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### Timing of Diversification, Dispersal, and Biogeography of Parrots in the Genus *Amazona* (Psittaciformes: Psittacidae) Throughout the Caribbean, Visualized in GIS

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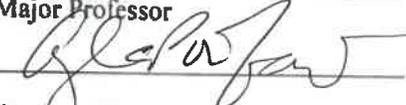
TIMING OF DIVERSIFICATION, DISPERSAL, AND BIOGEOGRAPHY  
OF PARROTS IN THE GENUS *AMAZONA* (PSITTACIFORMES:  
PSITTACIDAE) THROUGHOUT THE CARIBBEAN,  
VISUALIZED IN GIS

A Thesis Presented to the Graduate Faculty  
of Fort Hays State University in  
Partial Fulfillment of the Requirements for  
the Degree of Master of Science  
by

Christopher James Kingwill  
B.S. in Geography, University of Wyoming

Date 04/24/2023

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Approved   
Graduate Dean

**GRADUATE COMMITTEE APPROVAL**

The Graduate Committee of Christopher James Kingwill hereby approves his thesis as meeting partial fulfilment of the requirements for the Degree of Master of Science in Geosciences.



Chair, Supervisory Committee



Supervisory Committee



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On this date

04/24/2023

## ABSTRACT

Avian fossil records from across the Caribbean (Greater and Lesser Antilles) demonstrate higher avian diversity prior to extinction events due to climate change at the end of the Pleistocene and human impact across the Caribbean throughout the Holocene. Amazon parrots (*Amazona*) are a diverse genus of New World parrots found throughout Central and South America, as well as the Caribbean. Their phylogeny and evolutionary history, specifically for Caribbean species, has been debated in terms of source areas in Central and South America and the timing of and number of colonization events to different islands that preceded diversification into island-endemic forms. Taking a geospatial approach using GIS to study dispersal and biogeography of Caribbean amazon parrots, this study uses modified bathymetric data to model sea level fluctuations during the Late Pliocene (3.6 Ma – 2.58 Ma), the Pleistocene (2.58 Ma – 12 ka), and the Last Glacial Maximum (LGM) (~12 ka) to model potential paths of dispersal to islands of the Caribbean from inferred source regions on the mainland. Network Analyst and Euclidean raster data analysis in ArcGIS Pro 3.0 are utilized to create an optimal series of network pathways and inferred flight regions of the Caribbean at each time interval, based on an estimated maximum flying distance for amazon parrots. Previous phylogenetic information (for mainland and island forms) and *Amazona* fossil records are utilized as supplementary information to contemporary *Amazona* distributions in the Caribbean in this study. Network route, Euclidean distance, and fossil distribution mapping results added geographic context to the dispersion patterns of Greater Antillean amazons and offered a hypothesis for the diversification of Lesser Antillean amazons in spite of their paraphyletic status and poorly known evolutionary history.

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## TABLE OF CONTENTS

ABSTRACT	i
ACKNOWLEDGEMENTS	ii
TABLE OF CONTENTS	iv
LIST OF FIGURES	v
LIST OF TABLES	vii
INTRODUCTION	1
LITERATURE REVIEW	6
METHODS	27
RESULTS AND DISCUSSION	56
CONCLUSION	102
REFERENCES	110

## LIST OF FIGURES

Figure 1. Evolutionary tree for the five Greater Antillean amazons.....	9
Figure 2. Greater Antillean amazon species .....	10
Figure 3. Lesser Antillean amazon species.....	11
Figure 5. (A) The calculated maximum fuel-carrying capacities (ratio of total body mass to lean body mass, $h_{max}$ ; the filled circles) for 15 species of birds with known aerodynamic characteristics as a function of lean body mass. In addition, maximum observed fuel-carrying capacities in 41 species of free-living birds (open circles) in relation to lean body mass are depicted. (B) Calculated maximum flight range according to Pennycuick (1989) as a function of calculated maximum fuel-carrying capacities for the 15 species of birds with known aerodynamic characteristics. The red dashed marker on the $h_{max}$ and distance plot indicates the 1,500 km distance threshold used in this study.....	29
Figure 10. Bathymetry and elevation raster dataset for the Greater Antilles.....	33
Figure 11. Bathymetric raster dataset for the Lesser Antilles .....	34
Figure 12. The seascape polygon features of the Greater and Lesser Antilles, for the MG6 isotope period (top) and M2 (bottom) isotope period of the late Pliocene .....	38
Figure 13. The seascape polygon features of the Greater and Lesser Antilles, for the mid-Piacenzian Warm Period (mPWP) of the late Pliocene (top) and MIS 16 (bottom) isotope period of the middle Pleistocene.....	39
Figure 14. The seascape polygon features of the Greater and Lesser Antilles, for the MIS 2 isotope period (top) and MIS 1 (bottom) isotope period of the early Holocene.....	40
Figure 15. A flowchart documenting the creation of network datasets in this study. ....	42
Figure 16. Network datasets for the Greater and Lesser Antilles, during the marine isotope periods: MG6 (top) and M2 (bottom).....	43
Figure 17. Network datasets for the Greater and Lesser Antilles, during the marine isotope periods: mPWP (top) and MIS 16 (bottom). ....	44
Figure 18. Network datasets for the Greater and Lesser Antilles, during the marine isotope periods: MIS 2 (top) and MIS 1 (bottom). ....	45
Figure 20. Greater Antillean amazon fossil record, to the species level. ....	50
Figure 21. Lesser Antillean amazon fossil record, to the species level.....	50
Figure 22. Network mapping results for the Greater Antilles, during marine isotope stage, MG6 .....	59
Figure 23. Euclidean distance mapping results of the MG6 marine isotope stage in the Greater Antilles, for the distance thresholds of 1500 km and 500 km .....	60
Figure 24. Network mapping results for the Greater Antilles, focused in on Jamaica. During marine isotope stage, M2, of the late Pliocene, a brief glaciation event with global sea levels estimated as low as -65 m .....	61
Figure 25. Euclidean distance mapping results for the Greater Antilles, during the M2 glaciation event of the late Pliocene .....	63
Figure 26. Network mapping results for the Greater Antilles, during the mid-Piacenzian Warm Period of the late Pliocene. ....	64
Figure 27. Euclidean distance mapping results for the Greater Antilles, during the mid-Piacenzian Warm Period of the late Pliocene.....	66
Figure 28. Euclidean distance mapping results for the Greater Antilles, during MIS 16 (middle Pleistocene).....	68

Figure 29. Network route mapping results for the Greater Antilles, during MIS 16 (middle Pleistocene).	69
Figure 30. Euclidean distance mapping results for the Greater Antilles, during MIS 2, the Last Glacial Maximum .....	71
Figure 31. Routes of dispersion from Cuba to the Cayman Islands, Bahamas, and the Turks and Caicos Islands during the LGM. ....	72
Figure 32. Network dataset for the Greater Antilles, during the early Holocene .....	74
Figure 33. Potential island-hopping route for amazon parrots from northern South America, to different islands in the Lesser Antilles during the MG6 marine isotope stage for the late Pliocene. ....	76
Figure 34. Euclidean distance results for the Lesser Antilles during the MG6 isotope period. Sea levels were 20m higher than present .....	77
Figure 35. Hypothesized island-hopping route for amazon parrots from northern South America, to different islands in the Lesser Antilles during the M2 glaciation event .....	78
Figure 36. Euclidean distance mapping results for travel between different islands in the Lesser Antilles, during the M2 glaciation event.....	79
Figure 37. Euclidean distance mapping results for the Lesser Antilles, during the mid-Piacenzian Warm Period of the late Pliocene.....	80
Figure 38. Potential island-hopping route for amazon parrots from northern South America, to different islands in the Lesser Antilles during the mid-Piacenzian Warm Period.....	81
Figure 39. Euclidean distance mapping results for the Lesser Antilles, during the mid-Piacenzian Warm Period.....	82
Figure 40. Hypothesized island-hopping route for amazon parrots from northern South America, to different islands in the Lesser Antilles during the middle Pleistocene (MIS 16) .....	83
Figure 41. Euclidean distance results for the Lesser Antilles, during the LGM (MIS 2). ....	84
Figure 42. Network routes for the Lesser Antilles, during the LGM (MIS 2).....	85
Figure 43. Network dataset for the Lesser Antilles, during the early Holocene.....	86
Figure 44. Euclidean distance representing the Lesser Antilles during the early Holocene.....	87
Figure 45. Modern geographic range of the amazon parrot genus across the Greater Antilles, representing five extant species, with the spatial extent of the Greater Antillean amazon fossil record .	90
Figure 46. Modern geographic range of the amazon parrot genus across the Lesser Antilles, which represents four extant species, with the spatial extent of the Lesser Antillean amazon fossil record.....	93
Figure 47. Mesquite Tree and its associated legend for the first geographic character: landmass locations .....	97
Figure 48. Mesquite Tree and its corresponding legend, based on the second geographic character: nearest neighbor.....	98
Figure 49. Mesquite Tree and its corresponding legend, based on the third geographic character: West to East dispersion.....	99

## LIST OF TABLES

Table 1. Amazon parrot species in the Greater Antilles, mainland and island species, and their body masses (in grams and kilograms).....	28
Table 2. Amazon parrot species in the Lesser Antilles, mainland and island species, and their body masses (in grams and kilograms).....	28
Table 3. MIS values and their corresponding ages and sea level values. Ages are given in millions of years ago (Ma) or thousands of years ago (ka) while sea level is given in meters (m). .....	36
Table 4. Characters representing geographic attributes for each Greater Antillean amazon parrot. Only extant species/populations were used.....	55
Table 5. Results for total island area, interisland island network distance, interisland network distance according to the 500 km distance threshold, and the area of each flight region for the Greater and Lesser Antillean seascapes, by marine isotope stages (MIS) used in this study.....	57

## INTRODUCTION

Birds are the second most diverse group of vertebrates after fish. Remote islands can host endemic bird communities found nowhere else on Earth (Steadman 2006). Additionally, discoveries of extensive avian bones assemblages on islands, from Pleistocene or Holocene contexts help paint a picture of life on islands prior to the arrival of humans (Steadman 1995). The insular avian fossil record has been a field in significant development (Steadman & Martin 2003). Insular species, especially birds, are highly susceptible to extinction, due to invasive species and predation, including from humans (Steadman 2006).

In the Caribbean, the most diverse group of terrestrial vertebrates are birds (Steadman & Franklin 2015). According to the growing fossil and archaeological record of Caribbean islands, bird diversity in the West Indies was even higher than today, prior to human impact (Olson 1982; Steadman et al. 2007; Steadman & Takano 2013).

Among the birds in the Caribbean that experienced Quaternary extinctions on varying scales are parrots (Psittaciformes, Psittacidae), according to historic accounts and fossil information. Three parrot genera: *Ara* (macaws), *Aratinga* (conure parrots), and *Amazona* (amazon parrots) were once known throughout the Caribbean and once experienced higher diversity, in terms of island-endemic species (Williams & Steadman 2001). With *Amazona*, the Caribbean has two distinct groups of this genus: one group being found in the Greater Antilles and the other being in the Lesser Antilles. Caribbean fossil records and relationships to other amazon parrots found on the mainland may help answer questions of the evolutionary history of Caribbean amazons (Russello & Amato 2004).

*Amazona* is a species-rich genus of New World parrot, containing 27 – 31 recognized species, distributed throughout Central and South America (Mexico to Argentina) and throughout the Caribbean (Forshaw 2006). Amazon parrots in the Caribbean, most of which being single-island endemics, likely colonized the Antilles and Bahamas via overwater dispersal from Central and South America (Snyder et al. 1987).

Molecular dating based on phylogenetic studies of the diversification of amazon parrots has been related to known climatic and geologic events over the last five million years (Silva et al. 2014). Phylogenetic studies into the Caribbean species of amazon parrots determined that Greater Antillean species are distinct from Lesser Antillean forms (Russello & Amato 2004). In their phylogenetic analysis of Greater Antillean amazons, Kolchanova et al. (2021) determined from molecular dating that colonization of the Greater Antilles by amazon parrots likely occurred after 3.47 Ma while Silva et al. (2014) determined through phylogenetics that the diversification of the Greater Antillean and Lesser Antillean amazon clades did not occur before 5 Ma.

The group in the Greater Antilles has a well-reconstructed evolutionary history, with respect to molecular phylogenetic data and is considered a distinct, monophyletic group (Russello & Amato 2004; Kolchanova et al. 2021), and all five species are extant today (Williams & Steadman 2001). In contrast, the group in the Lesser Antilles has a poorly known evolutionary history, with several extinct taxa, and a lack of clarity on the relationships between the four extant species in the Lesser Antilles (Russello & Amato 2004).

Snyder et al. (1987) published extensively on conservation efforts of the endangered Puerto Rican amazon. With that, came hypotheses on the evolution of the Caribbean amazons as a whole. They proposed that amazons colonized the Greater and Lesser Antilles through

overwater dispersal. However, Kolchanova et al. (2021) note that amazon parrots are relatively poor dispersers.

## **Objective**

This study focuses on amazon parrots (Psittaciformes: *Amazona*) and their dispersion and biogeography in the West Indies. The study utilized fossil and modern records, and molecular dating from phylogenetic studies, in conjunction with sea level changes due to climate change during the Pliocene and Pleistocene to model the Caribbean in geographic information systems (GIS) to map out dispersal routes.

Using network analysis and Euclidean distance raster data processing in ArcGIS Pro 3.0, potential routes and avenues of amazon parrot dispersal, based on maximum distance travel estimations, were made for each region. Route and distance raster maps were created from modifying bathymetric raster data according to changes in global eustatic sea level during the Late Pliocene (after 5 Ma) and the Pleistocene, according to sea level curves derived from six marine isotope stages (MIS). Molecular dates (in millions of years) for Greater Antillean amazon parrot evolution, based on a phylogenetic study by Kolchanova et al. (2021), were used in conjunction with the ages of each respective MIS period. These phylogenetic divergence times were used to confirm the geographic nature of greater Antillean amazon dispersion while serving as an estimation for evolution of the Lesser Antillean amazon lineage. In addition, estimated range maps for Greater and Lesser Antillean amazons, prior to human arrival, were created, using aggregated paleontological occurrence information.

The results of this study produced optimal network pathways for dispersion that agree with previous phylogenetic findings, specifically for Greater Antillean amazons, for an island-

hopping style of dispersal put forth by (Kolchanova et al. 2021). Euclidean distance raster mapping produced optimized “flight regions” or avenues to consider total travel potential for amazon parrots. Meanwhile, the network route and Euclidean distance mapping for Lesser Antillean amazons produced hypothesized routes of dispersion that demonstrated a valid hypothesis for Lesser Antillean amazon parrot evolution, with respect to changes in sea level in the Lesser Antilles.

