



University Honors Program Theses

2020

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

Samera Lemma Mulatu
Georgia Southern University

Follow this and additional works at: <https://digitalcommons.georgiasouthern.edu/honors-theses>



Part of the [Botany Commons](#), [Evolution Commons](#), and the [Plant Biology Commons](#)

Recommended Citation

Mulatu, Samera Lemma, "Species Dispersal Modes in Amphotropical Plant Species of North and South America" (2020). *University Honors Program Theses*. 514.

<https://digitalcommons.georgiasouthern.edu/honors-theses/514>

This thesis (open access) is brought to you for free and open access by Digital Commons@Georgia Southern. It has been accepted for inclusion in University Honors Program Theses by an authorized administrator of Digital Commons@Georgia Southern. For more information, please contact digitalcommons@georgiasouthern.edu.

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

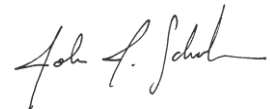
An Honors Thesis submitted in partial fulfillment of the requirements for Honors in the
Department of Biology

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 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 numerous shorter-distance-dispersal events via intermediate, favorable populations are an underappreciated mode of dispersal.



Thesis Mentor: _____

Dr. John Schenk

Honors Director: _____

Dr. Steven Engel

April 2020
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 &

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

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.

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

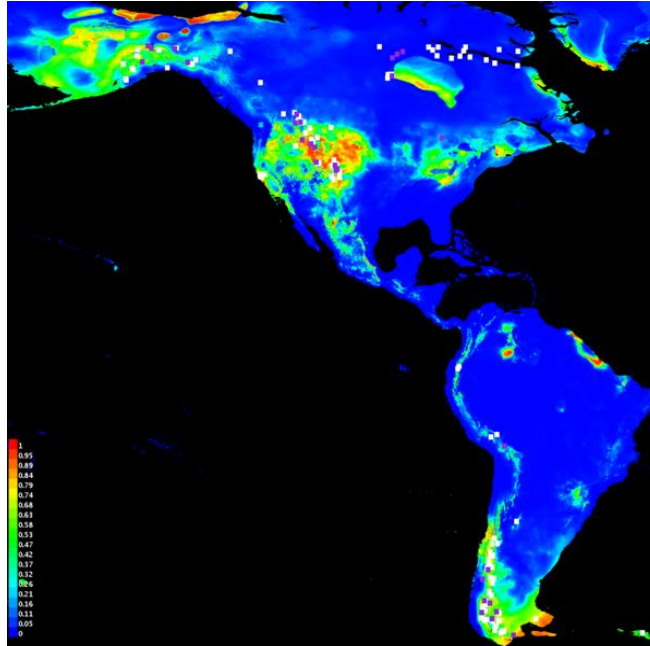


Figure 1. There were two amphitropical species that dispersed through stepping stone disjunct patterns during the current glacial maximum. The example presented above is *Alopecurus magellanicus*. We were able to identify this species as having stepping stone dispersal because of the high probability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

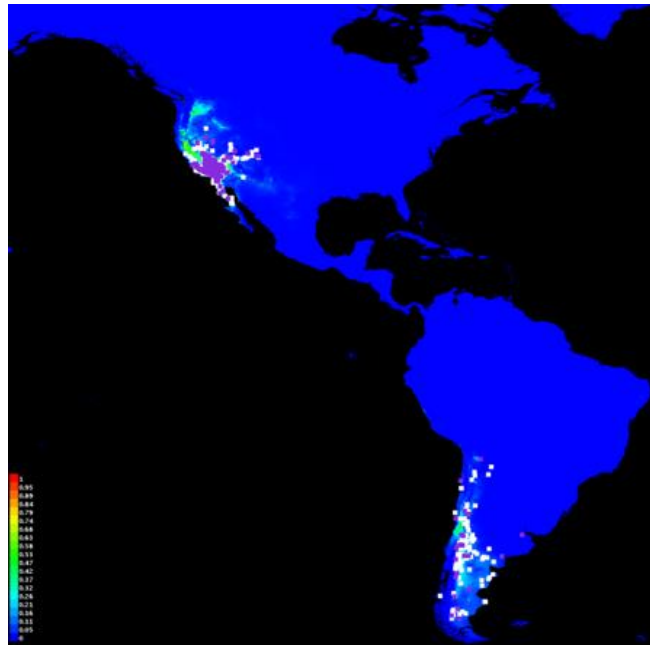


Figure 2. There were twenty- three amphitropical species that dispersed through long distance dispersal during the current glacial maximum. The example presented above is *Stipa speciose*. We were able to identify this species as having long distance dispersal because it's high probability of occurrence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

