Species Dispersal Modes in Amphitropical Plant Species of North and South America

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Species Dispersal Modes in Amphitropical Plant Species of North and South America

An Honors Thesis submitted in partial fulfillment of the requirements for Honors in the Department of Biology

By
Samera Lemma Mulatu

Under the mentorship of Dr. John Schenk

ABSTRACT
Amphitropical disjunct plants are species that occur in both North and South America but not in the intermediate equatorial region. How amphitropical species dispersed across the Americas to their current distribution remains uncertain. To explain amphitropical distributions, three hypotheses were developed to test that (1) species dispersed successively through island hopping across the tropical zone in temperate microhabitats (= stepping stones), (2) species came to their current distribution through vicariance, or (3) species dispersed by a single long distance dispersal event. Twenty-five species were studied to infer their historical distributions with species distribution models in MaxEnt. Distribution models for each species were estimated under three different timelines: the current climate, the last glacial maximum (22,000 years ago), and the last interglacial maximum (120,000–140,000 years ago). Ecological niche models were generated in MaxEnt with 19 bioclimate variables from the WorldClim database. Across the three time slices, the vicariance hypothesis was rejected in all but one species for one of its time slices. In thirteen experiments, the long-distance dispersal and vicariance hypotheses were rejected in favor of the stepping stone hypothesis. In thirty-seven experiments, the stepping stone and vicariance hypotheses were rejected in favor of long distance dispersal. There were three species that could have dispersed by shorter-distance-dispersal events via intermediate populations. Although our results suggest that long distance dispersal was the most dominant mechanism of dispersal among amphitropical species, they also convey that numerous shorter-distance-dispersal events via intermediate, favorable populations are an underappreciated mode of dispersal.

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Department of Biology
University Honors Program
Georgia Southern University
**Introduction**

A species range is determined in large part by its ability to disperse and its tolerance of novel environmental conditions (Holt, 2003). One of the most remarkable examples of species range distributions involve amphitropical species disjunctions. Amphitropical species reside in both North and South America, yet not in the connected, tropical region (termed American amphitropical disjuncts; Schenk & Saunders, 2017; Raven et al., 1963). Due to past geological development, certain areas in both North and South America are known to have cognate climates and landscape features (Johnson & Porter, 2017). Therefore, the same species can reside in suitable habitats on opposite sides of the tropics in both North and South America (Raven et al., 1963; Gray and Hooker, 1880). However, how amphitropical species dispersed across the Americas to their current distribution remains uncertain. Even though biologists have considered three possible hypotheses to explain amphitropical disjunct patterns, an explicit set of hypotheses have not been tested across amphitropical species (Schenk & Saunders, 2017; Raven et al., 1963).

We will use ecological niche modeling to test the hypotheses that (1) species dispersed by island hopping across the tropical zone in temperate microhabitats, (2) species came to their current distribution through vicariance, or (3) species dispersal by a single long distance dispersal event (Gray & Hooker, 1880). The island-hopping hypothesis postulates that species inhabited temperate microhabitats along the tropics and were able to form intermediate equatorial habitats between the two continents. Biologists have collected very little evidence in support of this stepping stone hypothesis (Schenk & Saunders, 2017; Raven et al., 1963). The variance hypothesis theorizes that these species originally had ranges that were widespread in both North America, South America, and the connecting tropical regions. Yet due to the climate change in the tropics, the species went extinct in these areas causing amphitropical disjunction (Schenk & Saunders, 2017; Johnson &
Biologists have never been able to collect empirical evidence in support of the vicariance hypothesis. The long-distance dispersal hypothesis is the most widely accepted hypothesis among the three above hypotheses (Schenk & Saunders, 2017; Nathan, 2006). The long-distance dispersal hypothesis postulates that populations of amphitropical species from one side of the North America equator dispersed through a single event onto one side of the South America equator with a similar habitat (Schenk & Saunders, 2017; Raven et al., 1963). Even though these hypotheses have been proposed by biologists to explain possible modes of dispersal among amphitropical species, they have never been explicitly tested for validation.

