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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
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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 dispersal from Mexico. Although our results suggest that long distance dispersal was the most dominant mechanism of dispersal among amphitropical species, they also convey that that numerous shorter-distance-dispersal events via intermediate, favorable populations are an underappreciated mode of dispersal.

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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 &

Porter, 2017). 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 maximums in response to changes in worldwide environmental conditions.

Materials and Methods

<u>*Sampling*</u>

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).

<u>*Species distribution models*</u>

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.

Species	**#Sampled in NA**	**#Sampled in SA**	**Total number of samples**	**Last Glacial Maximum**	**Current distribution**	**Last Interglacial Maximum**
Alopecurus magellanicus	2119	117	2236	stepping stone	stepping stone	stepping stone
Aloysia gratissima	22	290	312	long distance	long distance	stepping stone
Calamagrostis stricta	15152	83	15235	long distance	long distance	long distance
Crassula connata	1396	51	1447	long distance/mex intermediate	long distance/mex intermediate	long distance
Fragaria chiloensis	994	429	1423	long distance	long distance	long distance
Greeneocharis circumscissa	1663	18	1843	long distance/mex intermediate	long distance	long distance
Hoffmannseggia glauca	648	74	722	long distance	long distance	long distance
Hypericum gentianoides	427	13	440	stepping stone	long distance	stepping stone
Lappula redowskii	595	75	670	long distance	long distance	long distance
Lupinus microcarpus	3391	48	3439	long distance	long distance	long distance
Mentzelia albescens	49	12	61	long distance	long distance	long distance
Microcala quadrangularis	178	773	951	long distance	long distance	long distance
Microsteris gracilis	1067	99	1166	long distance	long distance	long distance
Muhlenbergia alopecuroides	697	103	800	long distance	long distance	stepping stone
Muhlenbergia asperifolia	1167	82	1249	long distance	long distance	long distance
Muhlenbergia schreberi	476	37	513	long distance	long distance	stepping stone
Osmorhiza chilensis	1317	47	1364	long distance	long distance	long distance
Perityle emoryi	1766	98	1864	long distance	long distance	long distance
Plantago patagonica	657	467	1124	long distance	long distance	long distance
Polemonium micranthum	294	53	347	long distance	stepping stone	long distance
Ranunculus bonariensis	99	124	223	long distance	long distance	stepping stone
Scleropogon katwinskyanus	374	15	389	long distance	long distance	long distance
Stipa speciosa	1528	320	1848	long distance	long distance	long distance
Thelesperma megapotamicum	1571	94	1665	long distance	long distance	long distance
Tiqullia nuttallii	299	38	337	long distance	long distance	vicariance

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 Tiqullia 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.

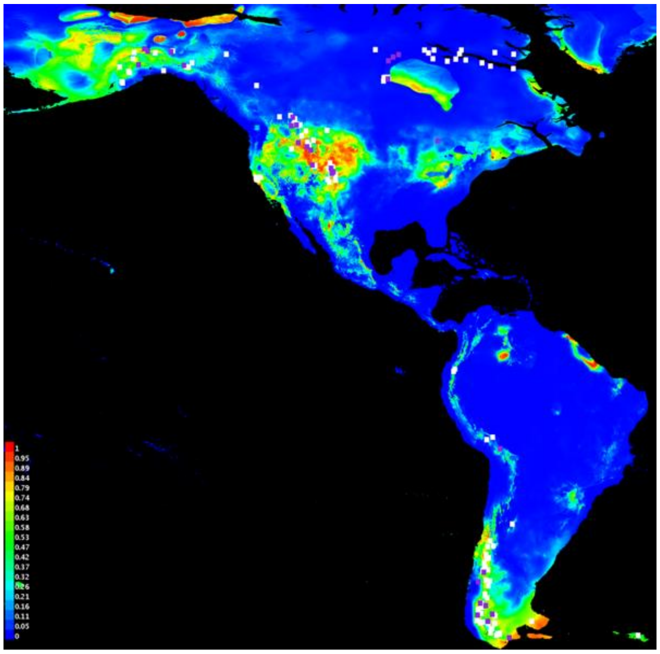

Figure 1. There were two amphitropical species that dispersed through stepping stone disjunct patterns during the current glacial maximum. The example presented above is *Alopecurus magellanicus*. We were able to identify this species as having stepping stone dispersal because of the because of the high probability of occurrence in both North and South America and the intermediate habitats formed along the tropical regions.