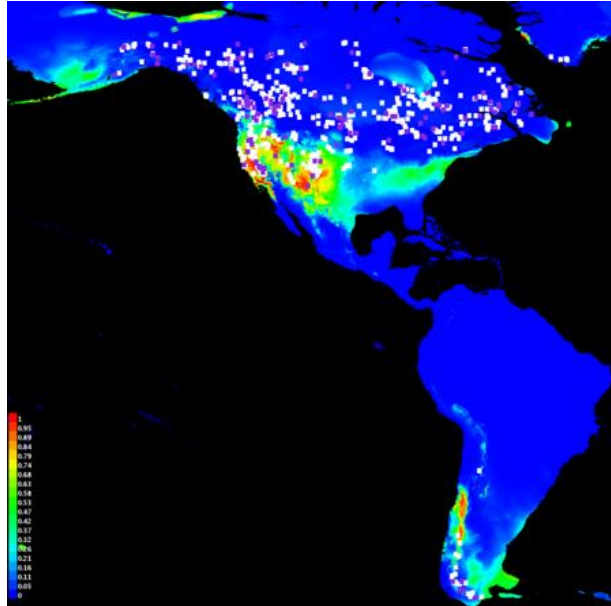


Figure 3. There were twenty- three amphitropical species that dispersed through long distance dispersal during the last glacial maximum. The example presented above is *Calamagrostis stricta*. We were able to identify this species as having long distance dispersal because it's high probability of occurrence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

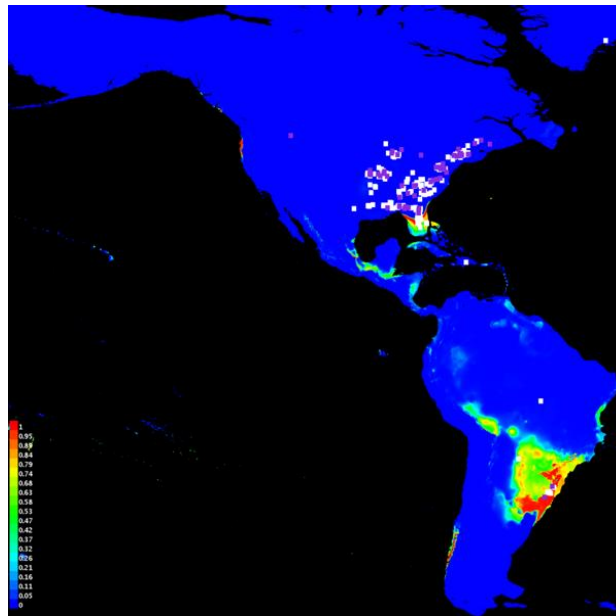


Figure 4. There were two amphitropical species that dispersed through stepping stone disjunct patterns during the current glacial maximum. The example presented above is *Hypericum gentianoides*. We were able to identify this species as having stepping stone dispersal because of the high probability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

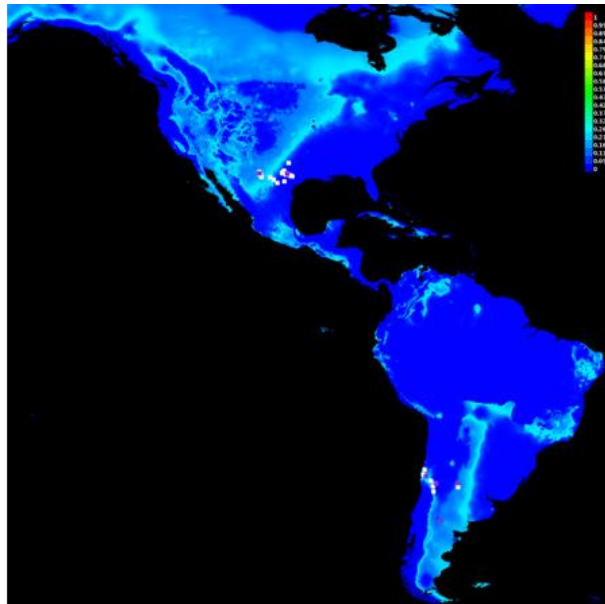


Figure 5. There were seven amphitropical species that dispersed through stepping stone disjunct patterns during the last interglacial maximum. The example presented above is *Mentzelia albescens*. We were able to identify this species as having long distance dispersal because of its high probability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