In addition, paths connecting islands exhibiting an absence in or minimal fossil evidence of *Amazona* (Williams & Steadman 2001) could be interpreted as evidence for paleontologists to further investigate and reconstruct avian fossil records of these islands, in the hopes of finding tangible evidence for the former occurrence of *Amazona*.

## **Study Area**

The Caribbean, also called the West Indies, include the Greater Antilles, the Lesser Antilles, and the Lucayan Archipelago (the Bahamas and the Turks & Caicos Islands). Geopolitically interchangeable with the ‘Caribbean’, some Central and South American mainland nations which have Caribbean coastlines, such as Belize, French Guiana, Guyana, and Suriname, and the Atlantic island nations of Barbados, Bermuda, and Trinidad and Tobago are grouped with the Caribbean as well. Geologically complex, the Caribbean consists of 7,000 islands and islets stretching over 3,000 km from the Florida peninsula of North America south-southeast to the northern coast of Venezuela.

The oldest geologically, islands of the Greater Antilles formed from old fragments of continental crust with some of the oldest rocks being located on Cuba. These fragments forming the Greater Antilles reached their present position after the Caribbean Plate collided with the

North American plate during the Paleocene (Meyerhoff & Khudoley 1971; Graham 2003). Islands of the Lesser Antilles formed from a volcanic arc system rising along the edge of the Caribbean Plate as it moves eastward, converging with the North American and South American Plates. The Lesser Antilles likely emerged no earlier than 20 Ma during the Miocene (Santiago-Valentin et al. 2004). The Lucayan Archipelago formed as a series of barrier reefs and low islands atop the Bahama Platform (a block of carbonate sediments that is part of the North American Plate). Emergent islands in the Bahamas and the Turks and Caicos accumulated sediment from wind-blown sediments at periods of eustatically-lowered sea level (Ricklefs & Bermingham 2008).

## LITERATURE REVIEW

### **Caribbean Paleontology**

Avian, mammalian, and reptilian fossil records demonstrate a greater diversity in insular taxa across the Greater and Lesser Antilles (Kemp & Hadly 2015; Steadman et al. 2019). Efforts to understand biogeographic patterns and evolutionary processes that produce endemic insular fauna on islands in the Pacific or the Caribbean have been hindered by the extensive late Quaternary (Pleistocene and Holocene) and historic extinctions that are often a consequence of human arrival to these island environments (Steadman 2006).

Terrestrial vertebrates of the Greater and Lesser Antilles, due to the region's complex geologic history, most likely colonized these islands throughout multiple episodes of overwater immigration (Bond 1963; Lomolino et al. 2017). Vertebrate extinctions across the West Indies occurred at different stages of time during the Quaternary. Establishing a chronology for avian extinction in the Bahamas, Steadman & Franklin (2015) determined that the Bahamas for instance experienced avian turnover during the Pleistocene-Holocene Transition (PHT; 15 - 9 ka), due to climate change and the associated changes in island area and sea-level following the rise in global eustatic sea-level. Following this was a second wave of extinction after the arrival of the first humans during the late Holocene (< 4 ka). Meanwhile, in Hispaniola, vertebrate fossil deposits of vertebrates that included mammals such as sloths, rodents, and monkeys, and birds like an extinct, undescribed woodcock (*Scolopax* sp.) from high-elevation sinkholes demonstrated a period of extinction that occurred after the first arrival of Amerindians to Hispaniola during the middle Holocene (Steadman & Tokano 2013). Following that was another

period of extinction, during and after the arrival of European and African peoples, in AD 1492 (= 458 cal. BP) (Deagan and Cruxent, 2002; Steadman & Tokano 2013).

### **Avian Fossil Record of the Caribbean**

Bird fossils from the West Indies indicate that bird diversity was much higher prior to human arrival. Suarez & Olson (2015) reviewed the giant, now extinct barn owls (Strigiformes: Tytonidae) that were once found on Caribbean islands including Jamaica, Cuba, the Bahamas, Hispaniola, and Barbuda. In other cases, avian fossils from the West Indies indicate a taxon now extirpated (extinct locally) from the region or one that has experienced range contractions. For instance, Steadman & Franklin (2017) looked at the extirpation of eastern bluebirds (*Sialia sialis*) and Hispaniolan crossbills (*Loxia megaplaga*) from the island of Abaco, in the Bahamas. Olson (2006) studied fossil remains of a raptor, identified as the Rufous Crab-Hawk (*Buteogallus aequinoctialis*) from Jamaica, that represent a now extirpated population from the island. Oligocene fossils of todies (Coraciiformes: Todidae) from western North America indicate that todies, while now restricted to the Greater Antilles, once had a wider distribution, including the North American continent, becoming extinct there but surviving today in the Caribbean (Olson 1976).

In addition, understanding taxonomic history and biogeography of West Indian birds can be strengthened with the fossil record. Olson & Wiley (2016) determined through fossil history, morphology, and zoogeography that the extant Blue-headed Quail-Dove (*Starnoenas cyanocephala*), endemic to Cuba, likely represents a relic of an earlier dispersion event of Columbiformes from the Old World to the New World.

## **Amazon Parrots**

Amazon parrots are midsized to large, stocky birds with predominantly green plumage and contrasting colors on the crown, face, and flight feathers. Individual plumage differences vary by species. Amazons also have short, slightly rounded tails and broad, rounded wings. These parrots exhibit strong, stout bills with a distinct notch in the upper mandible. Prominent bare ceres and eye-rings are seen, and barred appearances of most species derives from dark edging to their feathers. Amazon parrots exhibit little to no sexual dimorphism while juvenile birds have duller plumage than the adults (Forshaw 2006).

High Psittaciform diversity in South America and Australasia suggests that the order may be Gondwanan in origin, centered in Australasia with many Psittaciforms found in Africa as well (Wright et al. 2008). Hackett et al. (2008) determined a sister relationship between Psittaciformes and Passeriformes (songbirds/perching birds), through aligned nuclear DNA sequencing. This was reaffirmed by Suh et al. (2011), finding the same sister relationship between parrots and passerines, with Falconidae (falcons) sister to this clade.

Literature, grounded in paleontology, historic information, and phylogenetics suggests that multiple sympatric species of *Amazona* were once widespread across islands in the Caribbean (Williams & Steadman 2001; Russello & Amato 2004). Amazon parrots found on the mainland, from Central and South America, likely served as ancestors to the island-endemic species seen there in the Caribbean (Snyder et al. 1987; Russello & Amato 2004). Kolchanova et al. (2021) determined, through phylogenetics that Greater Antillean amazons are descended from Central American species, with their data supporting a stepping-stone dispersal and speciation period that lasted between approximately 3.47 Ma, during the late Pliocene, to 0.67 Ma BP, during the Pleistocene. The amazons of Greater Antilles form a distinct monophyletic group with

ancestors derived from Central America, including *Amazona albifrons* (the White-Fronted Amazon) (Figure 1).

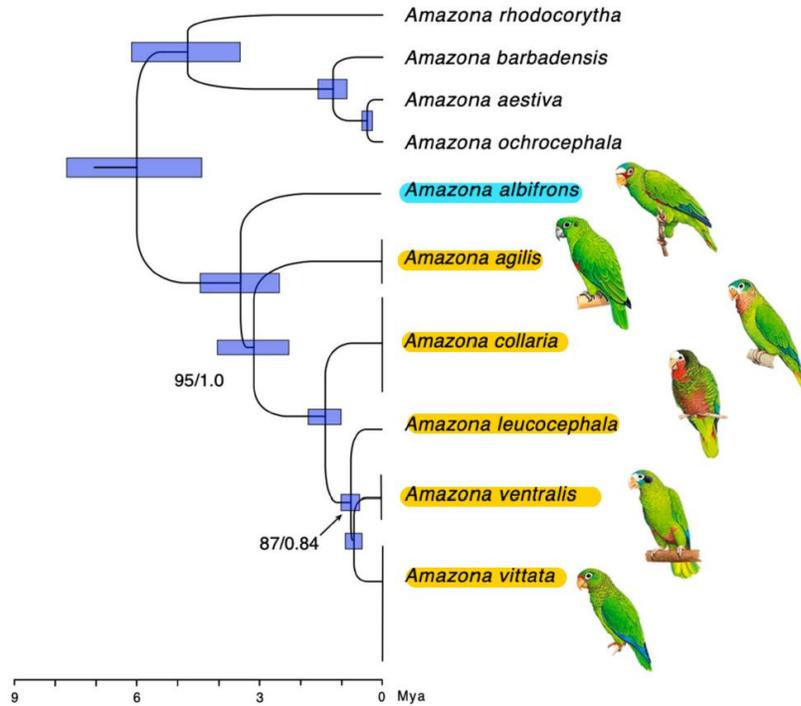


Figure 1. Evolutionary tree for the five Greater Antillean amazons (highlighted in yellow) and their common ancestor, *A. albifrons* (highlighted in blue) from mainland Central America. Divergence times are given in millions of years (Mya). Taken from Kolchanova et al. (2021).

There five species of *Amazona* found in the Greater Antilles. There are two Jamaican species: the Black-billed Parrot (*Amazona agilis*) and the Yellow-billed Parrot (*Amazona collaria*). The Rose-throated Amazon (*Amazona leucocephala*) is the only species found on multiple islands as there are multiple distinct subspecies found on Cuba, the Cayman Islands, and certain islands in the Bahamas. Amazon fossils recovered from islands of the Bahamas, including the Turks and Caicos identified as *A. leucocephala* indicate that this species was once more widespread in the Bahamas (Williams & Steadman 2001). The Hispaniolan Parrot (*Amazona ventralis*) is endemic to Hispaniola and the Puerto Rican Parrot (*Amazona vittata*) is found on Puerto Rico (Flieg & Sander 2016) (Figure 2 A-E).

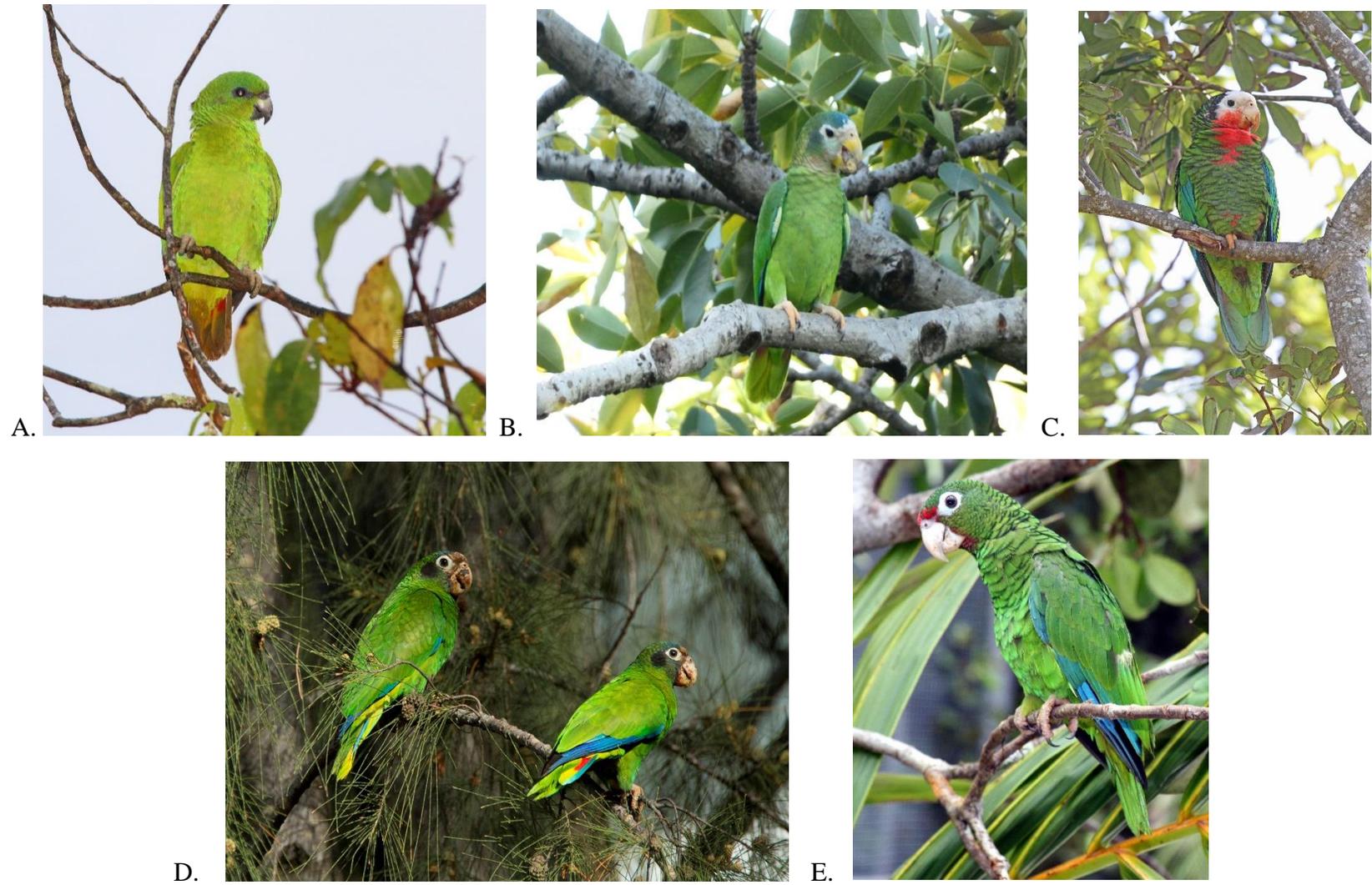


Figure 2. Greater Antillean amazon species. (A) : *A. agillis* (Jamaica). (B): *A. collaria* (Jamaica). (C): *A. leucocephala* (Cuba, Bahamas, Cayman Islands). (D): *A. ventralis* (Hispaniola). (E): *A. vittata* (Puerto Rico). Source: iNaturalist.

In the Lesser Antilles, there are two amazons: the Imperial Parrot and the Red-Necked Parrot (*Amazona imperialis* and *Amazona arausiaca*) endemic to the island of Dominica. Meanwhile, the St. Vincent Parrot (*Amazona guildingii*) is found on the island of St. Vincent while the St. Lucia Parrot (*Amazona versicolor*) is endemic to St. Lucia (Figure 3 A-D).



