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Recommended Citation

ÖNDER, BANU ŞEBNEM and PERKTAŞ, UTKU (2024) "The range dynamics of a cactophilic Drosophila species under climate change scenarios," *Turkish Journal of Zoology*: Vol. 48: No. 1, Article 5.
https://doi.org/10.55730/1300-0179.3158
Available at: https://journals.tubitak.gov.tr/zoology/vol48/iss1/5

The range dynamics of a cactophilic *Drosophila species* under climate change scenarios

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Abstract: In this study, we evaluated the historical demography of a cactophilic *Drosophila* species (*Drosophila gouveai*) based on previously published mitochondrial DNA (mtDNA) data ecological niche modelling. We particularly aimed to test the effect of climate change on the historical demography of *D. gouveai* during the late Quaternary and the future of the species. For this, we also modelled its host cacti species in its distribution range to reach a more robust biogeographic conclusion. Our results indicate that *D. gouveai* was as sensitive to climate change as its hosts were. This species experienced an almost complete range shift, range contraction after the Last Interglacial (130,000 years ago) but before the Last Glacial Maximum (22,000 years ago). Afterwards, its range contracted in the Present, and this species will experience complete range shift once again in the Future (based on 2050 and 2070 projections) as its hosts will do. In conclusion, the Last Interglacial played a significant role in shaping the demographic history of *D. gouveai* and its hosts, and this species will have a different distribution or will be extinct in the near future.

Key words: Phylogeography, mitochondrial DNA, *Drosophila gouveai*, Last Glacial Maximum, Last Interglacial, South America
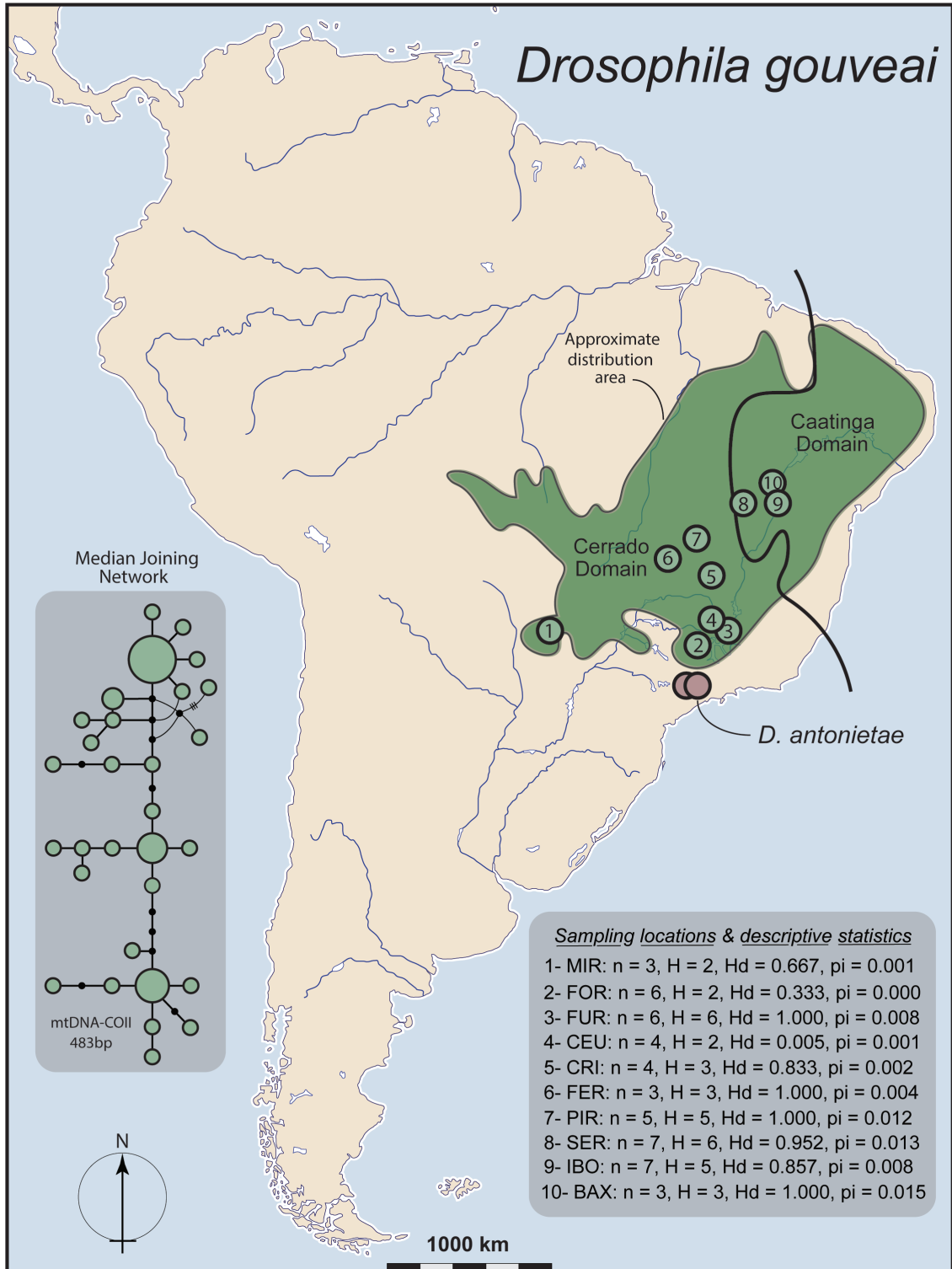
1. Introduction