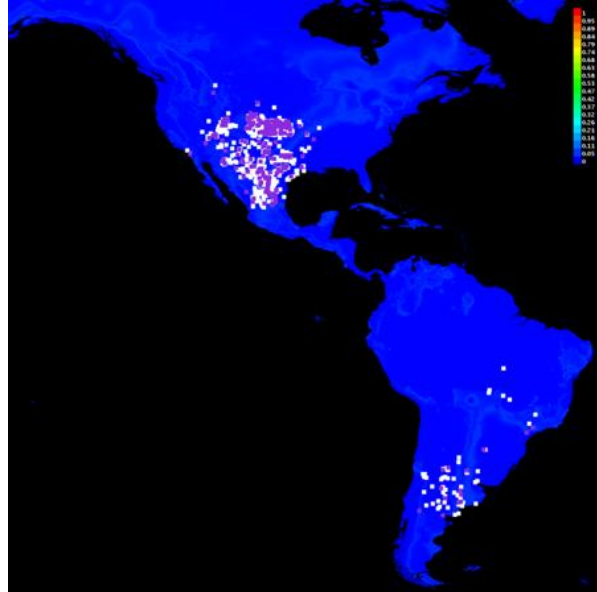


Figure 6. There were seventeen amphitropical species that dispersed through long distance dispersal during the last interglacial maximum. The example presented above is *Thelesperma megapotamicum*. We were able to identify this species as having long distance dispersal because it's high probability of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

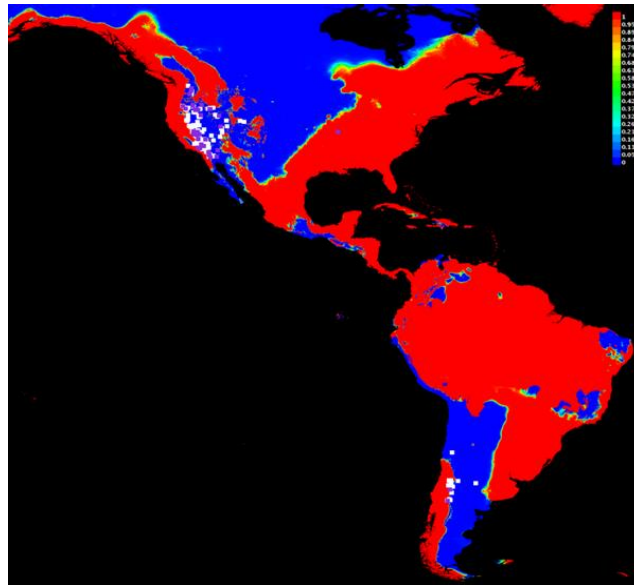


Figure 7. There was one amphitropical species that dispersed through vicariance during the last interglacial maximum. The example presented above is *Tiqullia nuttallii*. We were able to identify this species as having vicariance because of its widespread dispersal across North and South America.

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

Species Name	Mode of Dispersal		
	Current	LGM	LIGM
<i>Alopecurus magellanicus</i>	S	S	S
<i>Aloysia gratissima</i>	L	L	S
<i>Hypericum gentianoides</i>	L	S	S
<i>Mentzelia albescens</i>	L	L	S
<i>Muhlenbergia alopecuroides</i>	L	L	S
<i>Muhlenbergia schreberi</i>	L	L	S
<i>Polemonium micranthum</i>	S	L	L
<i>Ranunculus bonariensis</i>	L	L	S
<i>Tiquillia nuttallii</i>	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).