Species distribution models (SDMs) for each amphitropical species were estimated under three different timelines, current glacial maximum (CGM, current distribution patterns), last glacial maximum (LGM), and last interglacial maximum (LIGM). The LGM was about 22,000 years ago. It refers to the most recent time period when the glaciers’ global ice volume was at their thickest and global sea levels reached their lowest across the world (Otto-Bliesner & Brady, 2005). The LIGM was approximately 120,000–140,000 years ago. The LIGM is the warmest time period on Earth in the last 200,000 years. It was the last time in history when ocean sea levels were as high as current-day sea levels (Neumann & Hearty, 1996). Species dispersal patterns were observed before and after the movement of the glaciers to detect how the switch in climate between cold glacial and warm interglacial intervals would affect the species’ ability to disperse. There are very few empirical studies that evaluated divergence timing in amphitropical species dispersal; precisely 30% of amphitropical dispersal papers even recognize divergence timing (Simpson et al., 2017; Raven et al., 1963). We are interested in determining how amphitropical species dispersed to their current ranges, and the divergence timing of species over three glacial maxima in response to changes in worldwide environmental conditions.
Materials and Methods

Sampling

Twenty-five amphitropical species were studied to infer their historical distributions with species distribution models (SDM). Species were chosen through literature articles (e.g., Raven et al., 1963). Species were only selected if they had distribution ranges of fifteen occurrences or more in both North and South America, respectively. Distribution data of each species were downloaded from GBIF (http://gbif.org) and ranges were verified in ArcMap (http://esri.com) for consistency. Distribution patterns for all amphitropical species were also double checked for accuracy (Flora North America, floranorthamerica.org).

Species distribution models

Maximum entropy (MaxEnt) is a general statistical method used widely for ecological niche modeling. Species distribution models (SDM) were generated in MaxEnt (Phillips & Dudik, 2008) with a Pleistocene climate model (http://www.worldclim.org) that accounted for past bioclimatic variables using 19 WorldClim climate variables (Hijmans et al., 2005). 20% of test data were used to train the model. MaxEnt created a(n): area under the curve (AUC) plot, test data line, and image of the map of the study area. The AUC scores calculated how well the model differentiated presence from the background data. AUC scores were calculated for each species during all three timelines. The AUC scores were used to check the level of performance for each species model, and in our studies, we defined an ideal AUC score as 0.95 or higher. The test data line indicated how the model fit the data, and how well the model predicted the distributions of the species. Our theoretical presumptions were significant based off our random prediction line of AUC = 0.95. The study area image created through MaxEnt provided an indication on how well
the models predicted the distribution of each species, and a map indicating the probability of occurrence in the past time slices.

Species distribution models for each amphitropical species were estimated under three different timelines, current glacial maximum (CGM, current distribution patterns), last glacial maximum (LGM, approximately 22,000 years ago), and last interglacial maximum (LIGM, approximately 120,000–140,000). After SDM were created for all amphitropical species, SDM for each species during each of the three timelines were compared to observe and draw conclusions on how the species dispersed over time. The SDM were evaluated by studying the distribution points for each SDM then deciding which mode of dispersal/hypothesis could be rejected.

*Species mode of dispersal*

A hypothesis was rejected if the mode of dispersal observed in that species did not correlate with the three tested modes of dispersal. If species distribution models conveyed that the species had a high probability of occurrences in both continents and the tropical regions along the continents, we identified the species as having stepping stone dispersal in favor of long distance dispersal. If SDM conveyed a high probability of widespread occurrences of species in North America, South America, and the connecting tropical regions, we would fail to reject the vicariance hypothesis for that species. If SDM conveyed a high probability of occurrences on one side of the North America equator dispersed through a single event onto the opposite side of the South America equator, we would reject the stepping stone dispersal hypothesis in favor of long distance dispersal. Our approach did not allow us to test for long distance dispersal directly, as species could have dispersed over intermediate stepping stone habitats.
Table 1: The total number of species sampled in North and South America for all twenty-five species, and their mode of dispersal across all three maxima.