Figure 3. Lesser Antillean amazon species. (A): *A. arausiaca* (Dominica). (B): *A. guildingii* (St. Vincent). (C): *A. imperialis* (Dominica). (D): *A. ventralis* (St. Lucia). Source: iNaturalist.

From limited fossil records and historical accounts, there are accounts of numerous inferred, extinct amazons endemic to other islands in the Lesser Antilles. An extinct, undescribed amazon (†*Amazona* sp.) from Montserrat was identified from a coracoid, humerus, ulna, and a femur (Reis & Steadman 1999). From Grenada, Butler (1992) tentatively identified an extinct, undescribed amazon species (†*Amazona* sp.) while historic accounts retold by (Clark 1905) from the 18<sup>th</sup> century described a potentially extinct endemic amazon species (†*Amazona violacea*)

from Guadeloupe. Another hypothetical, extinct species, †*Amazona martinicana*, is not known from any fossil remains but was described from historical accounts from the 18<sup>th</sup> century as well (Rothschild 1907). The lack of fossil remains or other material from the two latter hypothetical species leaves their former existence disputed.

Unlike the Greater Antillean amazon species, the endemic amazon parrots of the Lesser Antilles are not one another's closest living relatives, phylogenetically speaking. *A. arausiaca* and *A. verisicolor* form a well-supported clade with *A. oratrix*, part of the larger *A. ochrocephala* (Yellow-Naped amazon) species complex, and *A. barbadensis*. Phylogenetic studies have also grouped *A. guildingii* and *A. imperialis* with *A. amazonica* (the Orange-Winged Amazon) and *A. brasiliensis* (the Red-tailed amazon) (Russello & Amato 2004). Bond (1978) proposed northern South America as being a source for Lesser Antillean avifauna, including amazons endemic to the Lesser Antilles. Russello & Amato (2004) used their phylogenetic analyses to infer that the difficulties in grouping the Lesser Antillean amazons could be attributed multiple, independent colonization events from northern South America. An evolutionary tree interpreting the limited knowledge of Lesser Antillean amazon evolutionary relationships from Russello & Amato (2004) is provided in Figure 4.

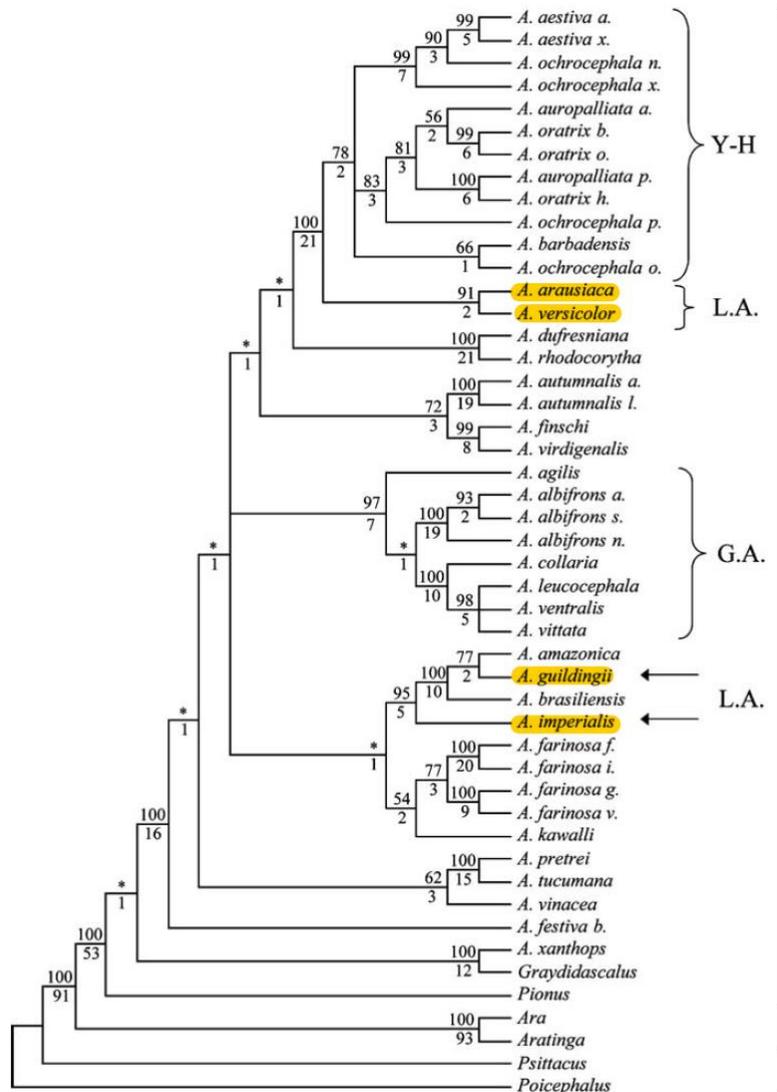


Figure 4. Amazona tree with the four Lesser Antillean taxa (highlighted in yellow). This tree addresses their status as a paraphyletic group. Taken from Russello & Amato (2004).

## Island Biogeography

Grounded in geography, biology, paleontology, and geology, biogeography is the study of the distribution of species and ecosystems over geographic space and geologic time. With respect to species turnover and change over time, there is no such real-life laboratory to observe biogeography more so than oceanic islands. Islands in oceanic settings are highly dynamic, subject to different climatic and geologic processes (i.e., sea level changes) that vary across

space and time. These processes have a profound influence on species diversity that islands can support (Whittaker et al. 2008; Fernández-Palacios et al. 2015).

Island biogeography has been largely governed by two ruling paradigms: vicariance biogeography and the equilibrium theory of island biogeography (ETIB) (MacArthur Wilson 1967; Heaney 2007). Geographical distributions of terrestrial or freshwater taxa separated by oceans can be explained by vicariance, or the fragmentation of a previously contiguous landmass (de Quiroz 2005). Geographic distributions of organisms on islands can also be explained with vicariance or dispersal, the active movement of organisms. Vicariance biogeography, part of historical biogeography, emphasized the process of diversification and argues that insular species will persist over millions of years, with little to no colonization by means of oceanic dispersal (Rosen 1978; Nelson & Platnick 1981).

In contrast, ETIB by MacArthur & Wilson (1967) postulated that island biotas are characterized by rapid turnover through on-going colonization and extinction, implying that rates of gene flow would often be high due to frequent dispersal events. The model proposed that the number of species inhabiting an island at any given time represented a dynamic equilibrium between the rates of immigration (the rate of species colonizing the island) and extinction (rate of species loss on the island).

In addition, two general patterns, the species-area relationship (Arrhenius 1921) and the species-isolation relationship (e.g., Forster 1778; Diamond 1972), which assume the tendency for species richness to increase with an island's area but also for that richness to decrease with increasing isolation of islands, governed island biogeography. The ETIB model incorporated the species-area relationship, species-isolation relationship, and another variable: species turnover,

or the rate of new species replacing those that go extinct. Despite their success with their equilibrium model, especially for its simplicity, MacArthur & Wilson (1967) drew criticism for the model being too simplistic and not accounting for dynamic change or more specifically, speciation and adaptive radiation. As argued by Fernández-Palacios et al. (2016), islands themselves are dynamic, and their area and isolation will change with time, something that the original equilibrium model by MacArthur & Wilson (1967) fails to account for.

### Sea Level Fluctuation & Island Biogeography

Geologic dynamism is responsible for the formation of islands like volcanic archipelagos or coral reef building creating atolls and raised limestone islands. However, as a result of eustatic sea level change due to Quaternary glacial cycles, islands have undergone significant changes in area, shape, isolation, and connectivity. An island's area and isolation can be affected by eustatic sea level change on critical evolutionary timescales (Steadman 2006).

Fernández-Palacios et al. (2016) reexamined ETIB through the lens of applying Pleistocene glacial cycles to the variable of time, in order to account for dynamic changes in sea level that affect area and isolation of oceanic islands. Their study argues that the ETIB paradigm is too static in accounting for island biodiversity that is a result of geologic and climatic processes that modify an island's environment and geography over both ecological and evolutionary timescales. Glacially lowered sea levels even affected the very existence of certain islands or small islets during the last glacial maximum (LGM), for instance (Kealy et al. 2018). Through the lenses of marine and island biogeography, glacial cycles throughout the last 2.6 Myr have raised and lowered eustatic sea level, driving biodiversity.

From a terrestrial and marine perspective, glacial cycles throughout the last 2.6 Myr have had profound effects and influences on biodiversity, specifically in terms of dispersal patterns and range expansion and contraction of biotas (Lomolino et al. 2017). For instance, the submerging of large island groups in Southeast Asia following the LGM resulted in the contraction in the geographic range of Sumatran rhinoceros (*Dicerorhinus sumatrensis*) and resulting decline in genetic diversity after populations became isolated (Mays et al. 2018).

Biogeographic corridors for dispersal and geographic range expansion were facilitated by lower sea levels during the Pleistocene (Lohman et al. 2011; Steadman & Franklin 2015). A case of lower sea levels during the Pleistocene commonly studied is the case of the Sunda Shelf, which, at lower sea levels, facilitated significant biotic dispersal between New Guinea and Australia, and landbridge islands such as the Aru Islands, whose vertebrate fauna, mainly Australo-Papuan groups, are present in southern New Guinea today as well (Hope & Aplin 2005; Lohman et al. 2011.)

## **Paleoclimate**

With molecular dating from phylogenetics, evolution and dispersal of amazon parrots in the Greater and Lesser Antilles can be correlated with known geologic and climatic changes throughout the Quaternary (Silva et al. 2014). In order to understand some of these geologic and climatic events, a look at the Upper Pliocene through the Pleistocene and Holocene and their associated climatic changes is needed.

### Pliocene

Throughout most of the Mesozoic and early Cenozoic (Paleogene) eras, the global climate was relatively warm and equable (Lomolino et al. 2017). Following the Paleocene-

Eocene Thermal Maximum (PETM), the planet gradually cooled throughout the Cenozoic, but Earth's global climate was still warmer than that in contemporary time. During the Pliocene epoch (middle Neogene, around 5 Ma), climatic oscillations increased, leading to a variation in warm and cool periods, and an overall decreasing trend in global temperatures. (Zachos et al. 2001).

During the most recent Pliocene warm period (ca. 3 Ma) global surface temperatures were 2-3° C warmer than those observed in the 20th century (Dowsett et al. 2013) and with estimates of atmospheric CO<sub>2</sub> concentrations similar to present (Bartolioli et al. 2011). In addition, this warm period was also distinguished by higher sea levels (10-20 m) and smaller ice sheets (Miller et al. 2019). Regional differences in the timing of cooling and evidence of high-latitude climate change imply that global cooling during the Pliocene was a gradual process, rather than a response to a single threshold or episodic event as previously suggested (Ravelo et al. 2004). During the Late Pliocene, this cooling event is known from marine oxygen isotopes and is typified by a glacial event and associated lowering of global sea level (Dolan et al. 2014).

#### Sea level estimates for the Pliocene

The middle and later Pliocene saw Earth's climate vary between warm and cold with an overall downward trend in global temperatures, which, would eventually help propagate the glacial cycles of the Pleistocene (Ravelo et al. 2004). Miller et al. (2019) estimated for Pliocene sea level estimates have a lot of error and that sea levels were 10-20m above present sea level. Meanwhile, from the M2 Isotope Stage for the Late Pliocene (Dolan et al. 2014), sea levels were estimated to have been 40-60m below present due to this Late Pliocene glaciation.

## Quaternary

The beginning of the Quaternary saw global temperatures dip substantially, impacting the climate system and the Earth became much colder (MacPhee & Schouten 2019). By the start of the Pleistocene, 65% of Earth's land surface was north of the Equator, creating a strong, asymmetric heat budget between the Northern and Southern hemispheres as the land absorbed more incoming solar radiation than the sea surface, setting the stage for increased climatic instability. Cyclical, astronomic changes in the characteristics of Earth's orbit (Milankovitch Cycles): obliquity (the tilt of Earth on its axis), eccentricity (the variation in the shape of Earth's orbit), and precession (orientation of the Earth's axis) affect the planet's total heat budget and the geographic and temporal variation of that heat, are the principal drivers of glacial-interglacial cycles (Milankovitch 1920). These cyclical variations in insolation across the Earth drive feedback processes that gradually cooled the planet, leading to an accumulation of sea ice and terrestrial glaciers (Lomolino et al. 2017).

### Sea level estimates for Pleistocene

The Pleistocene saw the Earth plunge into alternating periods known as glacial stages and interglacial stages, depending on the advancement of glaciers on land and sea ice in the ocean. With glacial stages, came different fluctuations in eustatic sea level (Lomolino et al. 2017).

For instance, past sea level estimates for MIS 11 (424 – 374 ka), derived from beach deposits in the Bahamas estimate that global sea levels were as high as 20m present (Hearty et al. 1999). Steadman & Franklin (2015) investigated changes in bird communities between the Pleistocene and Holocene, on Greater Abaco, Bahamas according to paleoclimate and sea level reconstructions, using a -120m below present sea level estimate from Yokoyama et al. (2000) for

the LGM. Yokoyama et al. (2000) estimated sea levels during the early Holocene (12-11 ka) to be 40m below present, using -35 to -45m for estimations of uncertainty. During the Paleolithic in North America, Gillam et al. (2006) used an estimation of -75m below present sea level for reconstructing shorelines of North America. Other major sea-level cycles occurred at intervals of approximately 100 ka over the past approximately 800 ka, with maximum amplitudes of 120–139m (Zong 2015).

### **Sea Level Fluctuations –Marine Isotope Stages**

Dynamic fluctuations in global sea level are one of the most profound results of Quaternary glacial-interglacial cycles (Yokoyama et al. 2000). Glacial-interglacial cycles and variations in the thermal expansion of seawater influence sea level rise and fall. During the Quaternary glacial-interglacial cycles, sea level change was facilitated by the exchange of oceanwater and ice and the planet's dynamic response to changes in surface load (Lambeck et al. 2014).

Marine Isotope Stages (MIS), or marine oxygen-isotope stages, represent alternating warm and cool periods of Earth's paleoclimate over the past 2.6 million years, derived from oxygen isotope data reflecting changes in temperature derived from deep sea core samples (Dolan et al. 2014; Zong 2015). In this exchange of ice and oceanwater (Lambeck et al. 2014), variations in the stable isotopes of oxygen record changes in sea level and sea surface temperature. Oxygen isotope records recovered in analyzing benthic foraminifera of deep-sea sediment cores paint the picture of the history of global continental ice volume and glacio-eustatic sea-level change. During a glaciation event, the oceans become enriched in the heavier  $^{18}\text{O}$  molecules while lighter  $^{16}\text{O}$  becomes trapped in the frozen water composing continental

glaciers. The more expansive ice sheets and glaciers are, the more  $^{18}\text{O}$  is left in the ocean while during a warmer interglacial, there is a greater concentration  $^{16}\text{O}$  in the ocean (Shackleton 1987).