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

- Blattner, F.R. 2006. Multiple intercontinental dispersal shaped the distribution area of *Hordeum* (Poaceae). *New Phytologist* 169: 603- 614.
- Clark, P.U., A.C. Mix. 2002. Ice sheets and sea level of the last glacial maximum. *Quaternary Science Reviews* 21: 1-7.
- Clark, P.U., A.S. Dyke, Shakun J.D., Carlson A.E., Clark J., Wohlfarth B., Mitrovica J.X., Hostetler S.W., McCabe A.M. 2009. The Last Glacial Maximum. *Science* 525: 710-714.
- Cox, C.B. 1990. New geological theories and old biogeographical problems. *Journal of Biogeography* 17: 117- 130.
- Cuffey, K. and S. Marshall. 2000. Substantial contribution to sea-level rise during the last interglacial from the Greenland ice sheet. *Nature* 404, 591–594.
- Donoghue, M.J. 2011. Molecular biogeography. *PNAS* 108: 6341-6342.
- Emiliani, C. 1971. The Last Interglacial: Paleotemperatures and Chronology. *Science* 171: 571-573.
- Figuerola, J., A.J. Green, L. Santamaria. 2002. Comparative dispersal effectiveness of wigeongrass seeds by waterfowl wintering in south- west Spain: quantitative and qualitative aspects. *Journal of Ecology* 90: 989-1001.
- Gasse, F. 2000. Hydrological changes in the African tropics since the last glacial maximum. *Quaternary Science Reviews* 19: 1-5.
- Holt, R.D. 2003. On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research* 5: 159- 178.
- Hershkovitz, M.A. and E.A. Zimmer. 1999. Riosomal DNA and disjunctions of western american *Portulacaceae*. *Molecular Phylogenetics and Evolution*: 15: 419-439.
- Hilbish T.J., A. Mullinax, S.I. Dolven. A. Meyer, R.K. Koehn, and P.D. Rawson. 2000. Origin of antitropical distribution pattern in marine mussels (*Mytilus* spp.): routes and timing of transequatorial migration. *Marine Biology*: 136 69- 77.
- Johnson, L. A. and J. M. Porter. 2017. Fates of angiosperm species following long-distance dispersal: Examples from American amphitropical Polemoniaceae. *American Journal of Botany* 104:1729– 1744.
- Kearney, M and W. Porter. 2009. Mechanic niche modeling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12: 334-350.

- Keely S.C. and A.W. Johnson. 1977. A comparison of the pattern of herb and shrub growth in comparable sites in Chile and California. *American Midland Naturalist* 97: 120-132.
- Kokko, H and A. Lopez- Sepulcre. 2006. From individual dispersal to species ranges: perspectives for a changing world. *Science* 313: 789- 791.
- Levin, D.A. 2006. Ancient dispersals, propagule pressure, and species selection in flowering plants. *Systematic Botany* 31: 443-448.
- Lia, V.V., V.A. Confalonieri, C.I. Comas, J.H. Hunziker. Molecular phylogeny of *Larrea* and its allies (*Zygophyllaceae*): reticulate evolution and the probable time of creosote bush arrival to North America. *Molecular Phylogenetics and Evolution*: 21: 309-320.
- Nathan, R. 2006. Long distance dispersal of plants. *Science* 313: 786- 788.
- Neumann, A. C. and P. J. Hearty. 1996. Rapid sea-level changes at the close of the last interglacial (substage 5e) recorded in Bahamian island geology. *Geology* 9: 775–778.
- Otto- Bliesner, B.L., and Brady E.C. 2005. The last glacial maximum and holocene climate in CCSM. *Journal of Climate* 19: 2526- 2544.
- Phillips, S. J. et al. 2005. Maxent software for species distribution modeling<<http://www.cs.princeton.edu/~schapire/maxent/>>.
- Phillips, S.J. and M. Dudik. 2008. Modeling of Species Distributions with Maxent: New Extensions and a Comprehensive Evaluation. *Ecography* 31:161-175.
- Popp, M., V. Mirre, C. Brochmann. 2011. A single Mid- Pleistocene long- distance dispersal by a bird can explain the extreme bipolar disjunction in crowberries (*Empetrum*). *PNAS* 108: 6520-6525.
- Raven, P. H. 1963. Amphitropical relationships in the floras of North and South America. *The Quarterly Review of Biology* 38: 151– 177.
- Rohling, E.J., K. Grant, C. Hemleben, M. Siddall, A.A. Hoogakker, M. Bolshaw and M. Kucera. 2007. High rates of sea-level rise during the last interglacial period. *Nature of Sciences* 1: 38-42.
- Sanmartiin, I., and F. Ronquist. 2004. Southern hemisphere biogeography inferred by event- based models: plant versus animal patterns. *Systematic Biology* 2: 216-243.
- Schenk, J. J., and K. Saunders. 2017. Inferring long-distance dispersal modes in American amphitropically disjunct species through adaptive dispersal structures. *American Journal of Botany* 104: 1756– 1764.

