A look into the past, present and future potential distributions of Talinopsis frutescens, a North American endemic lineage closely related to Cactaceae: Postprint

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Abstract

Talinopsis frutescens (Anacampserotaceae, a family that is close related to Cactaceae) is a succulent species endemic to North America. The aim of this study was to explore, using Ecological Niche Modeling (ENM), changes in potential distribution ranges considering different climate scenarios: past conditions during the Last Inter Glacial (LIG) and the Last Glacial Maximum (LGM), the present and projections for 2070 (RCP 2.6 to 8.5). A pattern of contraction is observed during the LIG, which agrees with other studies focused in species from arid environments. This pattern was followed by a migration towards the south during the LGM and a possible recent expansion to the north as is observed in the present scenario. All future projections show the same contraction and fragmentation patterns, resulting in three discontinuous areas: the northern part of the Chihuahuan Desert, the southern-central part of the Mexican Plateau, and the smallest one in the Tehuacán-Cuicatlán Valley. Our projections for future scenarios agree with other studies and support that global climate change tends to alter the current distribution of arid environment species.

Full Text

Preamble

A Look into the Past, Present, and Future Potential Distributions of *Talinopsis frutescens*, a North American Endemic Lineage Closely Related to Cactaceae

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Abstract: *Talinopsis frutescens* (Anacampserotaceae, a family closely related to Cactaceae) is a succulent species endemic to North America. Using Ecological Niche Modeling (ENM), this study explores changes in potential distribution ranges under different climate scenarios: past conditions during the Last Interglacial (LIG) and the Last Glacial Maximum (LGM), the present, and projections for 2070 (RCP 2.6 to 8.5). A pattern of contraction is observed during the LIG, which agrees with other studies focused on species from arid environments. This pattern was followed by a migration towards the south during the LGM and a possible recent expansion to the north as observed in the present scenario. All future projections show the same contraction and fragmentation patterns, resulting in three discontinuous areas: the northern part of the Chihuahuan Desert, the southern-central part of the Mexican Plateau, and the smallest one in the Tehuacán-Cuicatlán Valley. Our projections for future scenarios agree with other studies and support that global climate change tends to alter the current distribution of arid environment species.

Keywords: Anacampserotaceae; Caryophyllales; ecological niche modeling; succulent plants; potential distribution

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1 Introduction

Anacampserotaceae is a lineage closely related to Cactaceae (Hernández-Ledesma et al., 2015; Walker et al., 2018). Within Anacampserotaceae, the succulent species *Talinopsis frutescens* A. Gray is the earliest divergent taxon (Ocampo and Columbus, 2010). *Talinopsis frutescens* is endemic to North America and distributed from southwestern USA to the central-southern part of Mexico (Ocampo, 2011). The current known distribution corresponds to a discontinuous area from southern USA to the northern part of the Trans-Mexican Volcanic Belt (TMVB), including the Chihuahuan Desert (CD) and the Mexican Plateau (MP). Although most populations are found in the CD and MP, a few are located on the southern side of the TMVB in the Tehuacán-Cuicatlán Valley (TCV) (Fig. 1 [Figure 1: see original paper]).

The CD is the largest desert in North America and one of the most species-rich arid regions in the world (Morafka, 1977; Hoyt, 2002). Along with the MP, the CD has been suggested as a center of origin for modern desert taxa and appears to have existed since the middle Miocene (Morafka, 1977). The TCV belongs to the Mexican xerophytic region (Rzedowski, 2005) and is thought to be closely related to the CD. Together with the Actopan and Mesquital valleys, it represents one of the isolated arid areas in southern Mexico (Shreve, 1942). The TCV exhibits high plant diversity, representing 10.0%-11.4% of Mexican plant species (Valiente-Banuet et al., 2009), including a large number of endemic taxa (Dávila et al., 2002). The history of the TCV appears closely linked to the TMVB, whose emergence separated the northern-central part (northern tectonic domain) from the southern region (southern tectonic domain) of Mexico (Ferrari et al., 1999; Cevallos et al., 2012) and promoted differentiation of the CD and southwestern semi-desert relicts (De-Nova et al., 2018). The complex history of North American arid zones (Wilson and Pitts, 2010; Hafner and Riddle, 2011) and the distribution pattern of *T. frutescens* raise questions about the factors that shaped the species' disjunct distribution and whether this distribution has changed through time.