It is well-known that climatic factors, such as temperature (Cossins and Bowler, 1987), play a substantial role in determining the geographical distributions of species (Gaston, 2003). During the Late-Quaternary climatic oscillations, species changed their ranges to find climatically favorable areas to survive; otherwise, they became extinct. This argument has been well-tested for temperate region species, especially for vertebrates in the Nearctic and Palearctic (e.g., Hewitt, 2000; Waltari et al., 2007). Nevertheless, there is a scarcity of phylogeographic studies and ecological discussions concerning invertebrates such as fruit flies (genus *Drosophila*) (Franco and Manfrin, 2013; Sillero et al., 2014). This is due to the fact that, unlike phylogenetic systematics, similar studies in invertebrates are not widely observed, primarily because our focus lies in understanding the ecological causes of intra-species genetic diversity. These studies have concluded that temperature affects the ecological niches of drosophilids (Sillero et al., 2014), mainly because of their local adaptation.

Understanding species' responses to present climatic conditions is important to predict past and future climatic oscillations. Phylogeography plays a valuable

role here by using genetic information to investigate the demographic history of species. In addition, meaningful inferences about demographic history can be made through ecological approaches (e.g., ecological niche modeling, Perktaş and Gür, 2015). Hence, integrating phylogeography and ecological niche modeling at a species level provides a useful methodological perspective for biogeographical analysis of the published genetic and distributional information of any species (e.g., Metzger et al., 2015; Perktaş et al., 2017). Accordingly, in this study, we designed a historical biogeographic framework for the South American endemic fruit fly species, *Drosophila gouveai*, based on published DNA data (Moraes et al., 2009) together with species occurrences in a meta-analysis framework.

D. gouveai (Tidon-Sklorz and Sene, 2001), which is a cactophilic fruit fly species and member of the *D. buzzatii* cluster, includes seven species within the *repleta* group (Diptera: Drosophilidae). This species has a moderate distribution from midwestern to northeastern Brazil (Figure 1); in some parts of its range, the species shows a parapatric distribution pattern with other members of the *D. buzzatii* cluster (e.g., *D. antonietae* and *D. serido*). Distribution of this cluster in South America mostly

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Drosophila gouveai

Approximate distribution area

Caatinga Domain

Cerrado Domain

Median Joining Network

mtDNA-COII 483bp

D. antonietae

Sampling locations & descriptive statistics
1- MIR: n = 3, H = 2, Hd = 0.667, pi = 0.001
2- FOR: n = 6, H = 2, Hd = 0.333, pi = 0.000
3- FUR: n = 6, H = 6, Hd = 1.000, pi = 0.008
4- CEU: n = 4, H = 2, Hd = 0.005, pi = 0.001
5- CRI: n = 4, H = 3, Hd = 0.833, pi = 0.002
6- FER: n = 3, H = 3, Hd = 1.000, pi = 0.004
7- PIR: n = 5, H = 5, Hd = 1.000, pi = 0.012
8- SER: n = 7, H = 6, Hd = 0.952, pi = 0.013
9- IBO: n = 7, H = 5, Hd = 0.857, pi = 0.008
10- BAX: n = 3, H = 3, Hd = 1.000, pi = 0.015

N

1000 km

Figure 1. Approximate distribution of *D. gouveai* (green area) showed Caatinga and Cerrado domains and the localities sampled for the species (based on Moraes et al., 2009), descriptive statistics (n, number of individuals; H, the number of haplotype; H_d, haplotype diversity; pi, nucleotide diversity) and median joining network of 48 individuals of *D. gouveai*. All statistics based on nucleotide sequences were adopted from Moraes et al. (2009). MIR: Pirapotanga; FOR: Morro do Forno; FUR: Furnas; CEU: Vale do Céu; CRI: Cristalina; FER: Fercal; PIR: Pirenópolis; SER: Serrinha; IBO: Ibotirama; BAX: Baxio.