<table>
<thead>
<tr>
<th>Species</th>
<th>#Sampled in NA</th>
<th>#Sampled in SA</th>
<th>Total number of samples</th>
<th>Last Glacial Maximum</th>
<th>Current distribution</th>
<th>Last Interglacial Maximum</th>
</tr>
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<tr>
<td>Alopecurus magellanicus</td>
<td>2119</td>
<td>117</td>
<td>2236</td>
<td>stepping stone</td>
<td>stepping stone</td>
<td>stepping stone</td>
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<tr>
<td>Alyssia gratissima</td>
<td>22</td>
<td>290</td>
<td>312</td>
<td>long distance</td>
<td>long distance</td>
<td>stepping stone</td>
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<tr>
<td>Calamagrostis stricta</td>
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<td>83</td>
<td>15235</td>
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<td>long distance</td>
<td>long distance</td>
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<tr>
<td>Crassula connata</td>
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<td>51</td>
<td>1447</td>
<td>long distance/mex intermediate</td>
<td>long distance/mex intermediate</td>
<td>long distance</td>
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<tr>
<td>Fragaria chiloensis</td>
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<td>429</td>
<td>1423</td>
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<td>long distance</td>
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<tr>
<td>Greeneocharis circumsissa</td>
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<td>18</td>
<td>1843</td>
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<td>long distance</td>
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<tr>
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<td>74</td>
<td>722</td>
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<tr>
<td>Hypericum gentianoides</td>
<td>427</td>
<td>13</td>
<td>440</td>
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<td>stepping stone</td>
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<td>Lappula redowskii</td>
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<td>75</td>
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<td>773</td>
<td>951</td>
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<td>Microsteris gracilis</td>
<td>1067</td>
<td>99</td>
<td>1166</td>
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<td>Muhlenbergia alopecuroides</td>
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<td>800</td>
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<td>Muhlenbergia asperiolofa</td>
<td>1167</td>
<td>82</td>
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<td>stepping stone</td>
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<td>Osmorhiza chilensis</td>
<td>1317</td>
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<td>1364</td>
<td>long distance</td>
<td>long distance</td>
<td>long distance</td>
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<tr>
<td>Perityle emoryi</td>
<td>1766</td>
<td>98</td>
<td>1864</td>
<td>long distance</td>
<td>long distance</td>
<td>long distance</td>
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<tr>
<td>Plantago patagonica</td>
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<td>467</td>
<td>1124</td>
<td>long distance</td>
<td>long distance</td>
<td>long distance</td>
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<tr>
<td>Polemonium micranthum</td>
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<td>53</td>
<td>347</td>
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<td>stepping stone</td>
<td>long distance</td>
</tr>
<tr>
<td>Ranunculus bonariensis</td>
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<td>124</td>
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<td>long distance</td>
<td>stepping stone</td>
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<tr>
<td>Scleropogon katwinskyanus</td>
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<td>15</td>
<td>389</td>
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<tr>
<td>Stipa speciosa</td>
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<td>320</td>
<td>1848</td>
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<td>long distance</td>
<td>long distance</td>
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<tr>
<td>Thelesperma megapotamicum</td>
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<td>94</td>
<td>1665</td>
<td>long distance</td>
<td>long distance</td>
<td>long distance</td>
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<tr>
<td>Tiquilla nuttallii</td>
<td>299</td>
<td>38</td>
<td>337</td>
<td>long distance</td>
<td>long distance</td>
<td>vicariance</td>
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</tbody>
</table>
Results

*Current Glacial Maximum*

We rejected a vicariance hypothesis as a possible explanation of dispersal for all twenty-five species. In twenty-three species, we further rejected the stepping stone hypothesis in favor of the long distance dispersal. These twenty-three species were: *Aloysia gratissima, Calamagrostis stricta, Crassula connata, Fragaria chiloensis, Greeneocharis circumscissa, Hypericum gentianoides, Lappula redowskii, Lupinus microcarpus, Mentzelia albescens, Microsteris gracillis, Muhlenbergia alopecuroides, Muhlenbergia asperifolia, Muhlenbergia schreberi, Osmorhiza chilensis, Perityle emoryi, Plantago patagonica, Polemonium micranthum, Scleropogon katwinskyanus, Stipa speciosa, Thelesperma megapotamicum*, and *Tiquilia nuttallii*. Two species, *Alopecurus magellanicus* and *Ranunculus bonariensis*, were identified as having stepping stone dispersal. Our approach did not allow us to test for long distance dispersal directly. The AUC (area under curve) test average in the CGM was calculated as 0.986.
Figure 1. There were two amphitropical species that dispersed through stepping stone disjunct patterns during the current glacial maximum. The example presented above is *Alopecurus magellanicus*. We were able to identify this species as having stepping stone dispersal because of the high probability of occurrence in both North and South America and the intermediate habitats formed along the tropical regions.