Schneider, A. C., and A. J. Moore. 2017. Parallel Pleistocene amphitropical disjunctions in a parasitic plant and its host. *American Journal of Botany* 104: 1745– 1755.

Simpson, M. G., L. A. Johnson, T. Villaverde, and C. M. Williams. 2017. American amphitropical disjuncts: Perspectives from vascular plant analyses and prospects for future research. *American Journal of Botany* 104: 1600– 1650.

Simpson B.B., J.A. Tate, A. Weeks. 2005. The biogeography of *Hoffmannseggia* (Leguminosae, Caesalpinioideae, Caesalpinieae): a tale of many travels. *Journal of Biogeography* 32: 15-27.

Soons M.B., C. Vlugt, B. Lith, G.W. Heil, M. Klaassen. 2008. Small seed size increases the potential for dispersal of wetland plants by ducks. *Journal of Ecology* 96: 619-627.

Spalik K., M. Piwczynski, C.A. Danderson, R. Kurzyna- Mlynik, T.S. Bone, S.R. Downie. 2019. Amphiantartic disjunctions in Apiaceae subfamily Apioideae. *Journal of Biogeography* 37: 1977-1994.

Tank D.C. and R.G. Olmstead. 2009. The evolutionary origin of a second radiation of annual *Castilleja* (*Orobanchaceae*) species in South America: the role of long-distance dispersal and allopolyploidy. *American Journal of Botany* 10: 1907-1921.

Thorne, R.F. 1972. Major disjunctions in the geographic ranges of seed plants. *The Quarterly Review of Biology* 47: 365-411.

Thorne, R. 2004. Tropical plant disjunctions: a personal reflection. *International Journal of Plant Sciences* 165: 137-138.

Villaverde, T., P. González-Moreno, F. Rodríguez-Sánchez and M. Escudero. 2017. Niche shifts after long-distance dispersal events in bipolar sedges (*Carex*, Cyperaceae). *American Journal of Botany* 104: 1765– 1774.

Wagner, W.H. 1972. Disjunctions in homosporous vascular plants. *Annals of the Missouri Botanical Garden* 59: 203-217.

Wen, J. and S.M. Ickert-bond. 2009. Evolution of the Madrean- Tethyan disjunction and the North and South American amphitropical disjunctions in plants. *Journal of Systematics and Evolution* (5): 331-348.

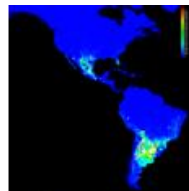
Wen, J., P.P. Lowry., J.L. Walck, and K. Yoo. 2002. Phylogenetic and biogeographic diversification in *Osmorhiza* (Apiaceae). *Annals of the Missouri Botanical Garden* 89: 414-428.

Wongsriphuek, C., B.D. Dugger, and A.M. Bartusze. 2008. Dispersal of wetland plant seeds by mallards: influence of gut passage on recovery, retention, and germination. *Wetlands* 28: 290-299.