depends on the presence of Cactaceae (Manfrin and Sene, 2006), this species is particularly associated with two cacti species (*Cereus hildmannianus* and *Pilosocereus machrisii*), because decaying cacti are the exclusive feeding resource for the larvae of this cluster (Pereira et al., 1983). Previous phylogeographic studies on *D. gouveai* show that the species' ancestral area was located in north-eastern Brazil and that it experienced a range expansion event (Moraes et al., 2009), although none of these inferences have been tested by any ecological analyses. Similar studies in North America based on allozyme and mitochondrial DNA (mtDNA) data showed substantial genetic differentiation between cactophilic *Drosophila* species, like *D. pachea*, *D. mettleri*, and *D. nigrospiracula* (Markow et al., 2002; Hurtado et al., 2004). However, mtDNA studies (Hurtado et al. 2004) on these species showed demographic expansion within each species that is similar to *D. gouveai* (see Moraes et al., 2009). Additionally, the expansion pattern has not been integrated with ecological analysis. Therefore, our objective in this study is to reevaluate previously published mitochondrial DNA data of *D. gouveai*, based on Moraes et al. (2009), through Isolation-by-Distance analysis and beside this, construct an ecological niche model in order to better understand *D. gouveai*'s species-specific demographic history and its future range dynamics. In addition to this, while revealing the demographic history of the species, we wanted to draw attention to a different point. Fruit flies live in their geographical distribution areas depending on host plants (Soto *et.al.,* 2007; Soto et al., 2008a, 2008b; Soto et al., 2010). For this reason, modeling the most suitable hosts for *D. gouveai* with an ecological niche modelling approach can help us better understand the future predictions of this cactus-dependent fruit fly species.

2. Methods

2.1. Historical demography
Isolation-by-distance - A matrix of genetic distances between all pairs of populations was estimated from the net average genetic distances (dA) between groups for mtDNA locus by MEGA version 7 (Kumar et al., 2016). A matrix of the geographic distances (km) between all pairs of populations from each sampling location were estimated using Geographic Distance Matrix Generator (version 1.2.3, https://biodiversityinformatics.amnh.org/open_source/gdmg/). A Mantel test with 10,000 random permutations was performed between the matrices of the net dA and geographic (log) distances (Slatkin, 1993; Rousset, 1997).

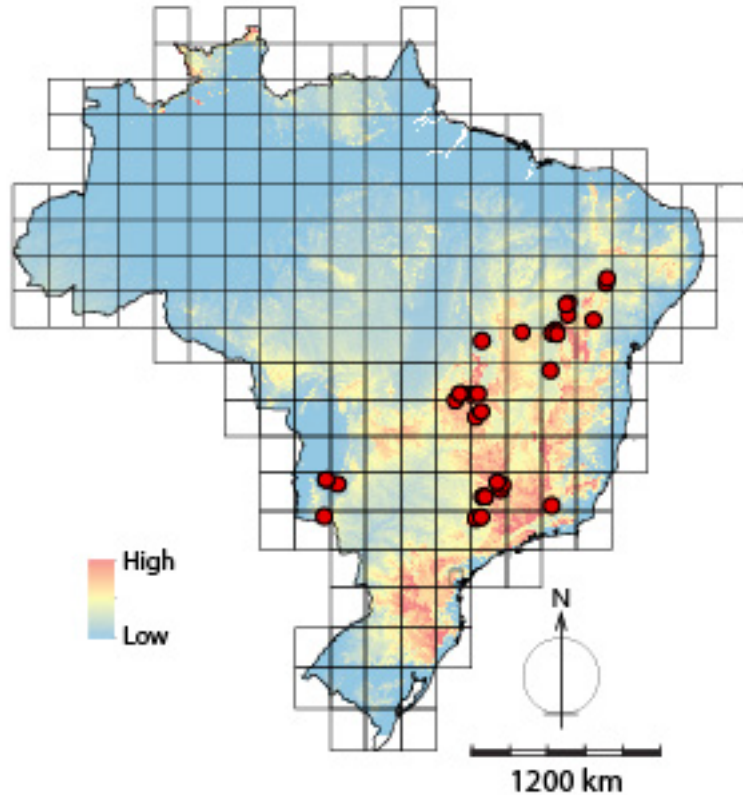### 2.2. Ecological niche modeling
Input data-The main components of the study were two different groups. One was the endemic *D. gouveai*; the other group was two cactus species, which are the host

of this species. For this reason, we got spatial occurrence records from different sources to use in the ecological niche modelling.

D. gouveai-Species occurrence data were compiled from the following sources: TaxoDros (www.taxodros.uzh.ch) and Moraes et al. (2009). The occurrence records showed more intense sampling in the northwest of the distribution range of *D. gouveai* and much less (or no sampling) in the southeast (Figure 2). As we only had a limited number of occurrence records (n = 34, see Supplementary Table S1 for raw data), we did not rarefy the data. Thus, a buffered minimum convex polygon of spatial occurrence records was created using a sampling bias distance of 200 km to produce a bias grid for the ecological niche modelling (Elith et al., 2010; Fourcade et al., 2014).