$\delta^{18}\text{O}$  records are derived from ocean cores and the shells of benthic foraminifera. In terms of measuring relative sea level change to continents, continental margins contain a record dating back over a billion years, in terms of water depth changes, observed as transgressions and regressions that reflect processes including eustasy, subsidence/uplift, and sediment input/loading (Miller et al. 2019).

## **Geographic Information Systems (GIS)**

A GIS is a computerized system designed to capture, store, manipulate, and present various types of location-based, geographic raster or vector data that users can visualize or use in analysis for mapping (What is GIS?, Esri). Raster data is cell-based while feature (vector) data is based on points, lines, and polygons. These forms of analysis are very applicable to using GIS for problem-solving.

### Networks in GIS

In GIS, a network is an interconnected set of points and lines, whereas a network dataset is a topologically connected collection of edges, junctions, and turns derived from a linear network (polyline data) (Wade & Sommer 2016). Analyses including finding the closest location along a network or the most optimal route between two nodes can be carried out with the Network Analyst extension in ArcGIS Pro. Operations including Route Solver utilize underlying algorithms such as Dijkstra's algorithm to examine network connectivity in order to determine the shortest path between two points, along said network (Nicoră & Haidu 2016).

Commonly used in urban or city mapping, the ArcGIS Network Analyst extension allows users to solve common network problems, such as finding the best routes across a city, finding the closest emergency vehicle, facility, or school, or identifying a service area around a specified location. The simplest operation in network analysis uses the variable of distance traveled between a starting and ending point and is weighted (Ahmed et al. 2017).

Ahmed et al. (2017) used ArcGIS Network Analysis to identify the most optimal route from an incident to any given emergency care center, in the Greater Cairo metropolitan area, in Egypt. Meanwhile, Prima et al. (2018) applied Network Analysis to ecology, modeling landscape connectivity for American bison (*Bison bison*) in GIS, using networking in ArcGIS. Their study described movement as a key process driving force of the distributions of animal species within heterogenous landscapes. A connected landscape or one that is fragmented or experiencing disjunctions can be observed in real-time or modeled in GIS (Graham 2001). Their study incorporated graph (network) theory and GIS in studying the movements of bison across pasturelands contained within a Canadian National Park. In addition to understanding and predicting landscape connectivity and animal movements, Prima et al. (2018) included time in their analysis. The study argued that a temporal dimension would add clarity to the observing of the space being used and landscape connectivity.

In other ecological and biological studies, the cost of migration or movement can be modeled using the cost of distance or other factors such as landcover (Graham 2001; Concepcion et al. 2020). Using adjusted bathymetric data, visibility ranges of humans, and reconstructed paleogeography (adjusted sea levels and coastlines, and rivers) of the greater Sundaland region, Kealy et al. (2018) used cost-distance to map the most likely paths of human travel across

Sundaland, from mainland Southeast Asia to Australia-New Guinea, during periods of glacially lowered sea level, according to coastlines and reconstructed island topography.

Webster et al. (2016) applied the cost of distance traveled in a twofold analysis using cost-distance and network mapping for calculating optimal travel corridors along rivers of the Peruvian Amazon, between different communities. Through their analysis, Webster et al. (2016) articulated that distance is commonly used to assess accessibility, interactions between individual entities in a network, and it is used to evaluate natural and social phenomena.

### Raster Analysis & Profile on Distance Analysis

In GIS, rasters are cell-based image files whose cells, also called pixels, all equally-sized, are gridded datasets with each pixel denoting a value and are associated with a specific geographic location (Esri, Introduction to image and raster data). Values that classify raster data can be associated with elevations, distances, or depths (Lemenkova 2020). One form of raster analysis associated with distance analysis is Euclidean distance.

Euclidean distance tools (direction, distance, and allocation) are Spatial Analyst tools for creating raster datasets pertaining to distance or direction. The distance-based outputs produced describe each cell's distance to a source or a set of sources based on the straight-line distance to that location and distances are measured from one cell center to another cell center (Esri, Understanding Euclidean Distance Analysis). The Euclidean distance algorithm calculates distance from the center of each source cell out to the center of each surrounding cell. For each cell, the distance to each source cell is determined trigonometrically by calculating the hypotenuse with  $x_{max}$  and  $y_{max}$  as the other two legs of a triangle. Each calculation derives the true Euclidean distance, and not the cell distance. Source data can be derived from a raster or

vector data that is converted to a raster as the tools run. Euclidean distance rasters are often utilized in further analysis such as suitability (Sengupta et al. 2022).

### Occurrence Mapping in GIS

Occurrence data for plant and animal species can be used for mapping geographic ranges in GIS, which can then be used in studying the movements of species or formulating protection plans. Some programs or studies, such as the Gap Analysis Project (GAP) from the U.S. Geological Survey (USGS) will map the occurrences of species alongside other geographic variables like slope, elevation, or landcover (USGS 2019). Occurrence datasets that can be visualized in a geographic information system (GIS) can be important in the studying of extinct lineages as well (Martin et al. 2017). Fossil data for the occurrence or distribution of a specific taxon or multiple taxa can be correlated with palaeoclimatological information as well.

In a study utilizing GIS for determining geographic ranges, an archaeological and paleontological approach for bison was taken by Martin et al. (2017). Their study compiled and mapped a prehistoric and historic geographic occurrence data for bison in GIS, sorting their dataset based on mean calendar years Before Present (cal yr BP), to determine the former geographic range extent for bison during the Pleistocene, in relation to present-day Grand Canyon National Park and nearby regions of the western United States where bison are native. Results indicated that based on fossil and modern *B. bison* occurrence data, bison should still be considered native to the Colorado Plateau, specifically the region that is now Grand Canyon National Park.

## Bathymetry and Sea Level Mapping in GIS

Elevation or hydrographic data in a GIS, specifically bathymetry can be used to map contemporary sea level, and it can be used to reconstruct past sea level depth or visualize future projections of sea level rise. Sea-level depth estimations, using bathymetry are widely accessible or relatively easy to model, at highly practical and large, continental scales using GIS (Smith & Sandwell 1997; Gillam et al. 2006).

Gillam et al. (2006) used map algebra functions in Esri ArcGIS 9.2 to modify the ETOPO2 digital elevation model (DEM) dataset (a 2-minute latitude/longitude grid with an approximated 3.7-km spatial resolution at the equator) of land elevations and seafloor bathymetry derived from the Global Land One-km Base Elevation (GLOBE), to model and recreate shorelines during the LGM and Paleoindian Period of North America. Sea level change and biotic dispersal to islands has been considered from the lens of GIS as well (Robles 2013).

Robles (2013) used Geographic Resources Analysis Support System (GRASS) GIS to reconstruct paleocoastlines of the Philippines during the LGM using contemporary bathymetric datasets from the Global Bathymetric Chart of the Oceans (GEBCO) dataset. The dataset was modified in QGIS to model lower sea level intervals (-10 to -120 meters below present) and calculate areas of islands that would have had higher land area exposed at lower sea levels. This study considered island connectivity at different sea level values and the effects it had on dispersal routes for vertebrate fauna, based on the biogeographic regions of the Philippines (Robles 2013). In North America, the Channel Islands' rich pygmy mammoth fossil record (*†Mammuthus exilis*) and reconstructions of the region at lower sea levels in GIS indicate that ancestral stocks of Columbian mammoths (*†Mammuthus columbi*) actively dispersed to the

Channel Islands via swimming from the coast of California based on studies assessing optimal pathways between mainland California and the Channel Islands (Muhs et al. 2015). Kealy et al. (2018) utilized least-cost pathway modeling to map human dispersal in the Wallacean Archipelago, from Sunda to Sahul according to different sea level values and the presence and absence of archaeological sites across the region, at 65 and 70 ka, respectively.

## **Phylogenetics**

When studying biodiversity and biogeography from a pre-human context, data from available fossil records, morphologic information, and molecular information from phylogenetics can offer insight into living or extinct lineages. Evolutionary relationships can be reconstructed using morphologic characters among taxa or genetic information in order to map out lineages, using Bayesian, maximum likelihood (ML), or maximum parsimony (MP) analyses. Parsimony analysis can be used to support or refute previous hypotheses on evolutionary relationships or divergences in a lineage (Brochu 1999). Mitochondrial (mtDNA) and nuclear (nuDNA) gene datasets can be sequenced with geographic data to add clarity to evolutionary relationships as well (Eaton et al. 2009).

Similar to trees and cladograms constructed based on discrete morphological characters (Brochu 1999) or molecular data (Eaton et al. 2009), evolutionary relationships for a group of taxa can be made based on geography, with different geographic lineages or populations reflecting biogeography. For biogeography, patterns of vicariant (geographical barriers separating populations) and geographic dispersion events can be expressed as trees, or area cladograms, using different taxa grouped by geographic regions. Relative times for the formation of geographic barriers or the joining of regions that encourage geographic dispersal can be determined (Lieberman 2003).

## **Avian Flight**

Powered-flight was a phenomenal achievement evolutionarily, for birds. Nearly all aspects of avian biology, internally and externally, are influenced by powered, flapping flight, or in the case of flightless taxa, the loss of such characters. Hollow bones, a keeled sternum and furcula for flight muscle attachment, wings supported by the carpometacarpus (the fusion of the carpal and metacarpal bone), and the airfoil shape to wings to generate lift are among the adaptations for powered flight (Tobalske 2016). Fuel load and body mass are critical in the flight capabilities for birds (Klaassen 1996). Flight, specifically for migration or long-distance travel can be a costly endeavor for birds, especially over long tracks of ocean (Concepcion et al. 2020).

As flighted vertebrates, birds are capable of active, overwater dispersal from the mainland, such as a continent, out to one or more islands. Regardless of migratory or non-migratory birds, long distance travel, especially over water, is very costly in terms of energy for birds (Tobalske 2016). Farther distances over large expanses of ocean can be difficult for some birds, depending on their flight capabilities (Concepcion et al. 2020). Wind patterns or storms, or simply long or short distances have an influence on migratory and travel behavior for birds, thus influencing their dispersion out to different islands (Concepcion et al. 2020; Gyllenhaal et al. 2020).

## METHODS

The objective of this study was to model and determine potential avenues and routes of amazon parrot dispersion in the Caribbean using a variety of raster and feature data analysis in ArcGIS Pro. Tools and methods utilized included Network Analyst and Spatial Analyst, specifically for raster processing including map algebra and Euclidean distance, and creating estimated ranges from aggregating together point feature data. Operations in this study were carried out using ArcGIS Pro version 3.0.0 and ArcMap 10.8.2. Sea-level fluctuations according to six MIS periods of the late Pliocene, Pleistocene, and early Holocene and molecular-dated evolution times were used in this study to create inputs and outputs in the different analyses.

### **Flight Distance Thresholds for Network and Euclidean Distance Mapping**

In order to plot out optimal network paths and create Euclidean distance raster datasets of each seascape at different sea levels for the Greater and Lesser Antilles, a maximum range for potential distance that amazon parrots could possibly fly was needed.

Pennycuik (1989) and Klaassen (1996) determined that the maximum fuel-carrying capacity (ratio of total body mass to lean body mass, or  $h_{\max}$ ) of migratory birds has an inverse relationship with increasing body mass. Thus, flight range will increase linearly with fuel load and the maximum flight range will also decrease with a bird's body mass.

Masses, in kilograms, of each mainland amazon parrot species that phylogenetic trees published by Russello & Amato (2004) and Kolchanova et al. (2021) group with Greater and Lesser Antillean amazons were taken from the American Ornithological Society's Birds of the World database (Birds of the World), if the record was available. In addition, masses for each insular amazon species in the Greater and Lesser Antilles were utilized as well (Tables 1 & 2).

While each seascape network and Euclidean distance analysis for each MIS ran in ArcGIS Pro began in either Central America (for the Greater Antilles) or northern South America (for the Lesser Antilles), the masses of each endemic island amazon species, if available were used to that species' potential to travel to other islands in the networks and distance surfaces, given by Euclidean distance.

Table 1. Amazon parrot species in the Greater Antilles, mainland and island species, and their body masses (in grams and kilograms).

	Species	Location	Mass (g)	Average Mass (g)	Average mass (kg)
Mainland	<i>Amazona xantholora</i>	Yucatan Peninsula; nearshore Mexico island of Cozumel	219 (males) - 212 (females) (Paynter 1955; Klass 1968)	215.5	0.2155
	<i>Amazona albifrons</i>	NW Mexico-S Mexico; Yucatan Peninsula to W Costa Rica.	176-242	209	0.209
Greater Antilles	<i>Amazona leucocephala</i>	Cuba, Bahamas, Cayman Islands	180-320	250	0.25
	<i>Amazona ventralis</i>	Hispaniola; introduced to Puerto Rico and the US Virgin Islands.	214	214	0.214
	<i>Amazona vittata</i>	Puerto Rico	250-312	281	0.281
	<i>Amazona collaria</i>	Jamaica	Not Available	—	—
	<i>Amazona agilis</i>	Jamaica	178-220	199	0.199

Table 2. Amazon parrot species in the Lesser Antilles, mainland and island species, and their body masses (in grams and kilograms).

	Species	Location	Mass (g)	Average Mass (g)	Average mass (kg)
Mainland	<i>Amazona amazonica</i>	Northern Columbia to Guyana, south to Brazil. Occurs on Trinidad and Tobago.	298-469	384	0.384
	<i>Amazona ochrocephala</i>	Panama to northern Bolivia; Venezuela to French Guinea, south to Brazil	340-535	437.5	0.438
	<i>Amazona barbadensis</i>	Northern Venezuela to Bonaire. Extirpated from Aruba, Margarita, and La Blanquilla.	Not Available	—	—
	<i>Amazona autumnalis</i>	Caribbean slope - N South America (Venezuela to NW Brazil).			
Lesser Antilles	<i>Amazona guildingii</i>	St. Vincent	485-880	682.5	0.683
	<i>Amazona versicolor</i>	St. Lucia	505-1000	752.5	0.753
	<i>Amazona imperialis</i>	Dominica	Not Available	—	—
	<i>Amazona arausiaca</i>	Dominica	Not Available	—	—

Using the plots for lean body mass and  $h_{\max}$  and  $h_{\max}$  and maximum potential flight range by Pennycuick (1989) and the masses of each amazon species considered in this study, a maximum potential flight range of around 1,500 km, which corresponded to a ratio  $h_{\max}$  value between 1 and 2, was determined and used as the estimated threshold in Network and Euclidean distance operations (Figure 5).