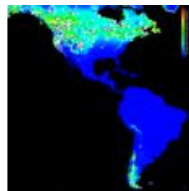
Supplemental Results

Current Glacial Maximum

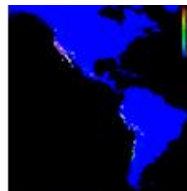
Long Distance Dispersal



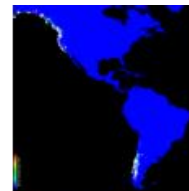
*Aloysia
gratissima*



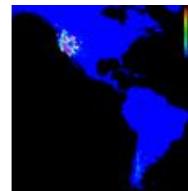
*Calamagrostis
stricta*



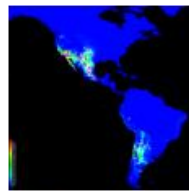
*Crassula
connata*



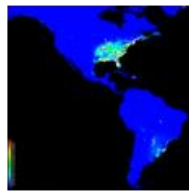
*Fragaria
chiloensis*



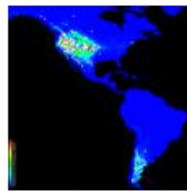
*Greeneocharis
circumscissa*



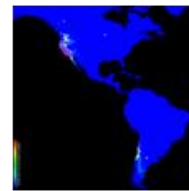
*Hoffmannseggia
glauca*



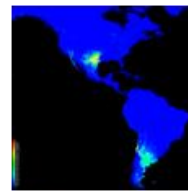
*Hypericum
gentianoides*



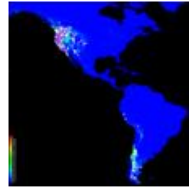
*Lappula
redowskii*



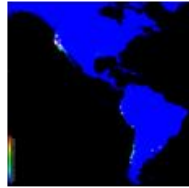
*Lupinus
microcarpus*



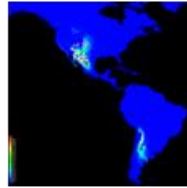
*Mentzelia
albescens*



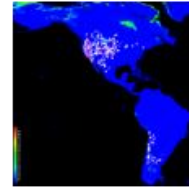
*Microcala
quadrangularis*



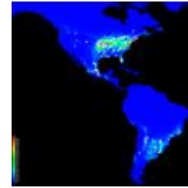
*Microsteris
gracilis*



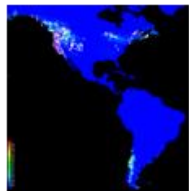
*Muhlenbergia
alopecuroides*



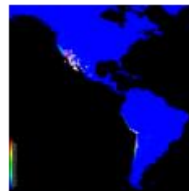
*Muhlenbergia
asperifolia*



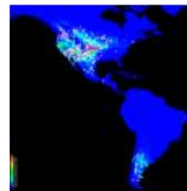
*Muhlenbergia
schreberi*



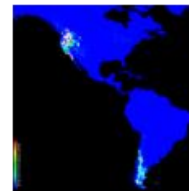
*Osmorhiza
chilensis*



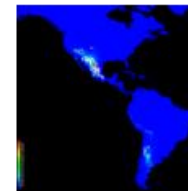
*Perityle
emoryi*



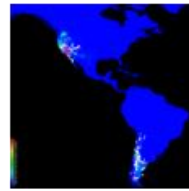
*Plantago
patagonica*



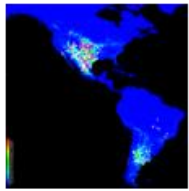
*Polemonium
micranthum*



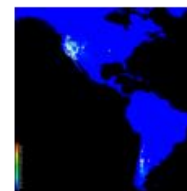
*Scleropogon
katwinskyanus*



*Stipa
speciosa*

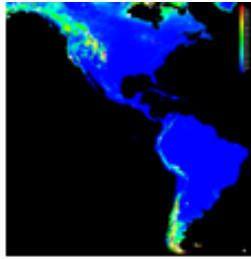


*Thelesperma
megapotamicum*

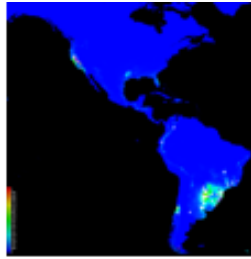


*Tiqullia
nuttallii*

Stepping Stone Dispersal



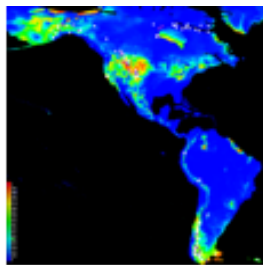