Figure 2. There were twenty-three amphitropical species that dispersed through long distance dispersal during the current glacial maximum. The example presented above is *Stipa speciosa*. We were able to identify this species as having long distance dispersal because it’s high probability of occurrence in only North and South America.
Last glacial maximum

We rejected a vicariance hypothesis as a possible explanation of dispersal for all twenty-five species. In twenty-three species, we further rejected the stepping stone hypothesis in favor of the long distance dispersal. These twenty-three species were: *Aloysia gratissima*, *Calamagrostis stricta*, *Crassula connata*, *Fragaria chiloensis*, *Greeneocharis circumsicissa*, *Hypericum gentianoides*, *Lappula redowskii*, *Lupinus microcarpus*, *Mentzelia albescens*, *Microsteris gracillis*, *Muhlenbergia alopecuroides*, *Muhlenbergia asperifolia*, *Muhlenbergia schreberi*, *Osmorhiza chilensis*, *Perityle emoryi*, *Plantago patagonica*, *Polemonium micranthum*, *Scleropogon katwinskyanus*, *Stipa speciosa*, *Thelesperma megapotamicum*, and *Tiquilla nuttallii*. Two species, *Alopecurus magellanicus* and *Hypericum gentianoides*, were identified as having stepping stone dispersal. Our approach did not allow us to test for long distance dispersal directly. The AUC test average during the LGM was calculated as 0.953.
Figure 3. There were twenty-three amphitropical species that dispersed through long distance dispersal during the last glacial maximum. The example presented above is *Calamagrostis stricta*. We were able to identify this species as having long distance dispersal because it’s high probability of occurrence in only North and South America.

Figure 4. There were two amphitropical species that dispersed through stepping stone disjunct patterns during the current glacial maximum. The example presented above is *Hypericum gentianoides*. We were able to identify this species as having stepping stone dispersal because of the high probability of occurrence in both North and South America and the intermediate habitats formed along the tropical regions.
Last interglacial maximum

We were unable to reject the vicariance hypothesis for *Tiquilia nuttallii*. In seventeen species, we further rejected the stepping stone hypothesis in favor of long distance dispersal. These seventeen species were: *Calamagrostis stricta, Crassula connata, Fragaria chiloensis, Greeneocharis circumscissa, Lappula redowskii, Lupinus microcarpus, Mentzelia albescens, Muhlenbergia asperifolia, Osmorhiza chilensis, Perityle emoryi, Plantago patagonica, Polemonium micranthum, Scleropogon katwinskyanus, Stipa speciosa*, and *Thelesperma megapotamicum*. Seven species were identified as having stepping stone dispersal. These species are: *Aloysia gratissima, Hypericum gentianoides, Lappula redowskii, Muhlenbergia alopecuroides, Muhlenbergia asperifolia, Muhlenbergia schreberi*, and *Scleropogon katwinskyanus*. Our approach did not allow us to test for long distance dispersal directly. The AUC test average in the LIGM was calculated as 0.953.

![Figure 5](image_url)

Figure 5. There were seven amphitropical species that dispersed through stepping stone disjunct patterns during the last interglacial maximum. The example presented above is *Mentzelia albescens*. We were able to identify this species as having long distance dispersal because of its high probability of occurrence in only North and South America.
Figure 6. There were seventeen amphitropical species that dispersed through long distance dispersal during the last interglacial maximum. The example presented above is *Thelesperma megapotamicum*. We were able to identify this species as having long distance dispersal because it’s high probability of occurrence in only North and South America.

Figure 7. There was one amphitropical species that dispersed through vicariance during the last interglacial maximum. The example presented above is *Tiquilia nuttallii*. We were able to identify this species as having vicariance because of its widespread dispersal across North and South America.
The results collected for each of the three timelines suggest that long distance dispersal was the most dominant mechanism of dispersal among amphitropical species. However, they also convey that numerous shorter-distance-dispersal events via intermediate, favorable populations are an underappreciated mode of dispersal in amphitropical species. Our results even suggest variance as being a possible main mode of dispersal among amphitropical species.