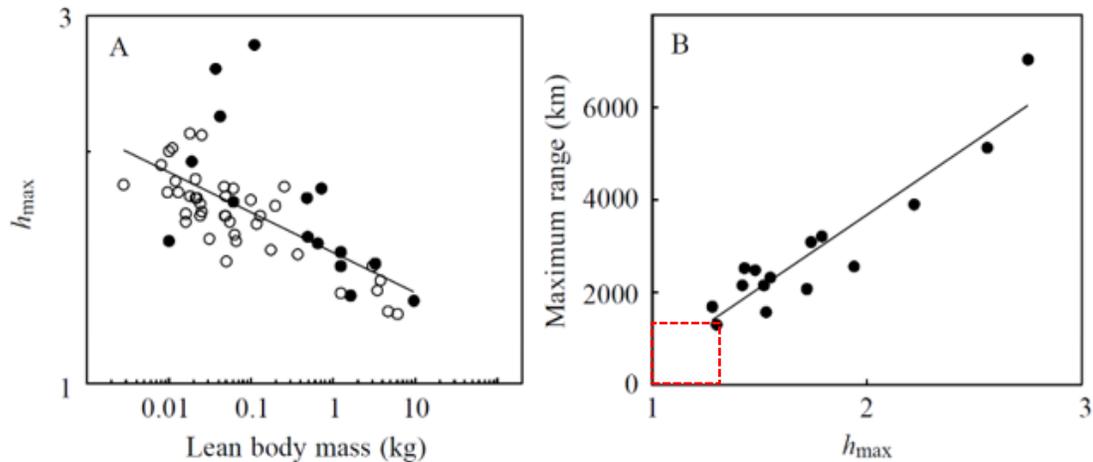


Figure 5. (A) The calculated maximum fuel-carrying capacities (ratio of total body mass to lean body mass,  $h_{max}$ ; the filled circles) for 15 species of birds with known aerodynamic characteristics as a function of lean body mass. In addition, maximum observed fuel-carrying capacities in 41 species of free-living birds (open circles) in relation to lean body mass are depicted. (B) Calculated maximum flight range according to Pennycuik (1989) as a function of calculated maximum fuel-carrying capacities for the 15 species of birds with known aerodynamic characteristics. The red dashed marker on the  $h_{max}$  and distance plot indicates the 1,500 km distance threshold used in this study.

The study from Klaassen (1996) considered only migratory bird species. Amazon parrots are non-migratory and are not equip for long-distance migration (Kolchanova et al. 2021). The flight range estimate of 1,500 km determined for the average masses of Caribbean amazons are used merely for modeling after I received outside consultation from Dr. Medhavi Ambardar, an ornithologist in the Biology Department at Fort Hays State University for this part of my methods (personal communication). In order to model for potential uncertainty with this estimation and address variables unable to be visualized in GIS, such as wind patterns, a second distance threshold of 500 km was used as well.

### ArcGIS Pro Software Description and Operations

ArcGIS Pro (Figure 6) is a desktop GIS software developed by Esri. First released in 2015, this software is the successor of Esri's previous ArcMap programs. ArcGIS Pro is notable

in having a 64 bit architecture, combined 2-D and 3-D mapping support, integration with ArcGIS Online, and it is supported by Python 3 (<https://www.esri.com/en-us/arcgis/products/index>).

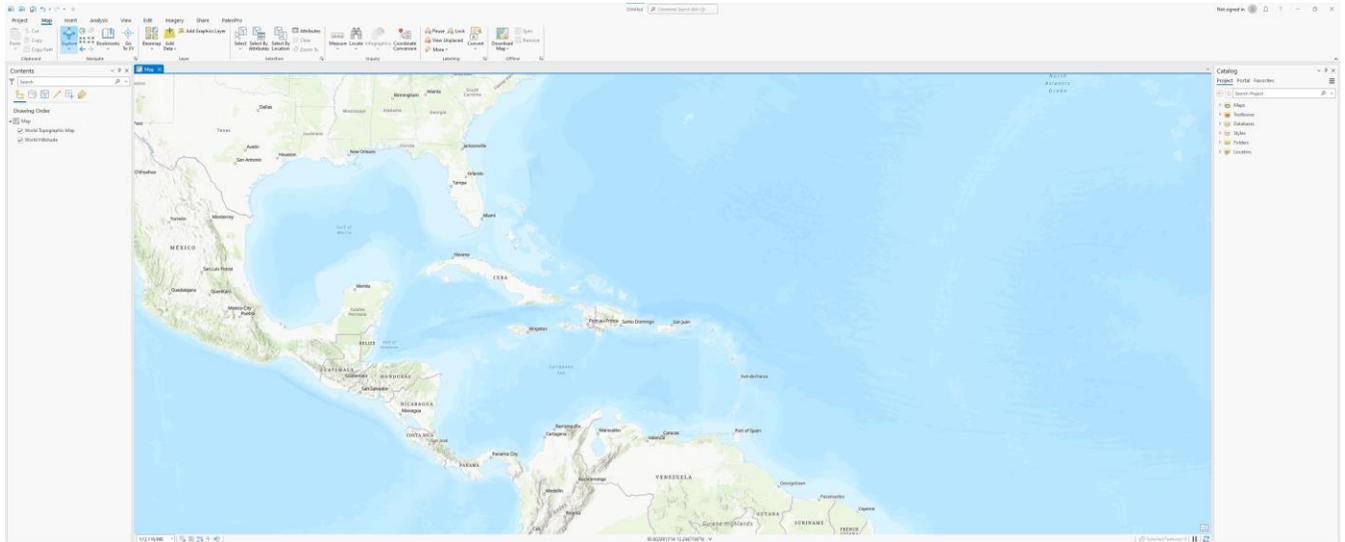


Figure 6. ArcGIS Pro 3.0 default map view. The Esri GIS software used in carrying out analyses in this study. <https://www.esri.com/en-us/arcgis/products/index>.

The Network Analyst extension is a feature in ArcGIS Pro that allows users to find the simplest routes along a network dataset – a series of nodes and edges that connect lines of a map (Wade & Sommer 2016). Analyses including finding the closest location along a network or the most optimal route between two nodes can be carried out with the Network Analyst extension in ArcGIS Pro (Figure 7). Operations including Route Solver utilize underlying algorithms such as Dijkstra’s algorithm to examine network connectivity in order to determine the shortest path between two points, along said network (Nicoră & Haidu 2016).

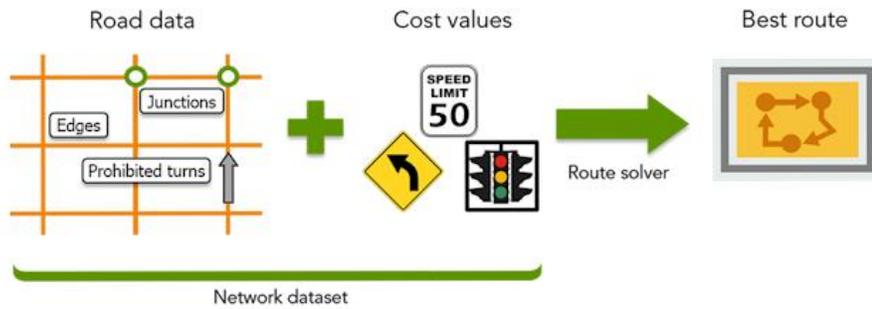


Figure 7. A graphic of network operations – junctions and edges with turns. Graphic source: Network Pro modules.

A Euclidean distance raster (Figure 8) contains the measured distance from every cell to the nearest source, a feature or raster from which the distance is measured in units of the raster (Understanding Euclidean Distance Analysis, Esri). Euclidean distance is a raster tool found in the Spatial Analyst extension in ArcGIS Pro.

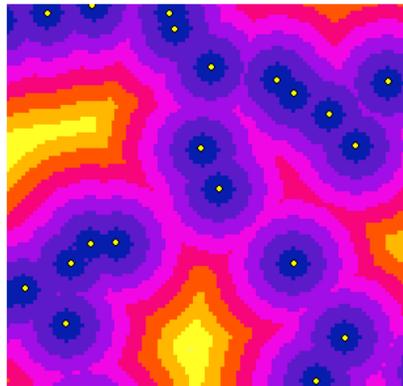


Figure 8. An example of a Euclidean distance raster operation and its output. Each cell denotes a distance value in relation to the nearness to each point feature. Graphic Source: Understanding Euclidean Distance Analysis – ArcGIS Pro.

Another tool for processing raster data is the Raster Calculator (found in the Spatial Analyst extension) which can be used to modify individual cell values (Figure 9). This tool was used extensively in this study as well.

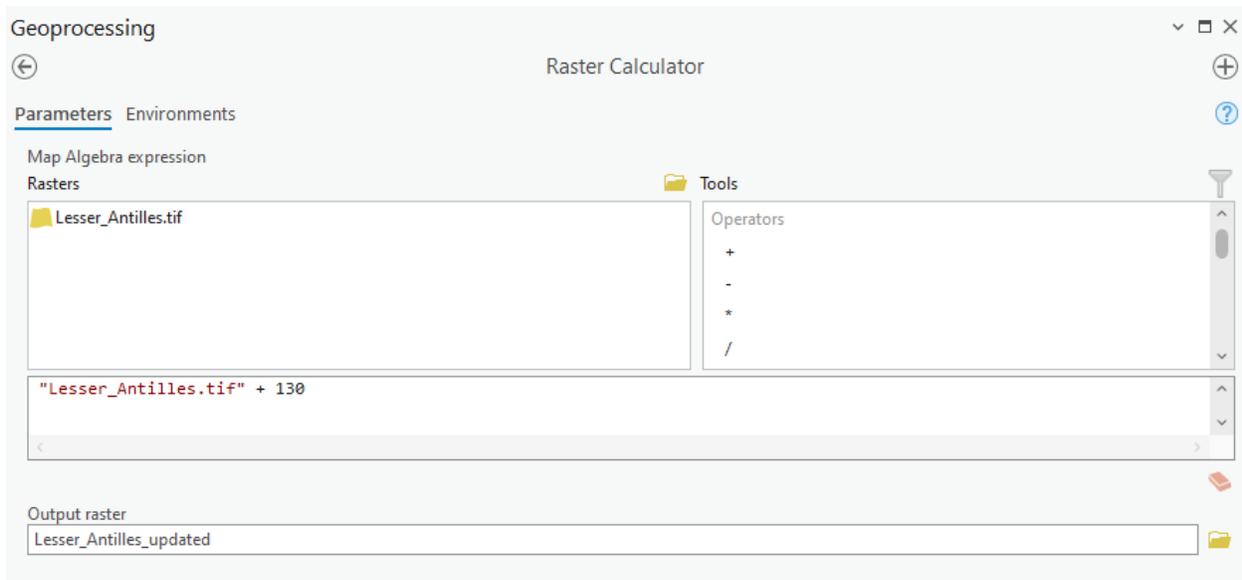


Figure 9. The Raster Calculator tool and an example of an operation to modify raster imagery. Graphic source: ArcGIS Pro.

## Datasets and Inputs

Inputs for network and raster operations in this study were derived from gridded elevation-bathymetry raster datasets from GEBCO (General Bathymetric Chart of the Oceans). GEBCO is an open-source provider of gridded bathymetric datasets, operating under the joint auspices of the International Hydrographic Organization (IHO) and the Intergovernmental oceanographic Commission (IOC) (GEBCO).

GEBCO bathymetric data was utilized in this study as an input for modeling sea level fluctuations of the Pliocene and Pleistocene in the Caribbean. Using GEBCO's Web Map Service, user-defined boundaries representing the Greater Antilles and Central America, and the Lesser Antilles and northern South America (specifically eastern Venezuela) were created (Figures 3 and 4). From the Web Map Service, two coverage file packages (the Greater Antilles + Bahamas and the Lesser Antilles) in GeoTiff and Esri ASCII raster were downloaded,

representing elevation and bathymetric data, in meters, on a 15 arc-second interval grid of GEBCO's current most bathymetric dataset, GEBCO\_2022 Grid.

The GEBCO bathymetry data used in this analysis represented the Caribbean, divided into the Greater Antilles and the Bahamas, and the Lesser Antilles. The first dataset for the Greater Antilles + Bahamas had a spatial extent of 27° 38' 30" North Latitude and 92° 50' 0" West Longitude to 12° 46' 0" North Latitude and 63° 28' 45" West Longitude. The second dataset for the Lesser Antilles had a spatial extent of 19° 3' 15" North Latitude, 63° 51' 45" West Longitude, and 8° 3' 30" North Latitude, 59° 9' 0" West Longitude. Each GeoTiff raster files had a cell resolution of  $4.17 \times 10^{-3}$  by  $4.17 \times 10^{-3}$  and projected in WGS 184 (GSC\_WGS\_1984) (Figures 10 and 11). The coordinate extents used for analysis for each GIS dataset utilized served as the compartmentalized study area for each operation.

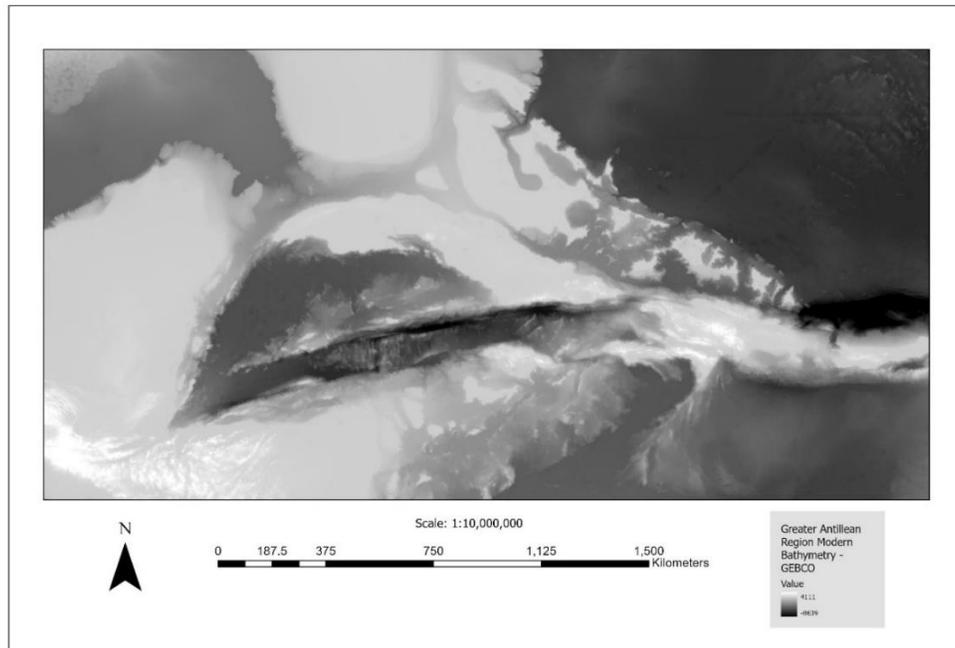


Figure 10. Bathymetry and elevation raster dataset for the Greater Antilles. Cell values in this raster dataset represent values (in meters) above (positive) or below (negative) sea level. Bathymetric values are represented by negative values. This served as the raw input for creating and modeling seascapes at six different MIS periods in this study as well as creating feature classes that served as inputs for the network and Euclidean distance operations. Source: GEBCO\_2022 Grid.