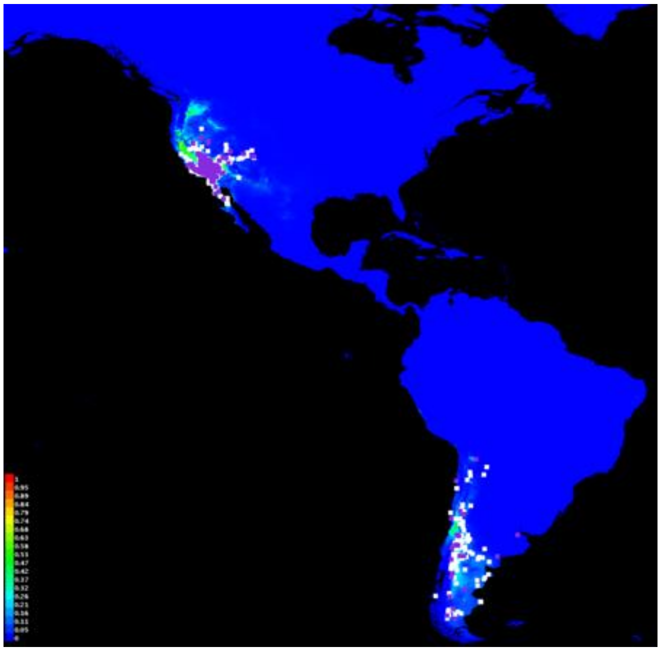

Figure 2. There were twenty- three amphitropical species that dispersed through long distance dispersal during the current glacial maximum. The example presented above is *Stipa speciose.* We were able to identify this species as having long distance dispersal because it’s high probability of occurrence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

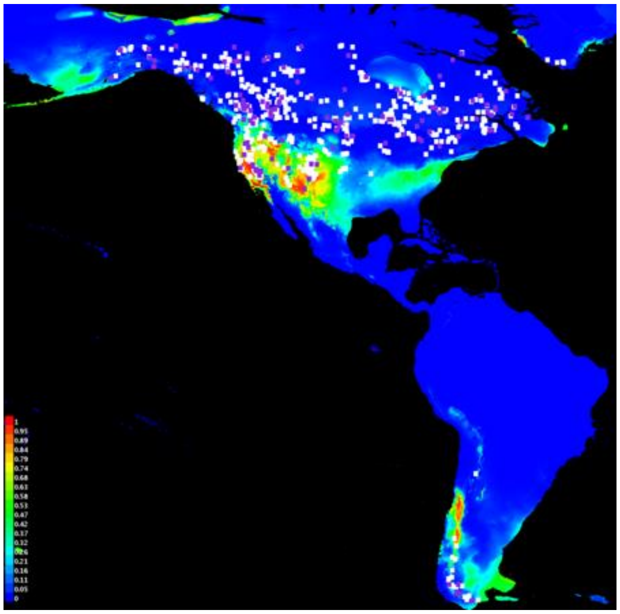

Figure 3. There were twenty- three amphitropical species that dispersed through long distance dispersal during the last glacial maximum. The example presented above is *Calamagrostis stricta.* We were able to identify this species as having long distance dispersal because it's high probability of occurrence in only North and South America.

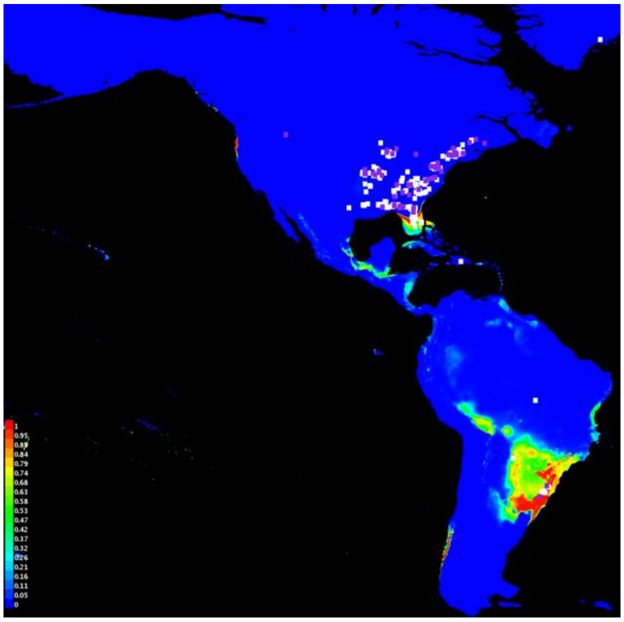

Figure 4. There were two amphitropical species that dispersed through stepping stone disjunct patterns during the current glacial maximum. The example presented above is *Hypericum gentianoides*. We were able to identify this species as having stepping stone dispersal because of the high probability 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 *Tiqullia 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.