There is evidence that arid environments experienced drastic climate changes during the last glacial period (Metcalfe, 2006), particularly during the Last Interglacial (LIG; 1.2×10 -1.4×10 years ago) and the Last Glacial Maximum (LGM; approximately 2.2×10 years ago). Studies show that several native species from arid environments have altered their distribution ranges in response to past climatic fluctuations, including *Berberis trifoliolata* (Berberidaceae; Angulo et al., 2017), *Ephedra compacta* (Ephedraceae; Loera et al., 2017), *Larrea tridentata* (Zygophyllaceae; Hunter et al., 2001), and *Lindleya mespiloides* (Rosaceae; Vásquez-Cruz and Sosa, 2016). Because *T. frutescens* is primarily distributed in arid environments, it is likely that these climatic oscillations affected its distribution range. Therefore, this study aimed to estimate whether climatic conditions during the LIG and LGM periods affected the distribution range of *T. frutescens*. Additionally, as an exploratory approach, we examined potential changes in the species' distribution range due to global warming caused by increased greenhouse gas emissions.

2.1 Study area

Talinopsis frutescens occurs in the CD, from the southern part of the USA to the TMVB, across the MP and into the TCV in central Mexico (Fig. 1). The CD is the largest desert in North America, covering an area of 6.48×10 km^2 and representing one of the most biologically diverse arid regions in the world (Morafka, 1977; Hoyt, 2002). The MP lies between the Sierra Madre Occidental and the Sierra Madre Oriental, with vegetation consisting of grass steppes dominated by *Bouteloua* and *Aristida*, interspersed among xeric scrubs and forests in plains and intermontane valleys (Morrone, 2005). The TCV floristic province is part of the Mexican xerophytic region (Rzedowski, 2005) and is located in southern Puebla and northern Oaxaca. The valley covers approximately 1.00×10 km^2 and represents a complex physiographic mosaic with internal valleys separated by numerous mountain chains. Plant diversity represents 10.0%-11.4% of national diversity with a high number of endemisms

(Dávila et al., 2002).

2.2 *Talinopsis frutescens*

Individuals of this species are small shrubs with tuberous roots; its succulent leaves are deciduous during the dry season, and inflorescences bear few yellow (e.g., Rzedowski, 2005; Ocampo, 2011) to pink (Kiger, 2003) flowers. The species primarily occurs in dry forest and xerophytic scrubs, although it has also been found in crops, grasslands, and secondary vegetation derived from coniferous and pine-oak forests at elevations ranging from 1000–1300 to 2300–2500 m a.s.l. (Ocampo, 2011).

Talinopsis frutescens has been poorly studied, and biological aspects such as pollination, dispersal, and interactions with other organisms remain unclear. However, field observations indicate that seeds of *T. frutescens* typically germinate near or under other plants such as cacti, *Parthenium* sp. (Asteraceae), and *Larrea tridentata* (Zygophyllaceae). Additionally, flowers bloom only once and remain open for just a few hours, suggesting limited opportunities for cross-pollination (Miguel-Vázquez and Ocampo, 2017).

2.3 Data and ecological niche modeling (ENM)

A total of 146 records of *T. frutescens* were obtained from biodiversity datasets, herbarium specimens, and our own collections (Table S1 of the Appendix). All records included in this study were at least 1 km apart. We employed the 19 environmental variables provided by WorldClim 1.4 for present and future conditions (year 2070); for the latter scenario, four different Representative Concentration Pathways (RCPs; 2.6, 4.5, 6.0, and 8.5) were considered (Hijmans et al., 2005). Past projections included LIG and LGM data (Otto-Bliesner et al., 2006). All datasets have a 1 km × 1 km spatial resolution except the LGM layers, which have a 5 km × 5 km resolution.

We performed simulations with Maxent v3.4.0 (Phillips et al., 2017) using the Community Climate System Model (CCSM4; Gent et al., 2011) with a convergence threshold of 10 , maximum iterations of 1000, regularization multiplier of 1, and default values for remaining modeling parameters. To evaluate model quality, we partitioned the data into training (75%) and testing (25%) datasets.