Host species-Species occurrence data for both cacti species (*C. hildmannianus*, *P. machrisii*) were compiled from the Global Biodiversity Information Facility (GBIF, www.gbif.org). Since the geographical information is limited for these two cactus species, we evaluated spatial occurrence records of the two species together in ecological niche models. The fact that both cacti species preferred arid places and that the ecological requirements of both species were similar did not prevent the analysis from being conducted together. A total of 47 spatial occurrence records was used for ecological niche modeling. We did not simplify the data, we just extracted the duplicate occurrence records from the dataset. Thus, a buffered minimum convex polygon of spatial occurrence records was created using a sampling bias distance of 50 km as the same procedure described for *D. gouveai*.

Climate data-The Future (2050 and 2070), the Present (1950-2000), the Last Glacial Maximum (22,000 years ago), and the Last Interglacial (130,000 years ago) bioclimatic data were downloaded from the WorldClim database (Hijmans et al., 2005, www. worldclim.org) at a resolution of 2.5 arc-min. Bioclimatic data for the Future were based on two time periods, 2050 (average for 2041–2060) and 2070 (average for 2061–2080), and 19 different simulations considering a middle-moderate climate change scenario (rcp45): ACCESS1-0, BCC-CSM1-1, CCSM4, CESM1-CAM5-1-FV2, CNRM-CM5, GFDL-CM3, GFDL-ESM2G, GISS-E2-R, HadGEM2-AO, HadGEM2-CC, HadGEM2-ES, INMCM4, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC-ESM, MIROC5, MPI-ESM-LR, MRI-CGCM3 and NorESM1-M. The Last Glacial Maximum was based on three general circulation model (GCM) simulations: CCSM4, MIROC-ESM, and MPI-ESM-P. The bioclimatic data include 19 bioclimatic variables derived from monthly temperature and precipitation values (for detailed descriptions of these bioclimatic variables, see www.worldclim.org/bioclim). After masking the data for South America, we checked

Figure 2. Occurrence points used for ecological niche modeling are shown in red. Squares equal approximately 2 decimal degrees and the background image on the map shows the elevational structure of Brazil.

that the correlations between the 19 bioclimatic variables were sufficiently strong (r ≥ 0.70 or ≤−0.90). For this, we made four different data sets and tested them in the model calibration process for *D. gouveai* and its host species.

Models-We defined the M area, that indicates the movement capacity of the species, for *D. gouveai* and its host species as suggested by Barve et al. (2011). For this, we followed the natural history of *D. gouveai* (Manfrin and Sene, 2006; Moraes et al., 2009; Franco and Manfrin, 2013) and its hosts. This approach is crucial because all ecological niches (e.g., fundamental or realized niches) can be estimated using both landscape and species occurrences in this landscape (Peterson and Soberon, 2012, for an example; see also Ülker et al., 2018). The projections for the Future, the Present, and the Past in the ecological niche models were performed with the mask set of South America. We used MaxEnt (the maximum entropy machine learning algorithm), version 3.3.3k (Phillips et al., 2006; Phillips and Dudik, 2008 www.cs.princeton. edu/~schapire/maxent) to construct the models of *D. gouveai*'s geographic distribution under the Future, the Present and the Past climatic conditions. We used receiver

operating characteristic (ROC) analysis in MAXENT, and followed the methodological process suggested by Peterson and Cohon (1999). For model calibration and afterwards for the final models, we followed recent advances in ecological niche modelling, and used the kuenm package (https://github.com/marlonecobos/kuenm; Cobos et al., 2019) in R 3.5.0 (R Core Team, 2018).

For model calibration, 928 candidate models, with parameters reflecting all combinations of 8 regularization multiplier settings (0.1, 0.2, 0.5, 0.8, 1, 2, 5, 8), 29 feature class combinations (L, Q, P, T, H, LQ, LP, LT, LH, QP, QT, QH, PT, PH, TH, LQP, LQT, LQH, LPT, LPH, QPT, QPH, QTH, PTH, LQPT, LQPH, LQTH, LPTH, LQPTH), and 4 distinct sets of environmental variables based on different correlation values (see above), have been evaluated for *D. gouveai* and its host species. We had 592 significant models for the calibration area (that is, M area) of *D. gouveai*, and 690 significant models for the calibration area of host species. These models were compared based on the corrected Akaike Information Criterion (AICc) produced by the kuenm package in R. The optimal model was selected based on its omission rate and the lowest AICc