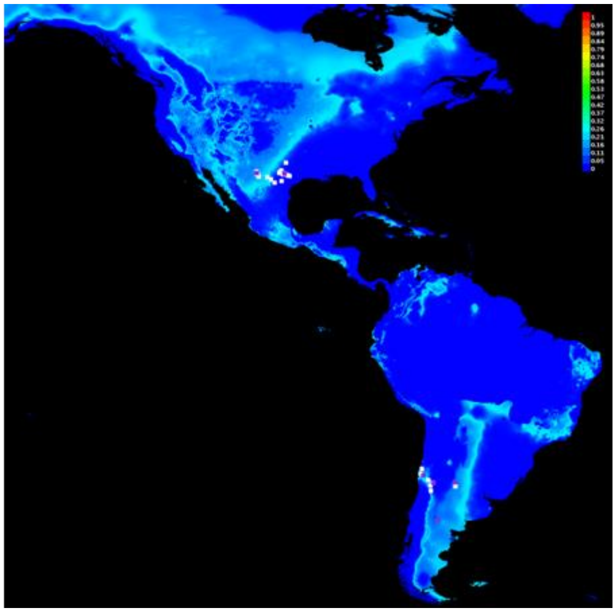

Figure 5. There were seven amphitropical species that dispersed through stepping stone disjunct patterns during the last interglacial maximum. The example presented above is *Mentzelia albescens.* We were able to identify this species as having long distance dispersal because of its high probability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

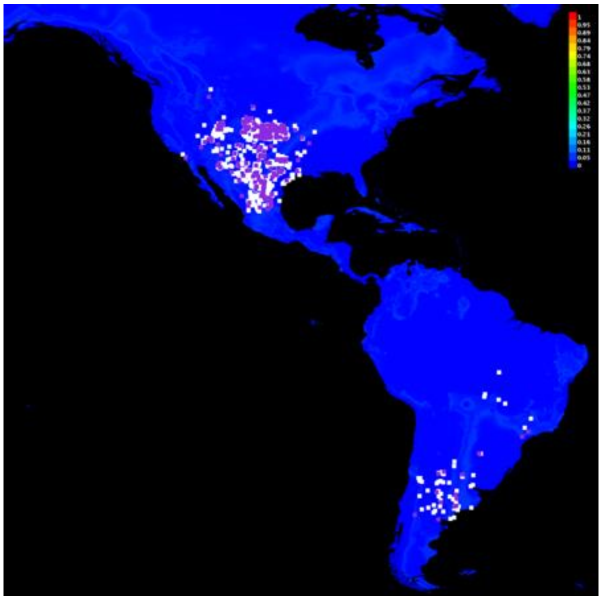

Figure 6. There were seventeen amphitropical species that dispersed through long distance dispersal during the last interglacial maximum. The example presented above is *Thelesperma megapotamicum*. We were able to identify this species as having long distance dispersal because it's high probability of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

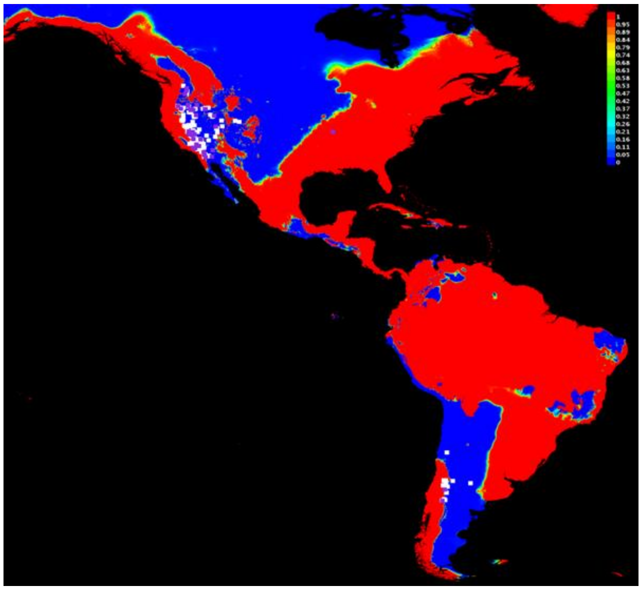

Figure 7. There was one amphitropical species that dispersed through vicariance during the last interglacial maximum. The example presented above is *Tiqullia nuttallii.* We were able to identify this species as having vicariance because of its widespread dispersal across North and South America.