*Alopecurus
magellanicus*



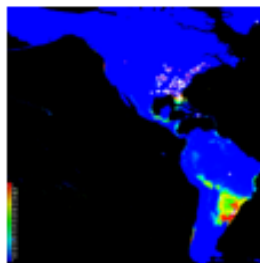
*Ranunculus
bonariensis*

Last glacial maximum

Stepping Stone Dispersal

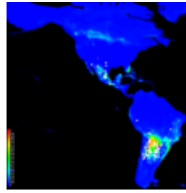


*Alopecurus
magellanicus*

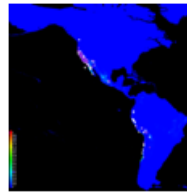


*Hypericum
gentianoides*

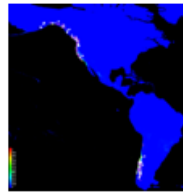
Long Distance Dispersal



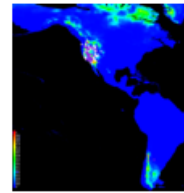
Aloysia gratissima



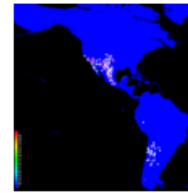
Crassula connata



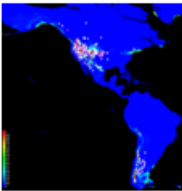
Fragaria chiloensis



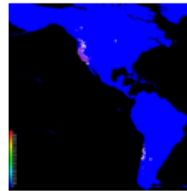
Greeneocharis circumscissa



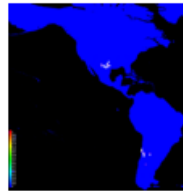
Hoffmannseggia glauca



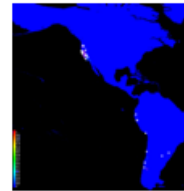
Lappula redowskii



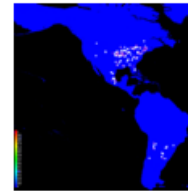
Lupinus microcarpus



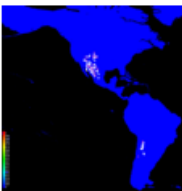
Mentzelia albescens



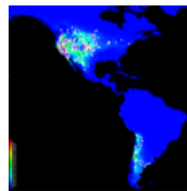
Microcala quadrangularis



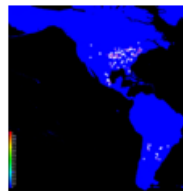
Muhlenbergia schreberi



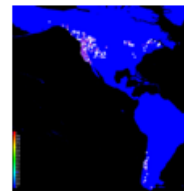
Muhlenbergia alopecuroides



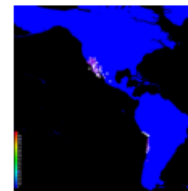
Muhlenbergia asperifolia



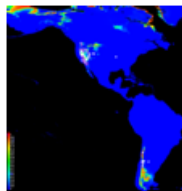
Muhlenbergia asperifolia



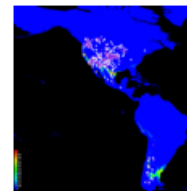
Osmorhiza chilensis



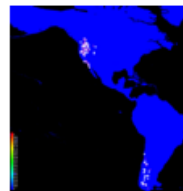
Perityle emoryi



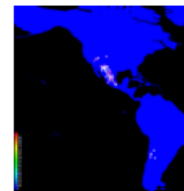
Microsteris gracilis



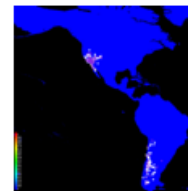
Plantago patagonica



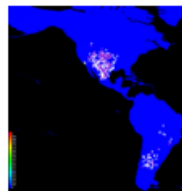
Polemonium micranthum



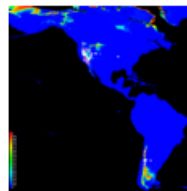
Scleropogon katwinskyanus



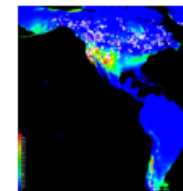
Stipa speciosa



Thelesperma megapotamicum



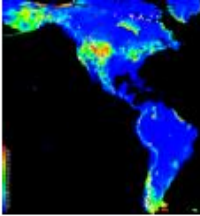
