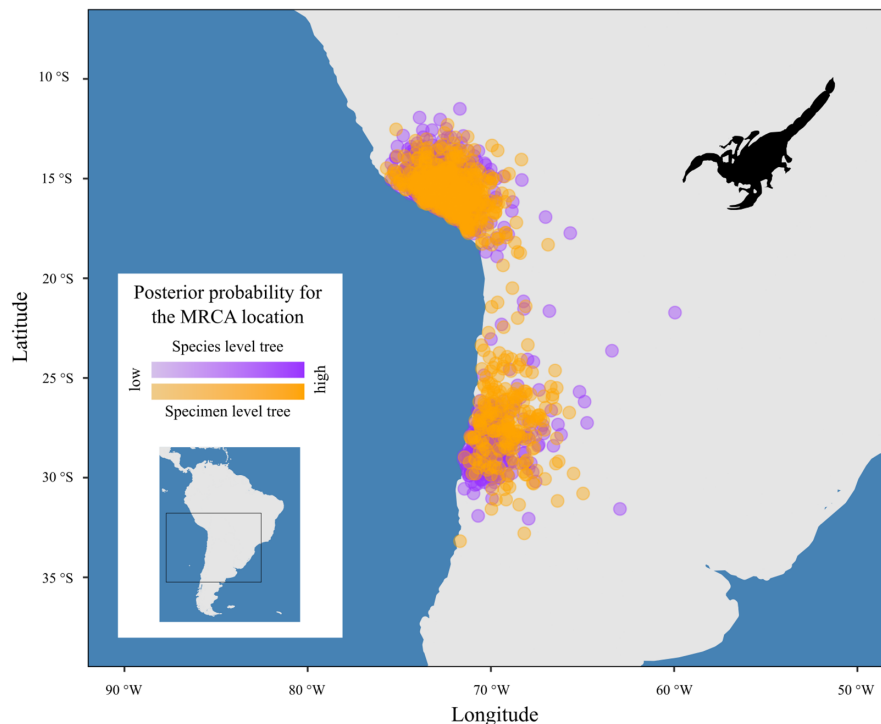


FIGURE 1 | Location for *Brachistosternus* common ancestor estimated from two phylogenetic trees. The most recent common ancestor of *Brachistosternus* (MRCA) was mainly distributed within the arid regions of South America. Specifically, along the central Andean Mountain of southern Peru and central 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.

who estimated the MRCA location in the area corresponding to the Puna and Coquimbo Provinces in the South American transition zone. Our results agree 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 linked to a branch. 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 least resistance to dispersal, 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 strong support for the idea that the species of the genus *Brachistosternus* have, historically, dispersed through routes

with least 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 with 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, first, on 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