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. *Tiqullia nuttallii* dispersed through long distance dispersal during CGM and LGM. However, during LIGM, *Tiqullia* 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.

	Mode of Dispersal		
Species Name	**Current**	**LGM**	**LIGM**
Alopecurus magellanicus	S	S	S
Aloysia gratissima	L	L	S
Hypericum gentianoides	L	S	S
Mentzelia albescens	L	L	S
Muhlenbergia alopecuroides	L	L	S
Muhlenbergia schreberi	L	L	S
Polemonium micranthum	S	L	L
Ranunculus bonariensis	L	L	S
Tiqullia nuttallii	L	L	V

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 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, *Tiqullia 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).

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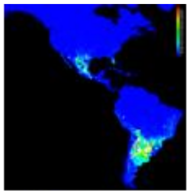
Supplemental Results

Current Glacial Maximum

Long Distance Dispersal



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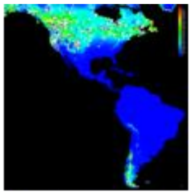

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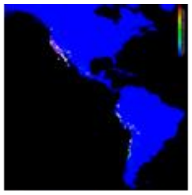

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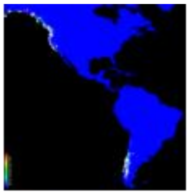

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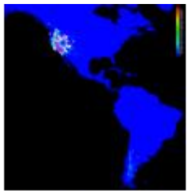

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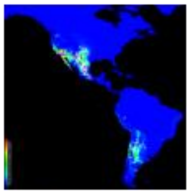

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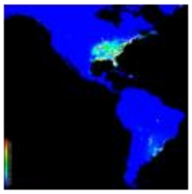

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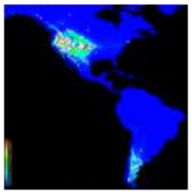

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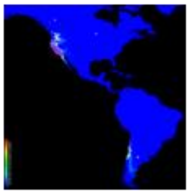

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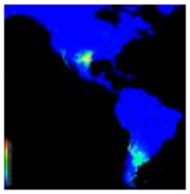
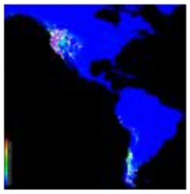


Mentzelia albescens



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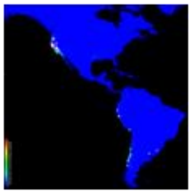

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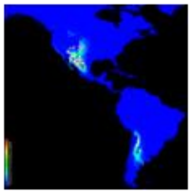

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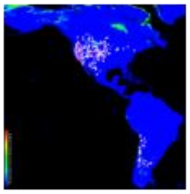

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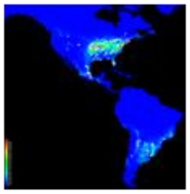

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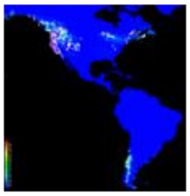

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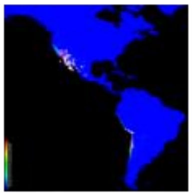

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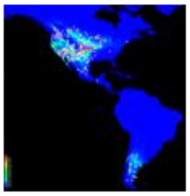
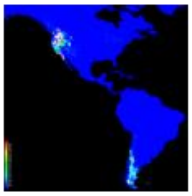


Plantago patagonica



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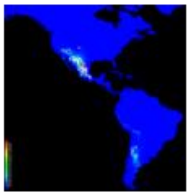
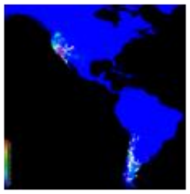
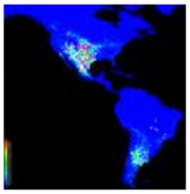