To confirm that variables with the highest contribution percentages for each of the seven models were not highly correlated ($r > 0.90$), we conducted a Pearson' s correlation analysis among the 19 variables using ENMTools (Warren et al., 2008). Additionally, this program was used to statistically compare the niche breadth (Nakazato et al., 2010) of the seven models obtained, using B1 and B2 metrics (Levins, 1968) to measure the uniformity of species distribution among resources (Rolando, 1990).

3 Results

Temperature seasonality contributed most to the ENM for both LIG and present scenarios (24.7% and 22.4%, respectively). In contrast, isothermality (temperature mean diurnal range/precipitation of the driest quarter; 25.7%-33.5%) contributed most to the LGM and all four future projections, followed by precipitation of the coldest quarter (18.9%-23.9%). Together, these two variables contributed nearly 50.0% to the models (Table 1). None of the most important variables for each model had correlation values (r) exceeding 0.90 (data not shown). For the niche breadth test, we used a standardized measure from the R package ENMTools, based on the B2 metric from Levins (1968).

We report but do not discuss B1 values because the package author notes that the current implementation in ENMTools is a standardized value that, in combination with the logarithmic equation of B1, can lead to incorrect interpretations of the metric that becomes dependent on sample size. The B2 metric is a standardized measure of niche breadth that only has meaning in the context of our resultant models; it works with suitability values from the same models rather than with the proportion of species found in a given space as originally described. B2 is reported as a general measure of how suitability values are distributed across all non-null cells, with values ranging from 0 to 1, where zero represents the most reduced breadth and one represents maximum breadth. The highest value was obtained for the LIG (B2 = 0.9231), while the lowest value was obtained for the LGM (B2 = 0.8875). The B2 value for the present was 0.9101, and values for the four future scenarios varied moderately relative to the present scenario (Table 2).

The area with highest occurrence probabilities for the LIG model is concentrated in the southern-central part of the MP and a very small area in the northern part of the CD; occurrence probability for the TCV is very low (Fig. 2a [Figure 2: see original paper]).

The LGM model estimated a shift in distribution range toward southern Mexico, showing high occurrence probabilities in three well-defined regions: the southern part of the MP, the TCV, and the southern part of the Sierra Madre del Sur (SMS; Fig. 2b).

The present scenario model properly predicted the known distribution range of *T. frutescens*, assigning high occurrence probabilities primarily to the southern-central part of the USA, the MP, and the TCV, while excluding the mountain region of the TMVB (Fig. 2c).

All future scenarios for *T. frutescens* distribution showed a general pattern of range reduction and fragmentation compared to the present (Figs. 2d-g). High occurrence probabilities are concentrated in the central and meridional part of the MP, while a very reduced and isolated suitable area in the northern part of the CD was predicted for three RCP scenarios (4.5, 6.0, and 8.5; Figs. 2e-g). Additionally, an important pattern of range reduction was detected in the

TCV, where areas with high occurrence probabilities were almost absent.

4 Discussion

The LIG projection shows high occurrence probabilities concentrated mainly in the central part of the MP, with small areas in the northern part of the CD. Although the niche breadth metric value for the LIG scenario was the highest, the area with high occurrence probabilities was concentrated only in the southern part of the MP, with very low probabilities in the TCV. This suggests a contraction event during the LIG period when compared to the present scenario. This pattern agrees with estimations for other arid environmental taxa such as *Agave lechuguilla* (Scheinvar et al., 2017), *Berberis trifoliolata* (Angulo et al., 2017), and *Ephedra compacta* (Loera et al., 2017), where present distribution is larger than that predicted for the LIG period. However, few examples show distribution ranges predicted for the LIG and present that are very similar, as observed for *Lindleya mespiloides* (Vásquez-Cruz and Sosa, 2016).