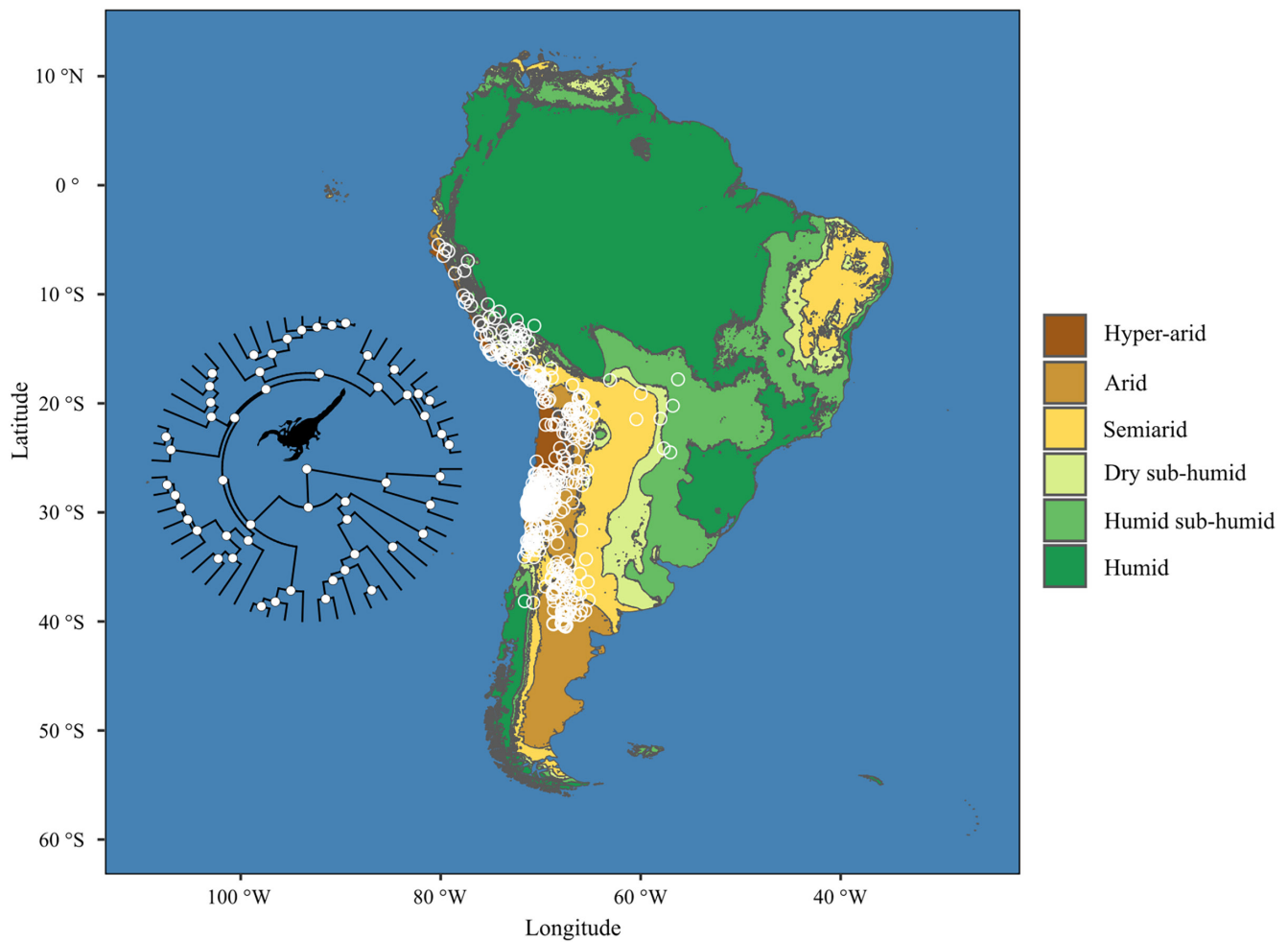


FIGURE 2 | Most of the phylogenetic internal nodes were inferred along the central Andes and the current arid zones of South America. As internal nodes in a phylogenetic tree represent the ancestral species and speciation events of a clade, our results support the idea that the ancestral species of *Brachistosternus* were dispersing and speciating mainly along the Central Andes and the arid zones of South America. White dots in the tree: Phylogenetic nodes for the phylogeny of *Brachistosternus* used in this study. White outlined dots in the map: Posterior geographic locations inferred across the 54 internal nodes of the tree with 55 species.

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 the 55 species.

Model	Geo model	Conductance euclidian	Conductance altitude	Conductance aridity	Conductance aridity+ altitude
Geo model	—	0	0	0	0
Conductance euclidian	0.68	—	0	0	0
Conductance altitude	0.59	0.62	—	0	0
Conductance aridity	0.33	0.6	0.4	—	0
Conductance altitude + aridity	0.73	0.94	0.8	0.62	—

Note: The table lower off-diagonals shows the correlation values. Upper off-diagonals show the *p* value.

America. This means that, in addition to elevation associated with the Andean uplift, aridity could have promoted the divergence into new species of *Brachistosternus*. If this idea is true, we should find a positive relationship between aridity and the speciation rates patterns of *Branchistosternus*.

Considering that species dispersed through the routes with less changes in 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