(Akaike's Information Criterion with a correction for small sample sizes) value. AICc serves as a model selection criterion, taking into account both the model's goodness of fit and complexity, with a preference for simpler models that provide a better fit. Finally, for *D. gouveai*, based on the best model of the calibration area, 24 different models were developed across the projection region for the set of 10 bioclimatic variables (Bio1, Bio2, Bio3, Bio5, Bio7, Bio12, Bio14, Bio15, Bio18, Bio19) based on 90% correlation coefficient for the Future (19 models), the Present (one model), the Last Glacial Maximum (three models), and the Last Interglacial (one model). MAXENT settings for the models were default while cross-validation was the replicated run type. Each model was run 10 times with a maximum of 500 iterations and a 1×10^{-5} convergence threshold. We used the 10-percentile training presence for both *D. gouveai* and its host species, and maximum training sensitivity plus specificity (max SSS) thresholding approaches for *D. gouveai* to convert model outputs to binary predictions (Liu et al., 2013; Radosavljevic and Anderson, 2014; Ülker et al., 2018). To assess the statistical robustness of the model predictions, the partial ROC statistic was taken into consideration. In our final model output, we prioritized low omission rates and AUC (Area Under the Curve) for the most accurate predictions. AUC is a metric employed in ecological niche modeling to gauge model performance, with higher values signifying increased accuracy. Raster calculation implemented in ArcGIS version 10.2 and some tools in SDMToolbox version 2.1 (Brown, 2014) were used to show overlap of the three different Last Glacial Maximum models.

3. Results
Although the haplotype network (Figure 1) showed moderately high genetic diversity within *D. gouveai*,

average genetic distances (Table 1) were positively but weakly correlated with geographic distance, which is evidence of isolation-by-distance (Figure 3).

Model calibration results based on the omission rate and AICc values showed that the best model included a regularization multiplier of 1 for *D. gouveai* and two feature types: linear and quadratic; and that the best model included a regularization multiplier of 8 for host species and 3 feature types: quadratic, product, and threshold. The ecological niche model performed better than a random prediction for both *D. gouveai* and its host species based on the most acceptable statistics (the omission rate, and the AUC). The AUC values were larger than 0.7 for training data [AUC for training data = 0.917 (±0.019) for *D. gouveai*, and AUC for training data = 0.745 (±0.038) for its host species] based on ten replicates cross-validation runs for *D. gouveai* and its host species. The prediction for Present bioclimatic conditions mostly matched the known geographic distribution of both *D. gouveai* and its host species, suggesting that the species is very near to equilibrium with climate. However, the prediction also included areas where these species have not been observed in South America, especially on the west coast and middle latitudes (Figure 4). The prediction for the potential distribution of *D. gouveai* did not change much between the Last Glacial Maximum and the Present whereas it did change between the Last Interglacial and the Last Glacial Maximum, and did substantially change between the Present and the Future. This result indicates that *D gouveai*'s distribution was more limited in the Last Interglacial than in the Present, and the species' future distribution will be more limited or the species will be extinct in near future. The projection results for the host species supported the range dynamics of *D. gouveai* for the past and the future

Table 1. The net average genetic distances (dA) among ten populations of *D. gouveai*. Highest values showed in bold.

	FOR	FUR	CEU	MIR	CRI	PIR	FER	BAX	IBO	SER
FOR	0									
FUR	0	0								
CEU	0	0	0							
MIR	**15.67**	2.85	**13.29**	0						
CRI	2.85	0.72	2.33	**9.00**	0					
PIR	1.63	0.72	1.56	−0.01	1.33	0				
FER	3.17	0.79	2.70	**5.67**	2.03	1.22	0			
BAX	1.33	0.52	1.27	0.09	1.22	−0.04	0.85	0		
IBO	1.33	0.28	1.22	1.44	1.17	0.37	0.41	0.06	0	
SER	0.89	0.23	0.89	0.61	0.85	0.14	0.49	−0.07	−0.06	0