Tiqullia nuttallii



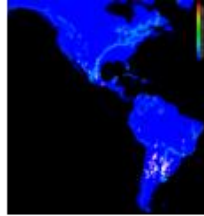
Calamagrostis stricta

Last interglacial maximum

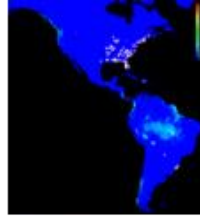
Stepping Stone Dispersal



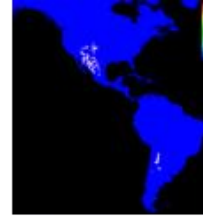
Alopecurus magellanicus



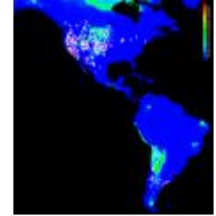
Aloysia gratissima



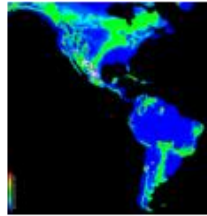
Hypericum gentianoides



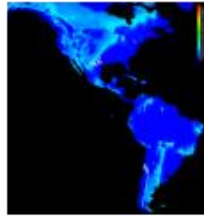
Muhlenbergia alopecuroides



Muhlenbergia schreberi

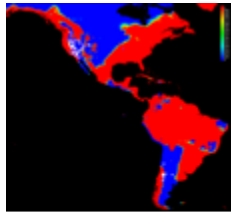


Scleropogon katwinskyanus



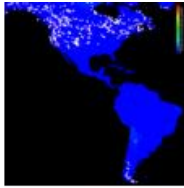
Mentzelia albescens

Vicariance

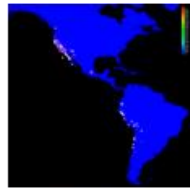


Tiqullia nuttallii

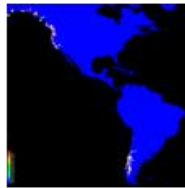
Long Distance Dispersal



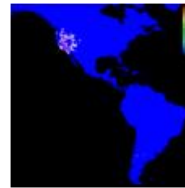
Calamagrostis stricta



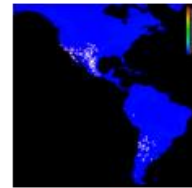
Crassula connata



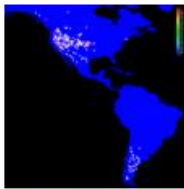
Fragaria chiloensis



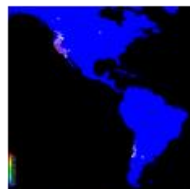
Greeneocharis circumscissa



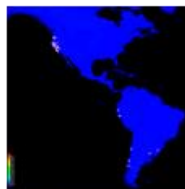
Hoffmannseggia glauca



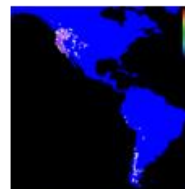
Lappula redowskii



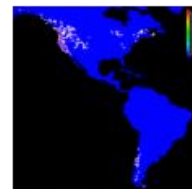
Lupinus microcarpus



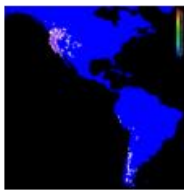
Mentzelia albescens



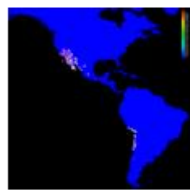
Muhlenbergia asperifolia



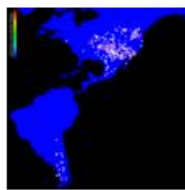
Osmorhiza chilensis



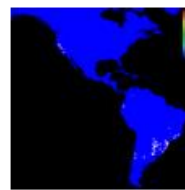
Microsteris gracilis



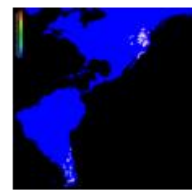
Perityle emoryi



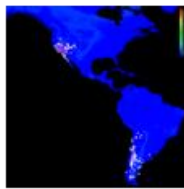
Plantago patagonica



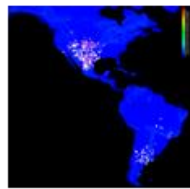
Polemonium micranthum



Ranunculus bonariensis



Stipa speciosa



Thelesperma megapotamicum