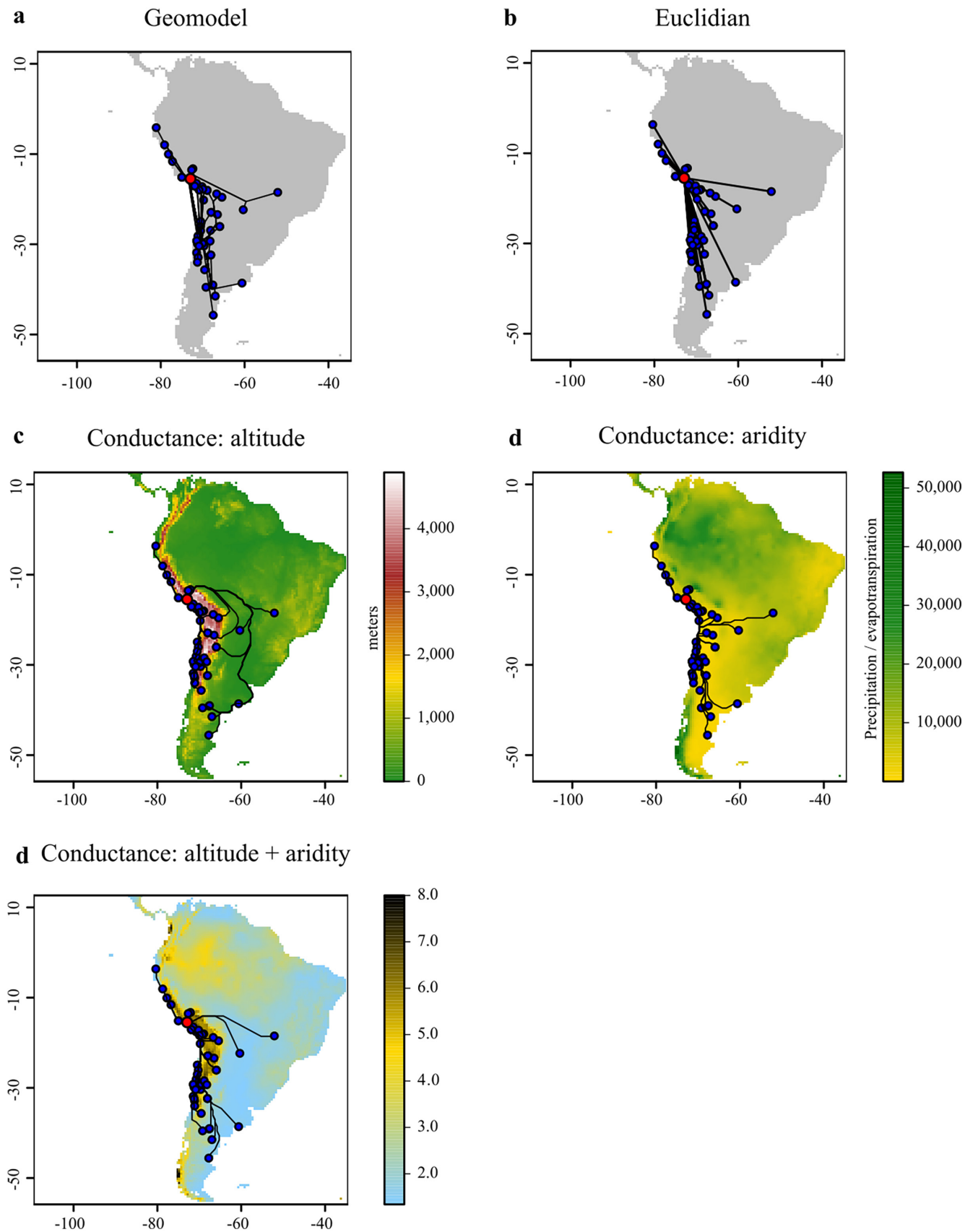


FIGURE 3 | Dispersal routes predicted for *Brachistosternus* according to different models. The red dot represents the location of the common ancestor, and the blue dots are the locations of extant species in the present. We show the routes from one tree in the sample of 100 phylogenetic trees for 55 species.

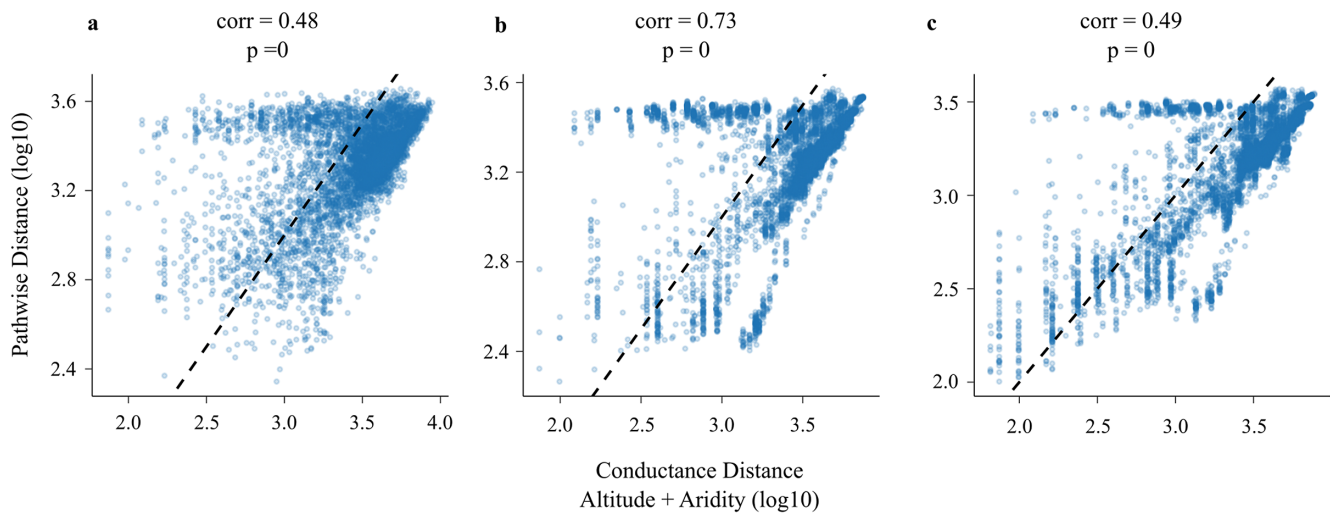


FIGURE 4 | Relationship between the Pathwise Distance and the Conductance Distance. a: Distances obtained from each coordinate in the posterior distribution, based on the analyses of the MCC tree with 55 species. b: Distances obtained from each centroid of the posterior distribution of coordinates, based 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.

both the Andes and the Arid Diagonal could have co-moulded 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, López, and Juez-Larré 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 those more arid conditions.

Author Contributions

All authors contributed to all aspects of this work.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All the data used in this study is available as [Supporting Information](#).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.