Scleropogon katwinskyanus



Stipa speciosa



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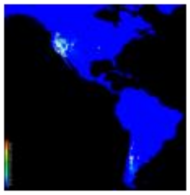
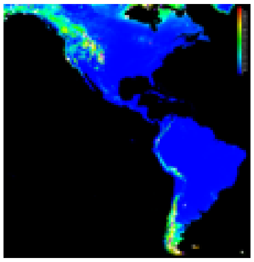
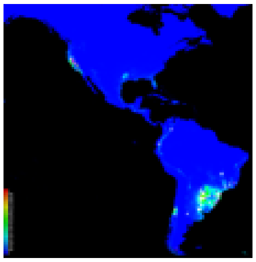


Tiqullia nuttallii

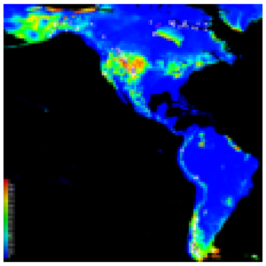
Stepping Stone Dispersal


Alopecurus magellanicus


Ranunculus bonariensis

Last glacial maximum

Stepping Stone Dispersal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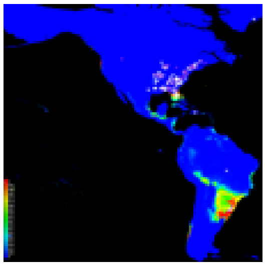
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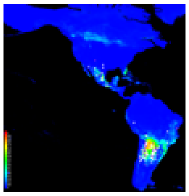
Long Distance Dispersal



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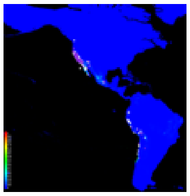

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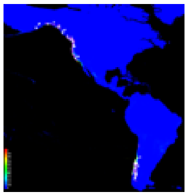
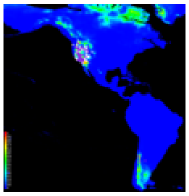


Fragaria chiloensis



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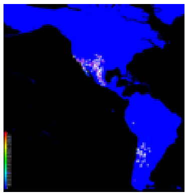
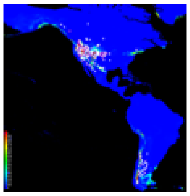


Hoffmannseggia glauca



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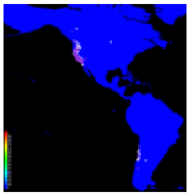

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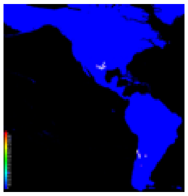

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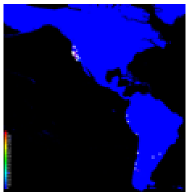
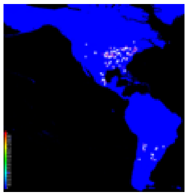
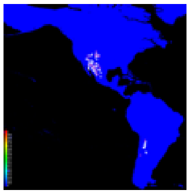


Microcala quadrangularis



Muhlenbergia schreberi



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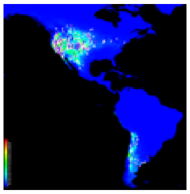
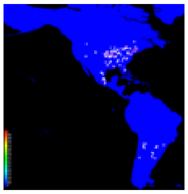


Muhlenbergia asperifolia



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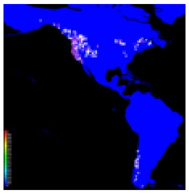
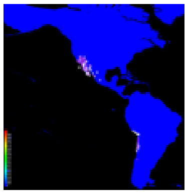
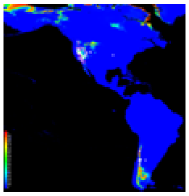


Osmorhiza chilensis



Perityle emoryi



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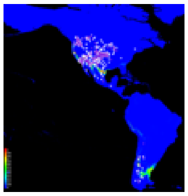
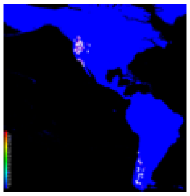


Plantago patagonica



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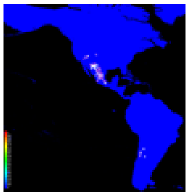

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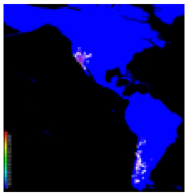

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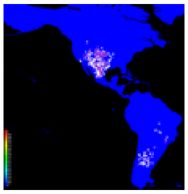

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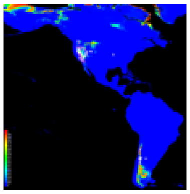
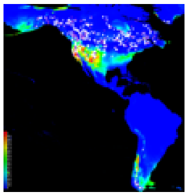