FOR: Morro do Forno; FUR: Furnas; CEU: Vale do Céu; MIR: Pirapotanga; CRI: Cristalina; PIR: Pirenópolis; FER: Fercal; BAX: Baxio; IBO: Ibotirama; SER: Serrinha.
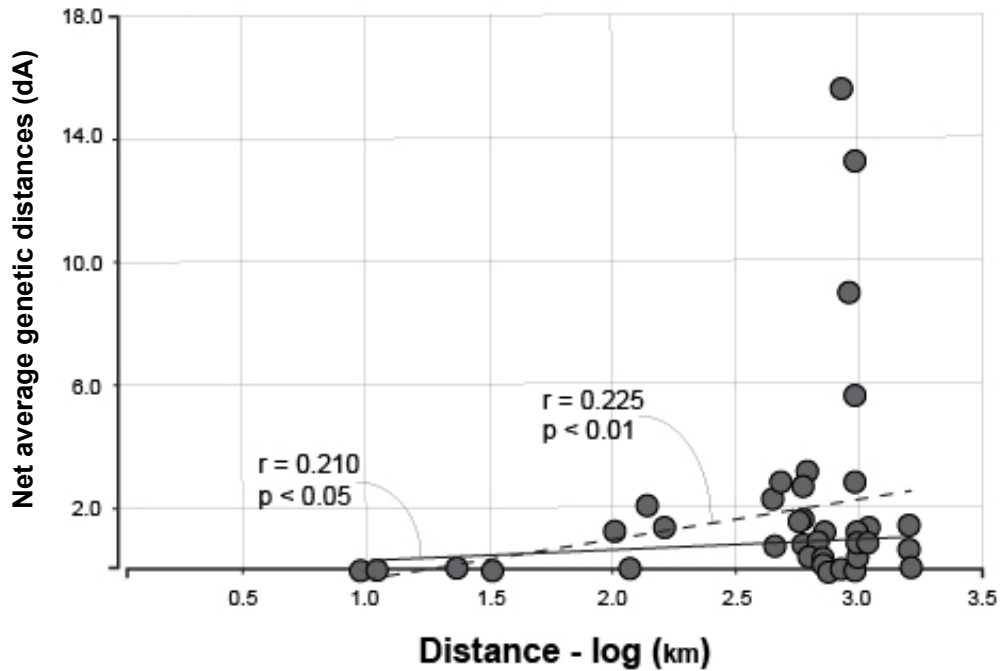
Figure 3. Isolation-by-distance of populations of *D. gouveai* based on mtDNA. Linear regression lines were drawn for all comparisons among populations (full line), and for populations not included MIR (dotted line).
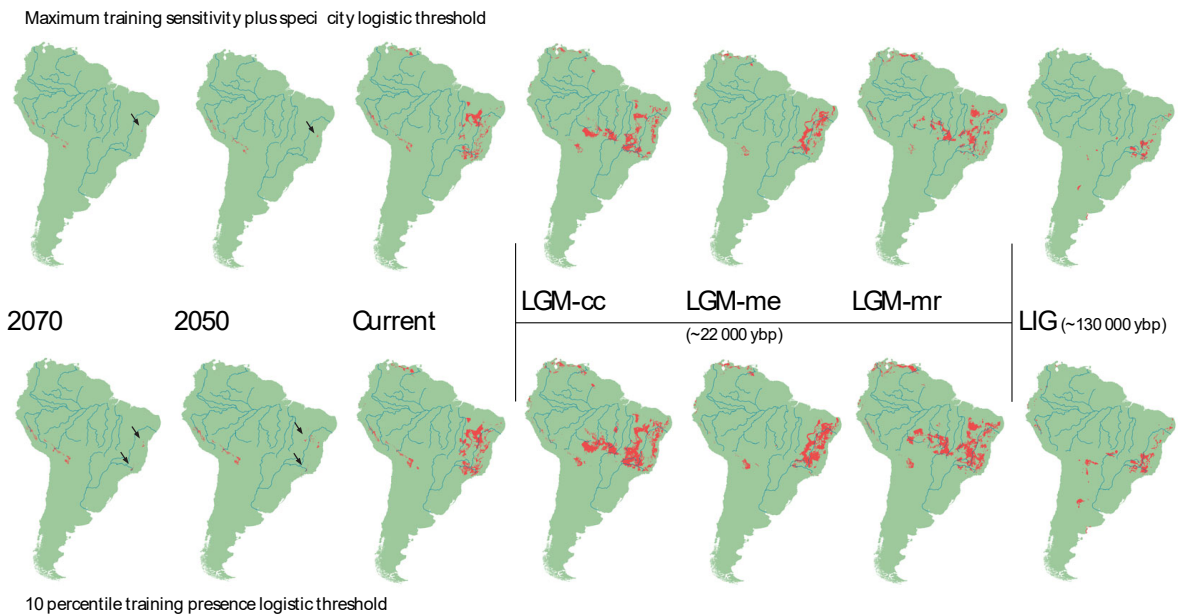
Figure 4. Last Interglacial, Last Glacial Maximum, Present (1960–1990), and the Future (2050 and 2070) predictions of the potential distribution of *D. gouveai* based on two thresholding approaches. Arrows shows very limited potential distribution of *D. gouveai* in 2050 and 2070. The abbreviations are defined as follows: LGM-Last Glacial Maximum, LIG-Last Interglacial. Additionally, specific climate models include LGM-cc (Community Climate System Model), LGM-me (MPI-ESM-P, General Circulation Models), and LGM-mr (Model for Interdisciplinary Research on Climate, Earth System version 2 for Long-term simulations).

(See Figure 5 for predictions). Host species will have a substantial range shift and range contraction in 2050 and 2070.

The percentage contribution or permutation importance suggests that 'Temperature of Warmest Month' (Bio5, 25.7% contribution to the model), 'Precipitation of Warmest Quarter' (Bio18, 16.9% contribution to the model), 'Precipitation of Coldest Quarter' (Bio19, 18.2% contribution to the model)" were the most significant bioclimatic variables in predicting the present distribution of *D. gouveai*; "Mean Diurnal Range (Bio2, 65.3% contribution to the model)" was the most significant bioclimatic variable in predicting the present distribution of two cacti species.

4. Discussion

This study integrated some phylogeographic insights and ecological niche modelling in order to understand how *D. gouveai* has responded to global climate changes through its evolutionary history during the Late Quaternary glacial–interglacial cycles. Including the possible host of *D. gouveai* in this integrity has also led to significant implications for the biogeographical history and future of the species.