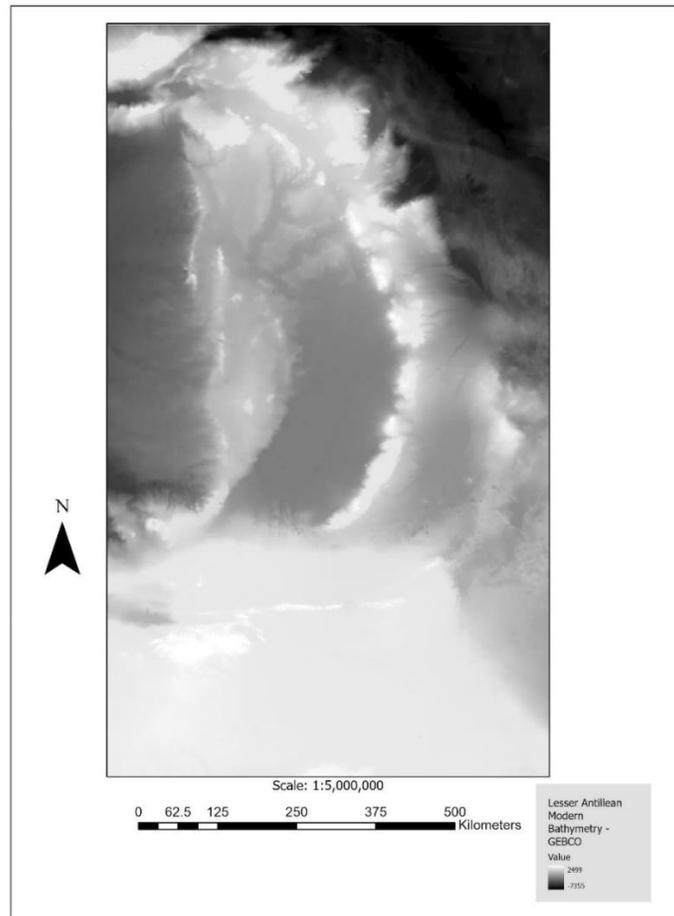


Figure 11. Bathymetric raster dataset for the Lesser Antilles. Cell values in this raster dataset represent values (in meters) above (positive) or below (negative) sea level. Bathymetric values are represented by negative values. This served as the raw input for creating and modeling seascapes at six different MIS periods in this study as well as creating feature classes that served as inputs for the network and Euclidean distance operations. Source: GEBCO\_2022 Grid.

## Molecular Ages + MIS Period Sea Levels

Molecular divergence times for Greater Antillean amazon evolution in a study by Kolchanova et al. (2021) supported stepping-stone dispersal for ancestral populations of amazons diversifying across the Greater Antilles starting 3.47 Ma and reaching Puerto Rico by 0.67 Ma. A monophyletic group (Russello & Amato 2004), Greater Antillean amazons being the result of a stepping-stone dispersal pattern may be connected to the exposure and drowning of the Nicaraguan Rise with sea level change (Kolchanova et al. 2021).

This timeframe for Greater Antillean amazon dispersal history was linked to four values for eustatic sea level change were derived from four MIS periods. The first four MIS periods and sea level values included - MG6: +20m above sea level (late Pliocene; ~ 3.47 Ma; Dumitru et al. 2021), M2: -65m below sea level (late Pliocene; ~ 3.3 Ma; Dwyer & Chandler 2009), the mid-Piacenzian Warm Period (mPWP): +30m above sea level (late Pliocene; ~3.25 – 2.9 Ma; Scheper et al. 2013), and MIS 16: -100m below sea level (middle Pleistocene; 636 – 625 ka; Hughes & Gibbard 2018). Two other MIS periods for dispersion and distributions of amazons during the Quaternary were utilized as well: MIS 2: -130m below sea level (LGM; 25 – 18 ka; Spratt & Liesecki 2016), and MIS 1: -40m below sea level (early Holocene; 12 – 11 ka; Steadman & Franklin 2015). These six MIS periods and their respective sea level values are given in Table 3.

Table 3. MIS values and their corresponding ages and sea level values. Ages are given in millions of years ago (Ma) or thousands of years ago (ka) while sea level is given in meters (m).

Marine Isotope Stage (MIS)	Age	Sea Level Value: lower (-) or higher (+)
MG6	~ 3.47 Ma	~ +20m higher (Dumitru et al. 2021)
M2	~ 3.3 Ma	-65m (Dwyer & Chandler 2009)
mid-Piacenzian Warm Period (mPWP)	~ 3.25 – 2.9 Ma	+ 20/30m (Scheper et al. 2013)
MIS 16	~ 636 – 625 ka	-100m (Hughes & Gibbard 2018)
MIS 2 (LGM)	~ 25 – 18 ka	-130m (Spratt & Liesekci et al. 2016)
MIS 1 (Early Holocene)	~ 12 – 11 ka	-40m (Steadman & Franklin 2015)

### Sea Level Modifications to Greater and Lesser Antilles Raster Datasets

First, these sea level values were used to modify the original GEBCO dataset of the Greater Antilles bathymetric raster data to serve as inputs for creating optimal routes of dispersal in Network Analyst and raster-derived flight regions from Euclidean distance analysis, to add geographic context for the dispersal history of Greater Antillean amazon parrots. Paleo sea-level depth values (-20, +65, -30, +100, +130, and +40) (Table 3) were added or subtracted from the z-values of each of the original GEBCO\_2022 Grid datasets, depending on the MIS with the Raster Calculator tool.

Following this, the status of Lesser Antillean amazons being a paraphyletic group with uncertainty on their evolutionary history (Russello & Amato 2004) was addressed. The same MIS period-derived sea level values, in conjunction with the molecular divergence times for Greater Antillean amazons were used to modify the GEBCO bathymetric-elevation data for the

Lesser Antilles to create network and Euclidean distance datasets, in order to provide a hypothesis on the dispersal and evolutionary history of the Lesser Antillean amazons. The MIS values utilized in this study were global mean sea level (GMSL) estimates, meaning they could be used for the entire Caribbean. In the Lesser Antilles, sea-level records related to global records can be found on the island of Barbados, an uplifted accretionary prism of seafloor turbidites, carbonate chalk, and outer layers of coral that are easy to date (Peltier & Fairbanks 2006).

Following the creation of raster datasets reflecting estimated bathymetry of six MIS periods for the Greater and Lesser Antilles, each raster dataset in ArcGIS was reclassified using the Reclassify tool (found in the ArcGIS Pro Spatial Analyst extension), into binary rasters with values of “1” and “2”. “1” represents all values for mean sea level (MSL) – defined here as all values less than or equal to zero, and “2” represents all values higher than MSL, or values denoting land above sea level. Each reclassified raster was then converted to a feature class (referred to as seascapes herein), using the Raster to Polygon function (Figures 12-14).

In raster to polygon conversions, users have the options to choose either simplified polygon geometry or they can maintain the geometry of the input raster. To best preserve the overall modeled island/land areas and extent, the polygons were not simplified in the conversion process. Feature class polygons were created for each MIS sea-level model, for the Greater and Lesser Antilles and their associated landmass sources: Central America (specifically the region closest to the Nicaraguan Rise) and northern South America, respectively.

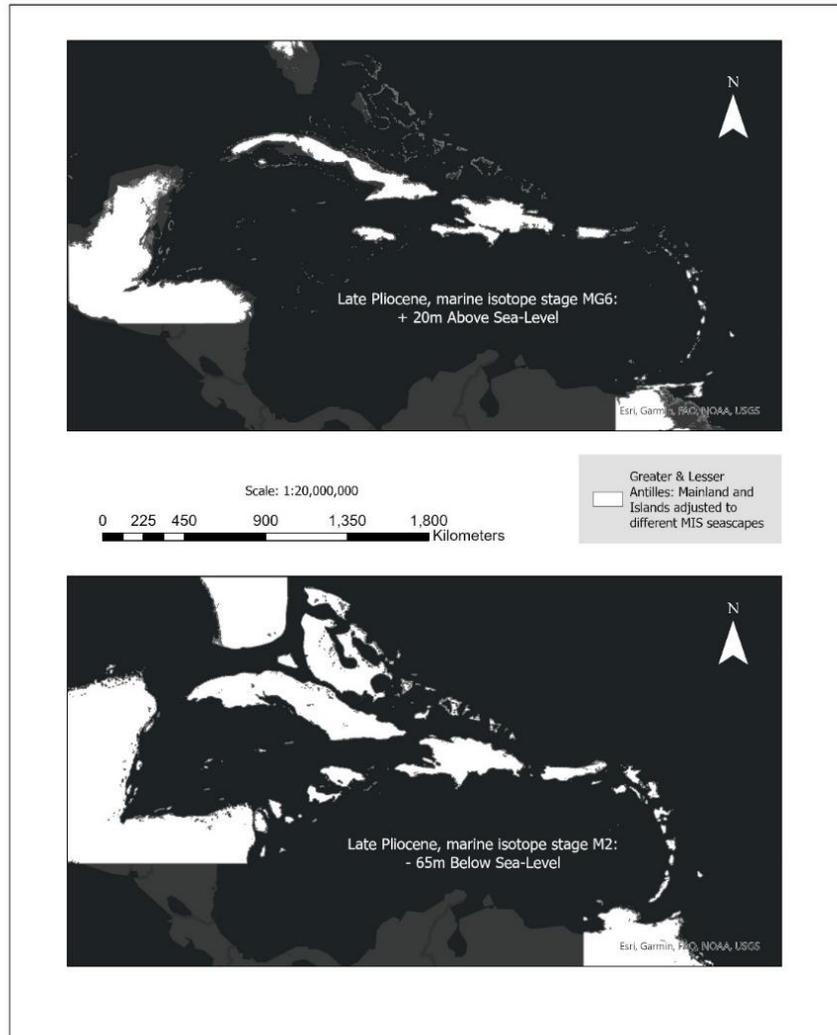


Figure 12. The seascape polygon features of the Greater and Lesser Antilles, for the MG6 isotope period (top) and M2 (bottom) isotope period of the late Pliocene. Boundary edges of the landmasses representing the mainland are the result of the spatial extent of the original bathymetric raster from which these polygons were derived through a raster to polygon conversion.

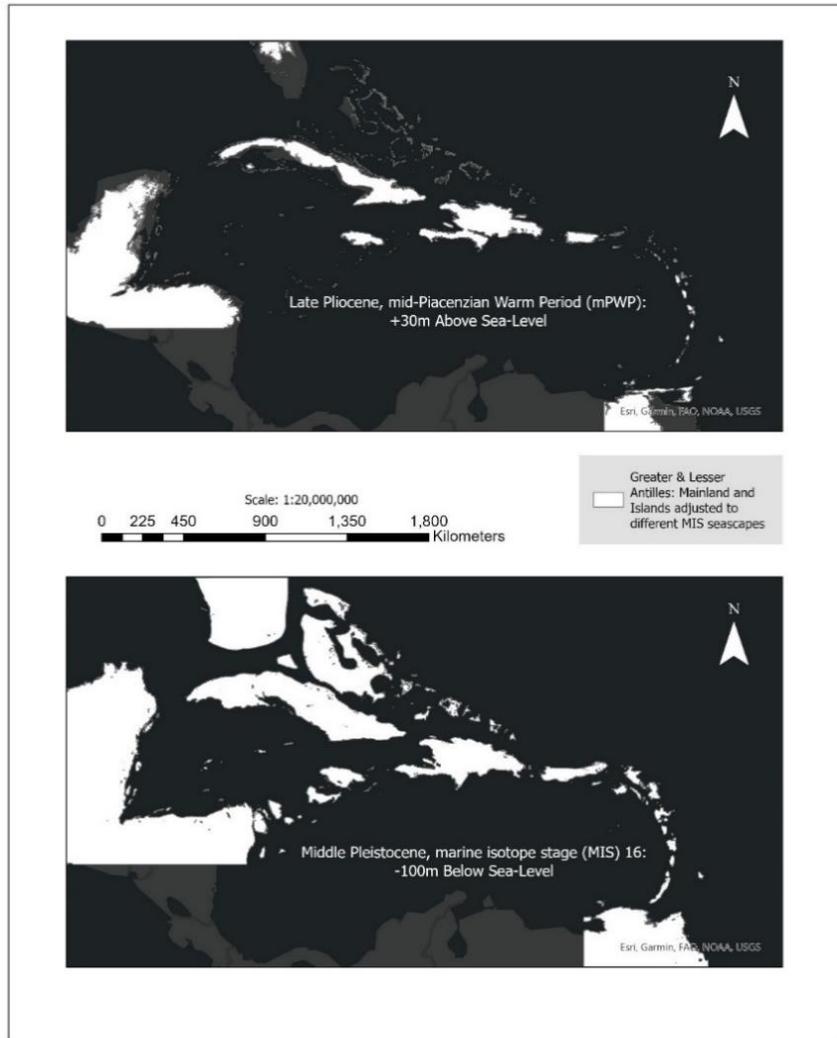


Figure 13. The seascape polygon features of the Greater and Lesser Antilles, for the mid-Piacenzian Warm Period (mPWP) of the late Pliocene (top) and MIS 16 (bottom) isotope period of the middle Pleistocene. Boundary edges of the landmasses representing the mainland are the result of the spatial extent of the original bathymetric raster from which these polygons were derived through a raster to polygon conversion.