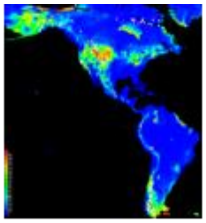
Tiqullia nuttallii



Calamagrostis stricta

Last interglacial maximum

Stepping Stone Dispersal



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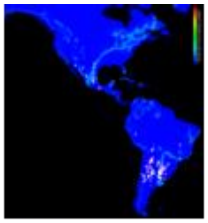
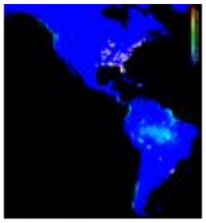
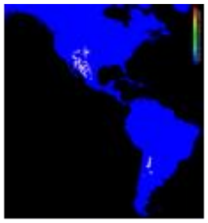


Aloysia gratissima



Hypericum gentianoides



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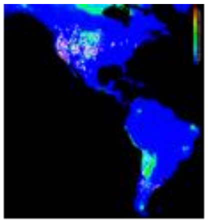

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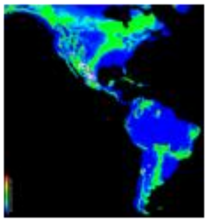
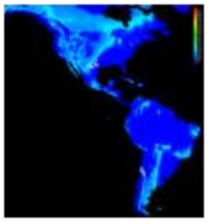
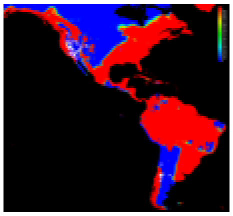


Scleropogon katwinskyanus



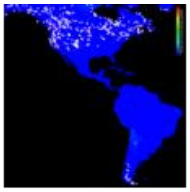
Mentzelia albescens

Vicariance

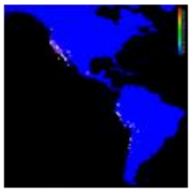


Tiqullia nuttallii

Long Distance Dispersal



Calamagrostis stricta



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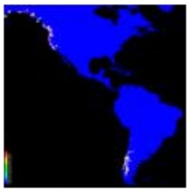
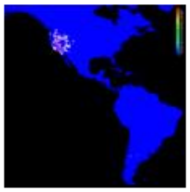


Fragaria chiloensis



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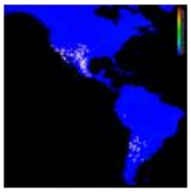
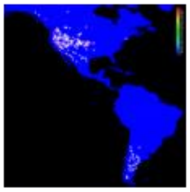
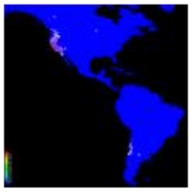


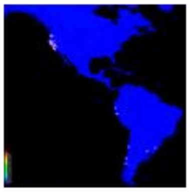
Hoffmannseggia glauca



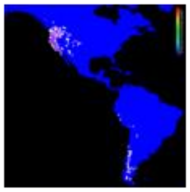
Lappula redowskii



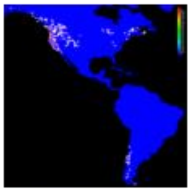
Lupinus microcarpus



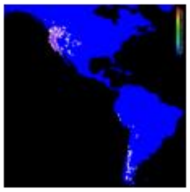
Mentzelia albescens



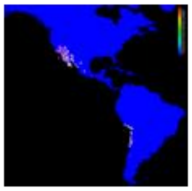
Muhlenbergia asperifolia



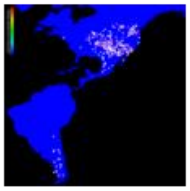
Osmorhiza chilensis



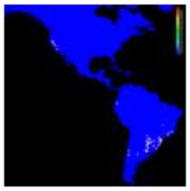
Microsteris gracilis



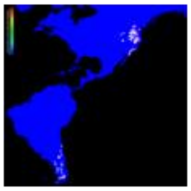
Perityle emoryi



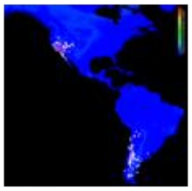
Plantago patagonica



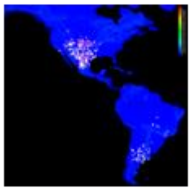
Polemonium micranthum



Ranunculus bonariensis



Stipa speciosa



Thelesperma megapotamicum