Discussion

*Aloysia gratissima, Mentzelia albescens, Muhlenbergia alopecuroides, Muhlenbergia schreberi, and Ranunculus bonariensis* could have dispersed through long distance dispersal during the current glacial maximum (CGM) or the last glacial maximum (LGM). However, during the last interglacial maximum (LIGM), these species exhibited patterns of stepping stone. *Hypericum gentianoides* dispersed through long distance dispersal during CGM, yet, during LGM and LIGM, *Hypericum* exhibited patterns of stepping stone. *Polemonium micranthum* exhibited signs of stepping stone dispersal during CGM, but during LGM and LIGM long distance dispersal was the only evident mode of dispersal. *Alopecurus magellanicus* was the only species to exhibit stepping stone patterns consistently throughout all three glacial maximums. *Tiquilia nuttallii* dispersed through long distance dispersal during CGM and LGM. However, during LIGM, *Tiquilia* failed to reject the vicariance hypothesis. The remaining sixteen species dispersed through long distance dispersal consistently throughout all three glacial maximums.

As mentioned earlier, a species range is determined in large part by its ability to disperse, and its tolerance of novel environmental conditions. A species range limits can shift due to ecological factors (e.g. climate, landscape, and interacting species) which can influence the species’ range limits (e.g. mode of dispersal). During both the current maximum and last glacial
maximum, only two species failed to reject stepping stone dispersal as a mode of dispersal (Figures 1–4). Yet during the last interglacial maximum, this was not the case. Seven species accepted stepping stone dispersal as a mode of dispersal and one species accepted vicariance as a mode of dispersal (Figures 5–7). By evaluating the species distribution models for all twenty-five amphitropical species across all three glacial maximums, it is evident that species had different probabilities of mode of dispersal during different times (Table 1). The last glacial maximum was when the glaciers’ global ice volume was at their thickest and global sea levels reached their lowest across the world (Otto-Bliesner & Brady, 2005). The last interglacial maximum was the warmest time period on Earth, and it was the last time in history when ocean sea levels were as high as current-day sea levels (Neumann & Hearty, 1996). As climates in both North and South America changed, the species range tolerance altered in response. Multiple species distribution models also showed slight, intermediate stepping stones in approximately the same area in Mexico. This area could have had physical factors suitable for inhabiting these species, making it within their species tolerance range.

The ecological changes observed across all three divergence timings altered the distribution patterns for more than a quarter of the twenty-five species of study (Table 1). These shifts in climate between cold glacial and warm interglacial intervals restricted the dispersal of individual species across the three glacial maxima. This is most evident during the last interglacial maximum. When comparing the results from all three maxima, the results collected from the last interglacial maximum was the most notably different and diverse (Figures 5–7). The number of species that dispersed through stepping stone dispersal increased drastically, and even one species accepted vicariance as a possible mode of dispersal (Table 1; Figure 7). This is very exciting news because biologists have never been able to collect empirical evidence in support of the vicariance
hypothesis (Raven et al., 1963). Even though long-distance dispersal was still proven to be the main mode of dispersal, evaluating the divergence timing for each amphitropical species has also proven that numerous shorter-distance-dispersal events via intermediate, favorable populations are an underappreciated mode of dispersal in amphitropical species (Schenk & Saunders, 2017).

Table 2: There were only nine amphitropical species whose mode of dispersal altered across the three glacial maxima.