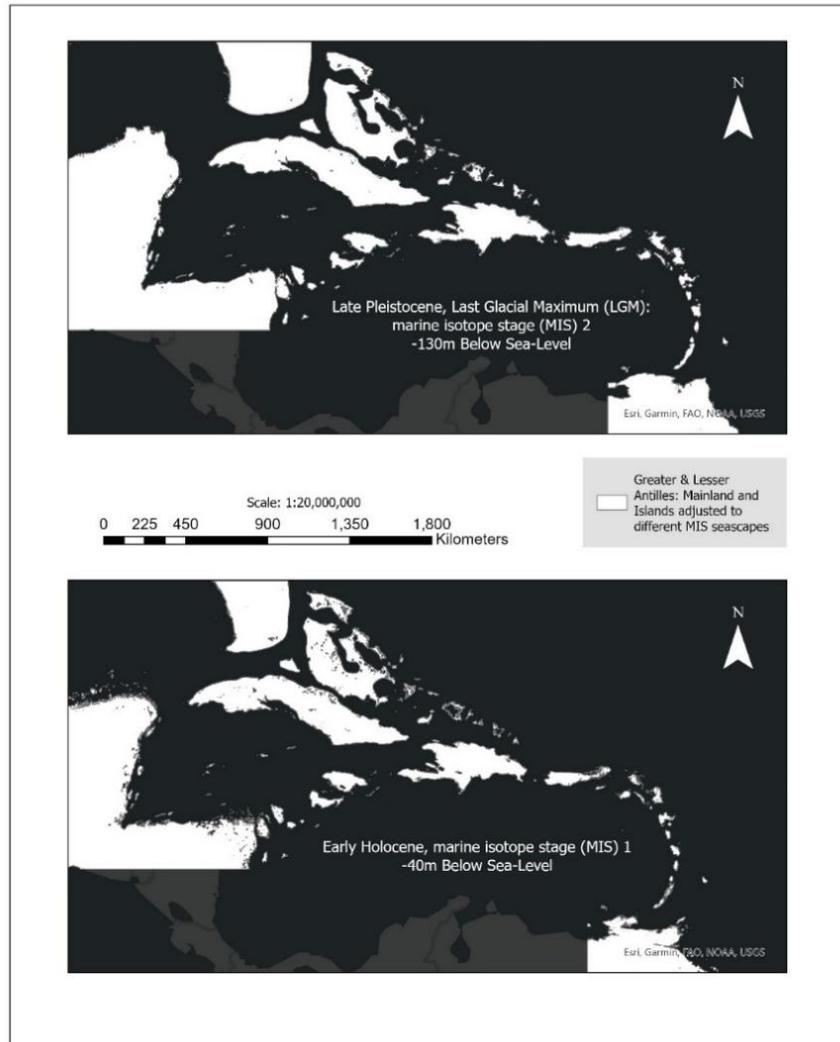


Figure 14. The seascape polygon features of the Greater and Lesser Antilles, for the MIS 2 isotope period (top) and MIS 1 (bottom) isotope period of the early Holocene. Boundary edges of the landmasses representing the mainland are the result of the spatial extent of the original bathymetric raster from which these polygons were derived through a raster to polygon conversion.

### Seascapes – Network Creation

Each MIS sea-level polygon dataset for the mainland and islands of the Greater and Lesser Antilles were exported to a new Feature Dataset. Following this, each of these feature classes were processed using the Optimal Region Connections tool.

The Optimal Region Connections tool in ArcGIS Pro creates an optimal network of paths between multiple input regions. The input regions data can be raster or feature datasets and the output derived is a topologically-corrected network of polylines and can therefore be used in further analysis, such as Network Analyst. In contrast to other tools such as Optimal Path as Line, Optimal Region Connections can be used if the user has several regions to connect and needs to create a network from the resulting polylines representing connections (Optimal Region Connections (Spatial Analyst), Esri).

These polyline connections needed to be clipped to the shoreline extents of the mainland and islands (for each seascape of the greater and Lesser Antilles, respectively). The feature lines generated from creating optimal connectivity paths between islands and the mainland for each region at each MIS were then edited through the Erase tool. Using the original input polygon feature classes, an Erase geoprocessing operation was run, to clip the polylines to only the boundaries of the islands and mainland.

Each seascape feature dataset was converted to polyline feature classes, so that only the outlines of the islands and mainland were retained. These polyline boundaries and the trimmed down connectivity lines were then joined using the Merge tool (found in Data Management Tools) to create complete, connected seascape networks. The boundaries of the individual islands were used as estimates for the birds traveling from island to island.

The vector datasets generated from connecting the seascapes together were converted into coverages using ArcMap 10.8.2. Coverages are an older Esri data model for storing geographic features. They typically represent a single layer and are stored as raw points, arcs,

and polygons (Wade & Sommer 2006). Each coverage's arc features (polylines) were converted back into features classes to be converted into network datasets.

Using my two distance thresholds of 1,500 and 500 km, I determined lengths only of those individual polylines in between different islands, to study how interisland distances changed with modifications to paleogeography with each MIS period seascape. All interisland polyline segments, representing interisland paths between islands were under my first threshold for maximum distance. However, seascapes showed greater variation in terms of the second query value, 500 km. A new feature dataset, when applicable for any polyline dataset with interisland polyline segments equal to or below 500 km was created. From here, both the original polyline dataset and ones queried for only values equal to or below 500 km were converted to network datasets. The general network datasets of each MIS seascape for the Greater and Lesser Antilles are given by Figures 16-18. Networks were tested using the standard Route function in network analyst to create optimal interisland pathways reflecting dispersal. The Figure 15 provides a graphic step-by-step process for my seascape-polyline and Network creation while final Network maps are provided in the Results section.

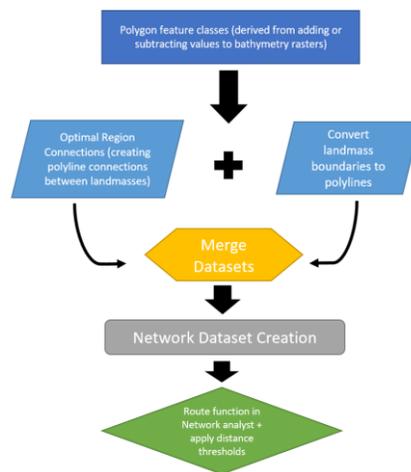


Figure 15. A flowchart documenting the creation of network datasets in this study.

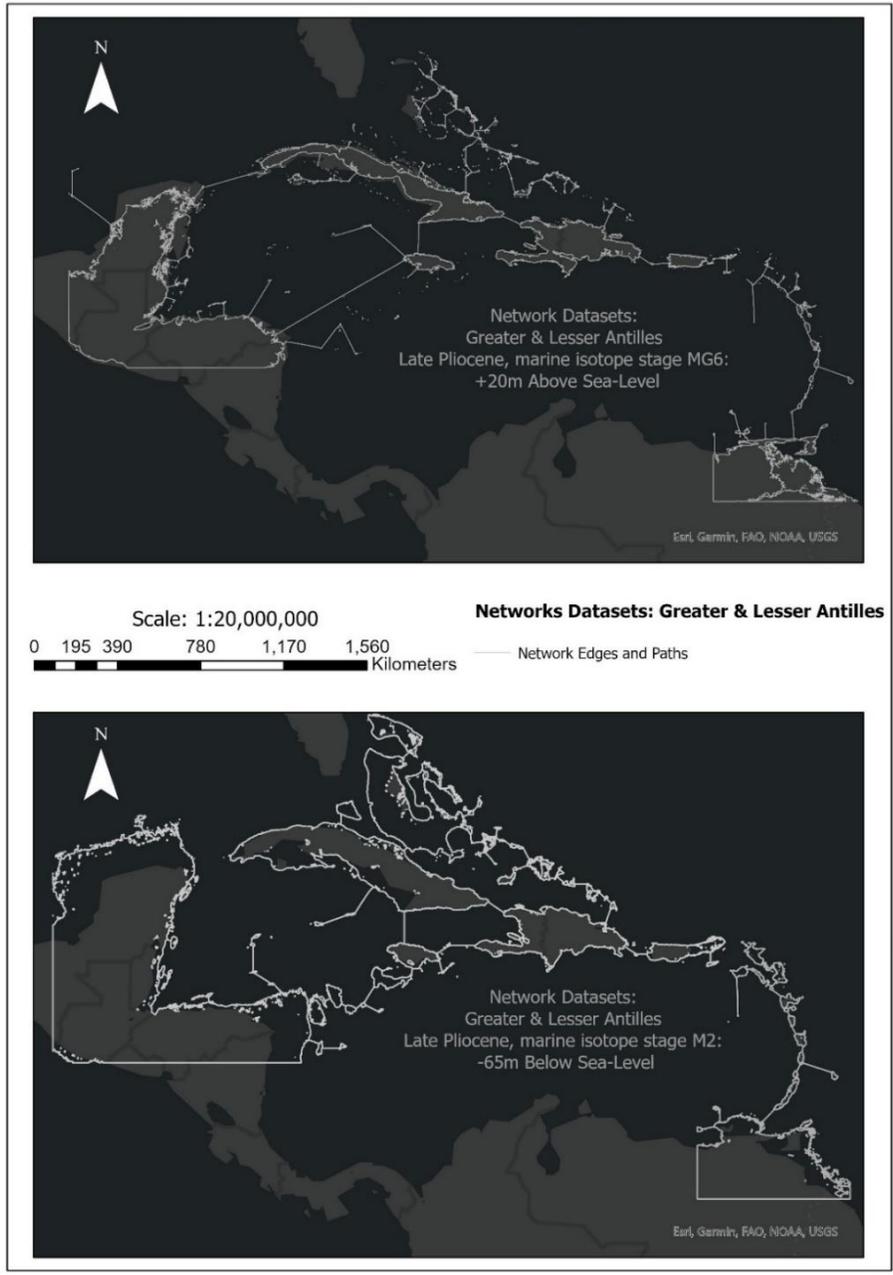


Figure 16. Network datasets for the Greater and Lesser Antilles, during the marine isotope periods: MG6 (top) and M2 (bottom).

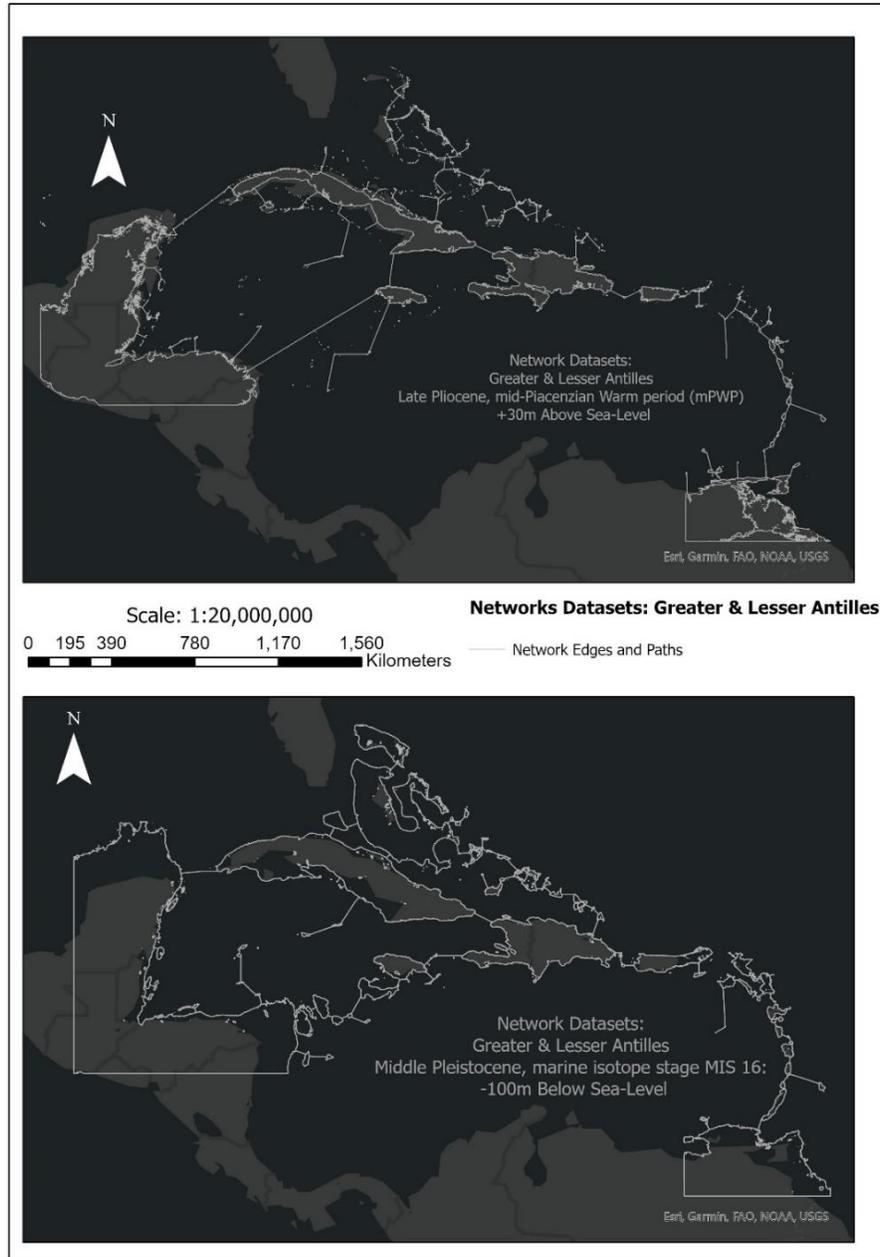


Figure 17. Network datasets for the Greater and Lesser Antilles, during the marine isotope periods: mPWP (top) and MIS 16 (bottom).