Demographic events (e.g., population fluctuations) should be concordant with climate-driven distributional shifts (e.g., expansion and/or contraction, see Brito, 2005). Our results here clearly show that the phylogeography of *D. gouveai* is mostly concordant with the ecological niche modeling results. However, demographic results based on mtDNA genes might have discordant patterns not only with different genes, but also for ecological niche modeling if the negative selection is to driving force (Hung and Zink, 2014; Lapierre et al., 2016). In this study, we only used published mtDNA data, and the neutrality tests

based on Tajima's *D* indicated that results did not depart from neutrality (see Moraes et al., 2009). Finally, these results show a mostly identical pattern to that previously described for cytochrome C oxidase subunit I (COI, Manfrin et al., 2001; de Brito et al., 2002) and II (COII, Moraes et al., 2009). The substantial difference in this study from previous ones is the main discussion on the historical demography of *D. gouveai*.

According to Moraes et al. (2009), the most common mtDNA haplotypes, which are central in haplotype network, occur in different geographic locations in species' distribution range. This means that all these haplotypes are probably ancestral, and that the species filled its distribution range very fast, probably during a very recent time period (e.g., before or after the Last Glacial Maximum). Details of Pleistocene climatic fluctuations in South America are not understood very well (Bush and Silman, 2004), and published information about this topic is very scarce (e.g., Bonatelli et al., 2014). The available predictions for South America indicate evidence of a drier climate in central and eastern Brazil during the Last Glacial Maximum (Ledru et al., 1996, 1998; Salgado-Labouriau et al., 1998; Barberi et al., 2000; Behling 2003). Findings by Barberi et al. (2000) suggested that semiarid climate was dominant in central Brazil during the Last Glacial Maximum. In addition to this, Collevatti et al. (2012) showed some Neotropical savanna tree species exhibited the distributional shrinkage during the Last Glacial period suggesting dry vegetation (e.g., Cactaceae) and its dependencies (e.g., *D. gouveai*) expansion in the same period. Similar to our case in this study, *D. pachea*, the other cactophilic species in the Sonoran Desert, showed a population expansion pattern way before the Last Glacial Maximum (Pfeiler et al., 2007), which was a kind of concordant demographic pattern for *D. gouveai* that we discussed in this study. The

Cereus hildmannianus &
Pilosocereus machrisii
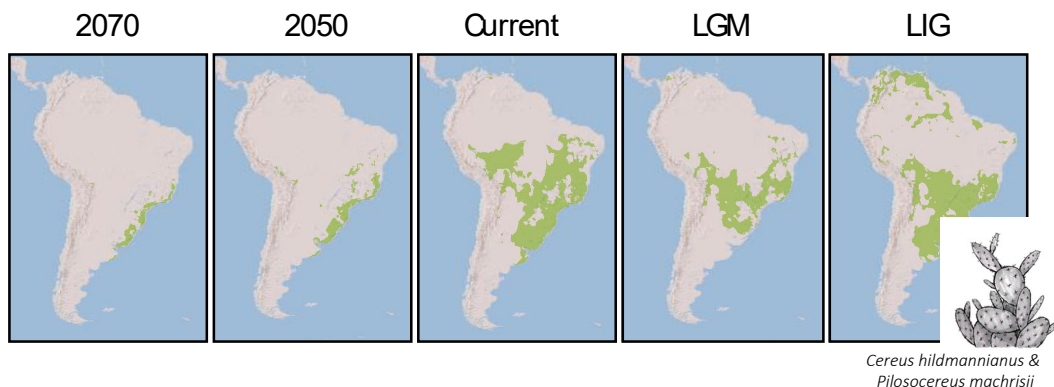
Figure 5. Last Interglacial, Last Glacial Maximum, Present (1960–1990), and the Future (2050 and 2070) predictions of the potential distribution of two cacti species (*C. hildmannianus* and *P. machrisii*) based on 10% thresholding approaches. The abbreviations are defined as follows: LGM-Last Glacial Maximum, LIG-Last Interglacial.

phylogeographic study of the other species, *D. mojavensis*, showed some signals for separate refugia located in the Mojave Desert and Sonoran Desert during the Last Interglacial (Smith et al., 2012).

Vertebrate species distributed in the southern part of the Western Palearctic temperate region (i.e. Mediterranean species) have different distribution patterns during the Last Glacial Maximum than temperate species (e.g., Gür, 2013; Perktaş et al., 2015). Even in the far eastern Palearctic, in China, one songbird species, the green-backed tit (*Parus monticolus*), shows a similar pattern to the Mediterranean species (Wang et al., 2013). Therefore, *D. gouveai* was a suitable species to test this biogeographic pattern in South America using phylogeography and ecological niche modeling.