<table>
<thead>
<tr>
<th>Species Name</th>
<th>Mode of Dispersal</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Current</td>
</tr>
<tr>
<td><em>Alopecurus magellanicus</em></td>
<td>S</td>
</tr>
<tr>
<td><em>Aloysia gratissima</em></td>
<td>L</td>
</tr>
<tr>
<td><em>Hypericum gentianoides</em></td>
<td>L</td>
</tr>
<tr>
<td><em>Mentzelia albescens</em></td>
<td>L</td>
</tr>
<tr>
<td><em>Muhlenbergia alopecuroides</em></td>
<td>L</td>
</tr>
<tr>
<td><em>Muhlenbergia schreberi</em></td>
<td>L</td>
</tr>
<tr>
<td><em>Polemonium micranthum</em></td>
<td>S</td>
</tr>
<tr>
<td><em>Ranunculus bonariensis</em></td>
<td>L</td>
</tr>
<tr>
<td><em>Tiquilia nuttallii</em></td>
<td>L</td>
</tr>
</tbody>
</table>


Conclusion

Most biologists currently assume that long distance dispersal is the only mode of dispersal among amphitropical species, however our results prove otherwise. Although the results for each of the three timelines suggest that long distance dispersal was the most dominant mechanism of dispersal among amphitropical species, they also convey that numerous shorter-distance-dispersal events via intermediate, favorable populations are an underappreciated mode of dispersal in amphitropical species. Our results even suggest the possibility of variance being the main mode of dispersal among amphitropical species. This is a new discovery in plant evolution and refutes past assumptions on species dispersal. Previous studies have concluded that there is not empirical evidence in support of the vicariance hypothesis (Schenk and Saunders, 2017; Raven et al., 1963). Yet, my results suggest that there is at least one species, *Tiquilia nuttallii*, that supports the vicariance hypothesis. Multiple species distribution models also showed slight, intermediate stepping stones in approximately the same area in Mexico. It was assumed that the climate in this area was suitable for numerous species, making it a popular hotspot in the tropics. Hopefully both my studies on amphitropical species and more to come will help to fix the many ambiguities that lay among plant species, specifically regarding naming amphitropical species (Simpson et al., 2017).
Acknowledgments

I would like to thank Dr. John Schenk for his phenomenal guidance and mentorship throughout my work on this project. These past several years under his mentorship I have grown tremendously in my capabilities and confidence as not only a student but a researcher. This was all because of his constant support, patience, and diligence. I would also like to thank the faculty and staff at the Biological Sciences Department at Georgia Southern University for providing me the resources and financial support to complete this project. I would like to give a special thank you to Dr. Xizhen Schenk who assisted tremendously with the GIS portion of the project. I would like to thank the Georgia Southern University Honors Program for encouraging students to not only succeed in academics but to also participate in academic research. Finally, I would also like to thank my friends and friends for their endless support which got me through both completing my thesis and degree program. Specifically, my parents (Mulatu Lemma, Aster Debebe, & Tsehaye Dejene) whose prayers and love have pushed me to work to the best of my abilities and to pursue every opportunity that comes my way, even the ones that seem impossible.
References


Supplemental Results

Current Glacial Maximum

Long Distance Dispersal
Stepping Stone Dispersal

Last glacial maximum

Stepping Stone Dispersal
Long Distance Dispersal

Aloysia gratissima
Crassula connata
Fragaria chiloensis
Greeneocharis circumscissa
Hoffmannseggia glauca
Lappula redowskii
Lupinus microcarpus
Mentzelia albescens
Microcala quadrangularis
Muhlenbergia schreberi
Muhlenbergia alopecuroides
Muhlenbergia asperifolia
Muhlenbergia asperifolia
Osmorhiza chilensis
Perityle emoryi
Microsteris gracilis
Plantago patagonica
Polemonium micranthum
Scleropogon katwinskyanus
Stipa speciosa
Thelesperma megapotamicum
Tiquilia nuttallii
Calamagrostis stricta
Last interglacial maximum

Stepping Stone Dispersal

Alopecurus magellanicus
Aloysia gratissima
Hypericum gentianoides
Muhlenbergia alopecuroides
Muhlenbergia schreberi

Scleropogon katwinskyanus
Mentzelia albescens

Vicariance

Tiquilia nuttallii
Long Distance Dispersal

Calamagrostis stricta
Crassula connata
Fragaria chiloensis
Greeneocharis circumscissa
Hoffmannseggia glauca

Lappula redowskii
Lupinus microcarpus
Mentzelia albescens
Muhlenbergia asperifolia
Osmorhiza chilensis

Microsteris gracilis
Perityle emoryi
Plantago patagonica
Polomonium micranthum
Ranunculus bonariensis

Stipa speciosa
Thelesperma megapotamicum