The shift toward southern Mexico predicted for the LGM period may have been facilitated by variations in precipitation regime (amount and seasonality), temperature, and sea level, which promoted migration of many arid environmental taxa to lower latitudes (Metcalfe, 2006). Notably, the three areas with predicted high occurrence probabilities during the LGM were apparently isolated from each other. Formation of the TMVB, specifically its last volcanic episode (from the late Pliocene to the Holocene; Gómez-Truena et al., 2007), may be responsible for this pattern in the southern part of the distribution range, where populations were potentially isolated from those located in the MP. Coupled with this pattern, the niche breadth metric obtained for the LGM was the lowest, suggesting a reduction in area potentially occupied by the species during that period. In general, the models and niche breadth test values support the hypothesis that the distribution range of *T. frutescens* changed throughout the last interglacial and glacial periods.

Studies on native species from arid environments have shown that their distribution ranges experienced contraction and fragmentation patterns during the LGM period. For instance, *Larrea tridentata* is one of the most common and important elements in the CD and currently has a broad distribution range in the MP; however, its distribution range experienced contractions and expansions and has recently (Holocene) expanded to the northern part of the CD (Duran et al., 2005). The fact that *L. tridentata* may act as a nurse plant for *T. frutescens* (Miguel-Vázquez and Ocampo, 2017) and that both species show a similar pattern of recent expansion to the northern CD could indicate a close relationship between these taxa, suggesting potential correlation in distribution changes during the LIG and LGM periods. Similar nursing interactions of *L. tridentata* with other arid environmental plant species, especially cacti, have been documented (Samour-Nieva, 2012). Implications of Pleistocene glacial and interglacial period effects have been addressed in other studies, including gene flow limitation, decline or loss of genetic variation, isolation in refugia, and recent expansions (Nason et al., 2002; Ruiz-Sánchez et al., 2012; Scheinvar et al., 2017).

The four future scenarios and observed reduction and isolation events agree with models estimated for other taxa whose distribution ranges have been affected by climate change (Kelly and Goulden, 2008). Our study shows that isothermality (the variable with highest contribution to all future scenarios, ranging from 25.7% to 33.5%) and precipitation in the coldest quarter (19.4%-23.9% contribution) could be factors affecting the species' distribution range. These results have strong implications because climate change produces not only aridification but also changes in precipitation regime (IPCC, 2007). These two processes will likely severely impact the distribution range of *T. frutescens* and its associated species; for instance, the distribution of *L. tridentata* has already been affected by temperature changes due to climate change (Ballesteros-Barrera, 2008). Another ENM study focusing on *Neobuxbaumia tetetzo* (Cactaceae), an endemic species from the TCV, showed a pattern of distribution range contraction in future projections (Dávila et al., 2013). Recently, Sosa et al. (2018) proposed areas of interest with high endemism in Mexico, most occurring in places with some conservation status; however, it is concerning that areas located in the CD are not under any legal protection. *Talinopsis frutescens* is found in two of the most biodiverse arid regions in North America (CD and TCV) and establishes associations with plants emblematic of these areas (i.e., cacti and creosote bush (*L. tridentata*)). Therefore, data obtained in this study may provide valuable information for conservation purposes, contribute to understanding the evolution of North American arid zones, and support creation of new natural protected areas within this important habitat.

5 Conclusions

Our results indicate that the distribution range of *T. frutescens* may have changed in the past and is potentially prone to range reduction and fragmentation due to climate change effects. The pattern observed for past scenarios agrees with results reported for other species from arid environments, supporting the Pleistocene refugia hypothesis where organisms remained isolated during these periods. The present scenario shows a recent possible expansion in the northern part of the CD, which may have occurred after the LGM once climatic conditions in the CD changed and aridification of that region began. Finally, all future projections show distribution range contraction and fragmentation, including considerable reduction or even local extinction of the southernmost *T. frutescens* populations located in the TCV.

This preliminary study provides information about the possible behavior of a North American endemic species during glacial and interglacial periods and simultaneously offers estimations of possible global warming effects on taxa from arid environments. Our results agree with other studies demonstrating the negative effect of this factor on species distribution ranges, which tends to modify them and may induce local extinctions in the worst scenarios. We hope this information will help draw more attention to changes and effects of higher carbon emissions on deserts and other arid environments—ecosystems that are very important due to their high numbers of endemic plant and animal species and their support of a substantial fraction of North American biota.

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Note: Figure translations are in progress. See original paper for figures.