Our results showed that *D. gouveai* experienced unusual demographic and range expansion because of the Late Quaternary glacial–interglacial cycles. This is likely to have occurred during the cooling transition between the Last Interglacial and the Last Glacial Maximum, approximately at the beginning of the Last Glacial Period. The present patchy distribution of *D. gouveai* could have been because of independent expansion from different refugia (see Moraes et al., 2009) during the Last Interglacial. Moraes et al. (2009) gave a detailed discussion about haplotype distribution within *D. gouveai*, and underscored the absence of gene flow between geographical regions. In this study, we conducted an isolation-by-distance analysis and it showed a significant positive correlation between average genetic distance and geographical distance. This result clearly supports the claim of an expansion event from different refugia because of the more than model haplotypes, as discussed by Moraes et al. (2009); and this result might be significant due to isolation in allopatric refugia in the Last Interglacial.

Integrating phylogeography with ecological analysis is crucial to understand species' recent demographic history (Perktaş and Gür 2015, for an example, please refer to Capainolo et al. 2023). In this study, we added ecological niche modeling analysis to the previously published demographic panorama. Moraes et al. (2009) suggested that all demographic events experienced by *D. gouveai* occurred before the Last Glacial Maximum. This claim is clearly supported by our ecological niche modeling results. The pre-Last Glacial Period has been discussed as an age of range expansion for various organisms in this region (Wüster et al., 2005; Almeida et al., 2007) and in the Palearctic Region, as mentioned above (Perktaş et al., 2015; Wang et al., 2013). This raises the scenarios of how and why the Last Interglacial affected the distribution of *D. gouveai* in South America.

During the Last Interglacial, climate conditions supported a similar vegetation structure to that observed today (Li et al., 2006; Qu et al., 2011). Thus, we first expected that the predicted distribution for *D. gouveai* should be similar during the Last Interglacial to its present-day distribution. However, very interestingly, the results of our ecological niche modelling analysis did not support this hypothesis for *D. gouveai* in South America. Instead, the predicted refugial area was almost consistent with previously published genetic analysis and our historical demography analysis. The expansion started before the Last Glacial Maximum and continued until about 22,000 years ago. This exactly matches the conclusion of Moraes et al. (2009). Allopatric refugia are located on the east bank of the Paraná River and the other on the west bank. These results mean that all dry vegetation was more common than today. Average temperatures during the Last Interglacial are known to have been about 2 °C–5 °C warmer than present (Otto-Bliesner et al., 2006). This warmer temperature led to the dry areas within the distribution range of *D. gouveai* becoming larger. However, especially precipitation during the coldest quarter, which was the most important variable in the model of the distribution range of *D. gouveai*, must have been very high during most of the Last Interglacial. Therefore, a warming climate could have made *D. gouveai* more widespread in its distribution range. However, the precipitation pattern may have pushed their distribution to the refugia or something else may have happened. The most evident conclusion regarding this situation becomes apparent when we concentrate on *D. gouveai*'s host. Two different species of cacti (*C. hildmannianus* and *P. machrisii*) were those that shaped the vegetation where *D. gouveai* was found. *D. gouveai* lives to some extent dependent on these cacti species. Therefore, when the possible scenarios are combined with the results of the ecological niche modelling of the potential hosts of *D. gouveai*, it turns out that the species probably lost most of its distribution range in the south after the Last Interglacial, and made an almost complete range shift during the Last Glacial period. In other words, *D. gouveai* possibly started to increase its effective population size during the last 55,000 years, and following its hosts, especially due to the displacement of arid areas. The conclusion we reached in this study draws attention to an important point. In order to understand the biogeographic responses of host-dependent endemic species such as *D. gouveai* to climate change, we must first understand the biogeographic responses of their hosts to climate change.

Previous phylogeographical studies have suggested that responses to Pleistocene climate fluctuations vary among species and regions. However, there is now concordance between South America, the Mediterranean Region, and East Asia for different organisms. Our results strongly show that the Last Interglacial played a significant role in shaping the demographic history of not only *D. gouveai*,

but also its hosts. Thus, this study contributes to the idea that species' responses to Pleistocene climate fluctuations have been more varied than previously thought. Overall, this study makes a significant contribution to the growing literature on the effect of the Last Interglacial on the distribution patterns of different organisms.

Regarding climate change in the future, our results confirmed that *D. gouveai* will certainly be affected by global warming in the near future. This is substantially important for conservation actions in South America, because this species uses a specific habitat based on specific vegetation in this region, and has relatively narrow physical limits for resource utilization like other drosophilids (Parsons, 1982). Therefore, this specification makes this species

more sensitive to climate change, and, of course, *D. gouveai* may experience the extinction risk or a substantial range shift and range contraction once again, depending on the range-shift and contraction event of the host to which it is associated (Figure 5). The extinction risk is also important for the region where this species distribute because global warming will finally lead to a reduction in biodiversity by eliminating this kind of specialist, and conservation strategies need to be taken care of this effect in this kind of high biodiversity region in the world.

Author contribution

UP and BSO conceived of the study; and both authors prepared and edited the manuscript.

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