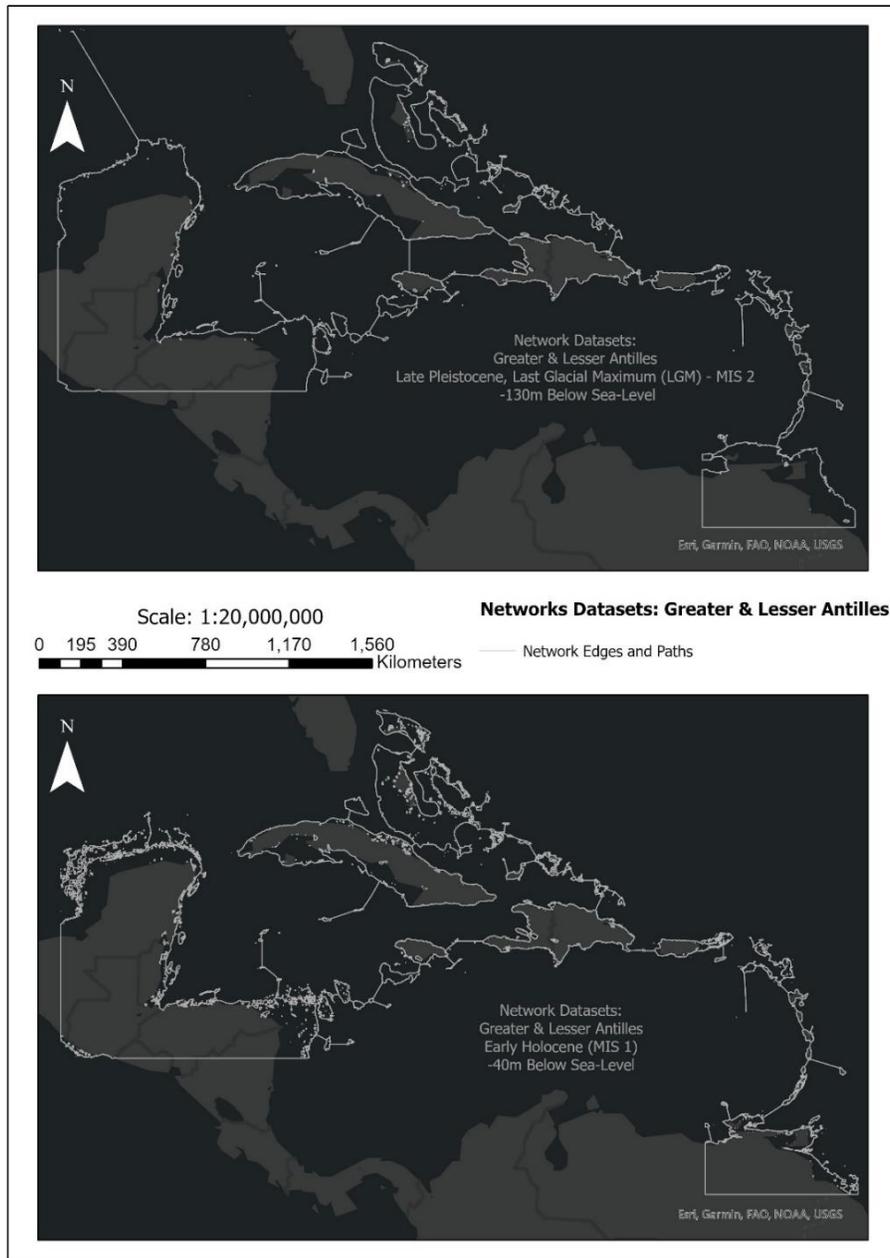


Figure 18. Network datasets for the Greater and Lesser Antilles, during the marine isotope periods: MIS 2 (top) and MIS 1 (bottom).

## Seascapes - Euclidean Distance

In conjunction with creating route maps for amazon parrot dispersal in the west Indies, Euclidean Distance raster functions were used for creating optimal “flight regions” or avenues of travel for each seascape as well.

Seascapes of each of this study’s desired MIS sea level reconstructions were exported as new features to a new file geodatabase and a feature dataset in the UTM Zone 20N for Puerto Rico. In addition, each individual polygon feature representing the mainland “source” for dispersion in the Greater and Lesser Antilles (Central America versus northern South America, respectively) in each MIS seascape were exported as new separate polygon feature classes. The purpose of this was to run a second Euclidean distance operation to map only flight regions with respect to the animals beginning from the mainland. For each raster produced, default cell size parameters were used, based on the input polygons and a planar distance method was used (for the input feature classes being in a projected coordinate system). The cell values generated for each seascape Euclidean Distance raster represented distances between the shoreline boundaries of individual islands, in meters while the Euclidean Distance raster datasets generated using only the mainland reflected distances from the mainland, in meters.

Using my two model distance thresholds, conditional statements using the Con tool in ArcGIS Pro (found in the Conditional toolbox, of Spatial Analyst) were applied to each Euclidean distance raster. With this, this operation selected all cells whose value was 1,500,000 m or less (using the conversion, 1,000 m = 1 km) and reclassified them as having a value of “1”. Cell values exceeding the 1,500,000 threshold were reclassified as “0” as false values. A second conditional statement was run, this time applying the 500 km (500,000 m). This was done for

comparison purposes and to model hypothesized flight regions for amazons and account for variables unable to be modeled in GIS such as climatic variables like wind.

Each resulting raster dataset from running the Con tool for each region’s MIS seascape were converted to feature classes using the Raster to Feature tool. For each mainland-Euclidean distance raster dataset, any island or group of islands falling outside of the 1,500 or 500 km threshold polygons in a given MIS seascape offered support that amazon parrots would be incapable of travel beyond the respective distances in this geospatial model, validating the concept of island-hopping dispersal patterns for amazons (Russello & Amato 2004). Visual steps for the Euclidean distance and Con operations are provided in Figure 19.

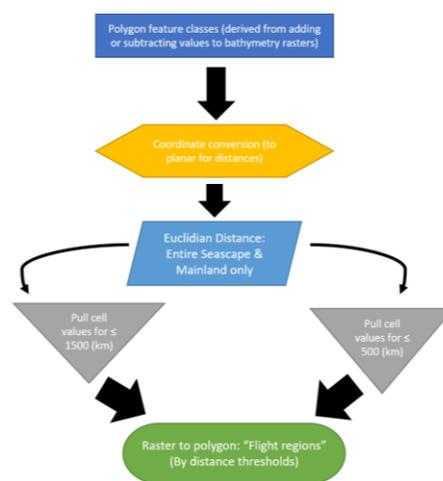


Figure 19. A flowchart depicting the creation of suitable flight regions, using Euclidean distance raster processing.

## Geographic Range Maps

As previously reviewed, point data can be used to visualize occurrences of plant or animal taxa for biogeographic studies and geographic ranges can be inferred (Martin et al. 2017). In this study, network analyst and Euclidean distance were used to model dispersion pathways with respect to sea-level fluctuation over time. However, occurrence information in the form of

point data from historic and prehistoric records were used to estimate the total geographic range for amazon parrots in the Greater and Lesser Antilles as well.

Synthesizing West Indian occurrences of different parrot genera, Williams & Steadman (2001) used records derived from paleontological, zooarchaeological, and post-Columbian historical records to detail the multiple sympatric species of *Amazona* once widespread in the Caribbean.

Taking a similar but geospatial approach, occurrence information from prehistoric and historic records from databases and literature were used to create polygon feature data denoting total geographic range extents for *Amazona* in the Greater Antilles and the Lesser Antilles (Figures 20 and 21).

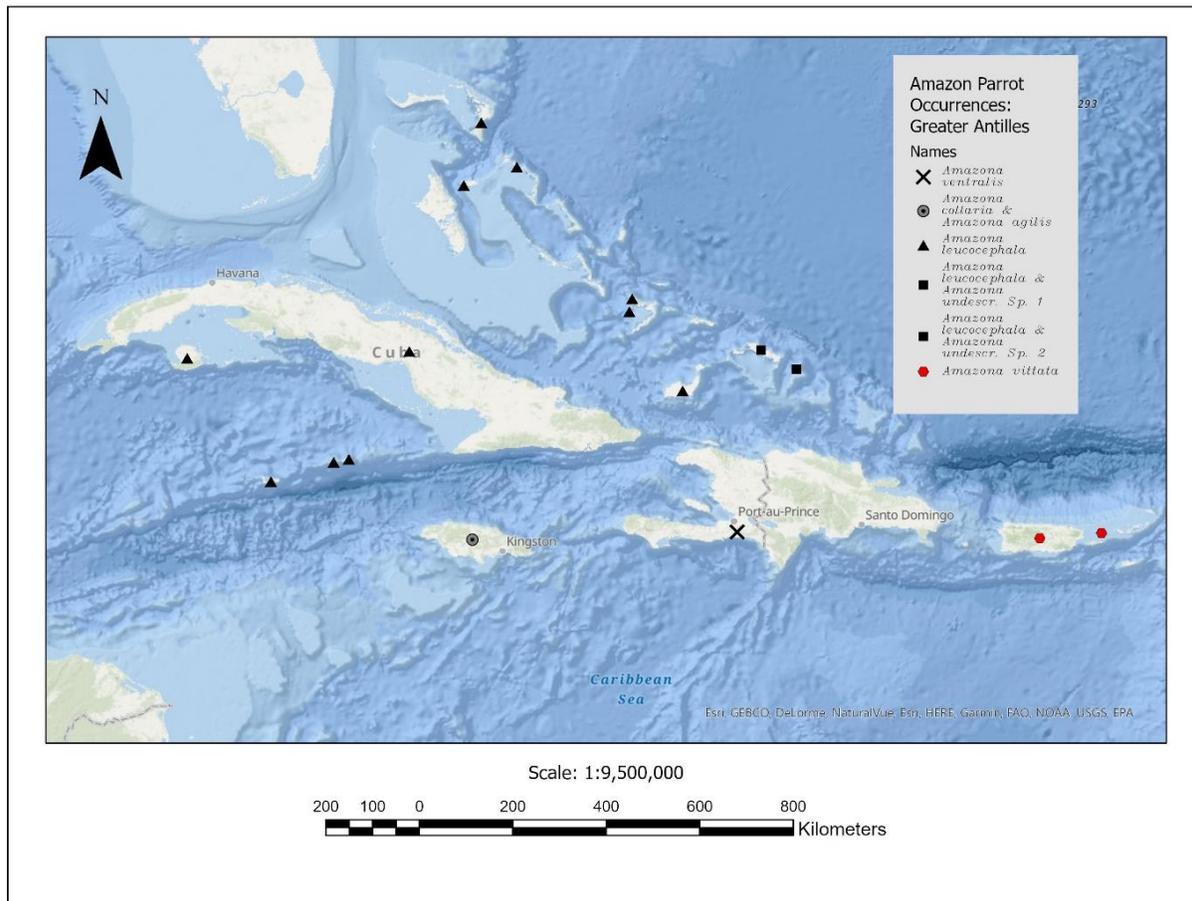


Figure 20. Greater Antillean amazon fossil record, to the species level. The fossil record suggests that amazons were more widespread prior to the arrival of humans to the West Indies.

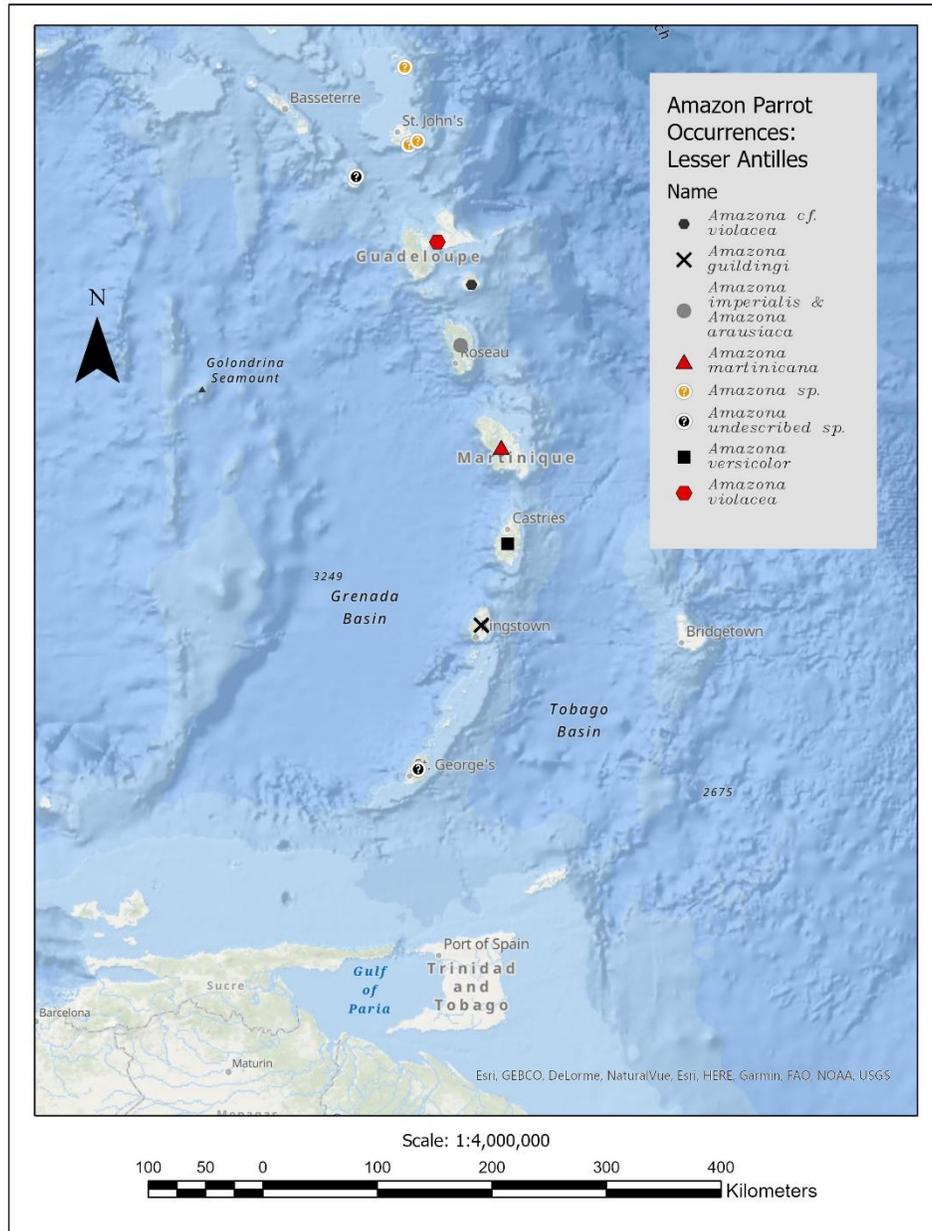


Figure 21. Lesser Antillean amazon fossil record, to the species level. The fossil record suggests that amazons were more widespread prior to the arrival of humans to the West Indies.

Fossil occurrence data for Caribbean amazons were derived from the Paleobiology Database (PBDB), iDigBio, and primary literature. Records downloaded from the two databases came in a comma-separated value (CSV) file format which was then converted to a 97-03 Excel

file format to be brought into ArcGIS Pro as point data. Points in ArcGIS Pro software have one x-value and one y-value to define their geographic locations (Wade & Sommer 2006). The latitude and longitude, in decimal degrees, was utilized for all occurrence data, including those pulled from literature. Literature-derived locations either had precise latitude and longitude provided in publications or if no location was available, an estimate was used, specifically by deriving a point in the middle of islands from Google Earth, in decimal degrees.

A finalized list-style 97-03 Excel file spreadsheet was prepared with all occurrence records pulled from the online databases and literature. A separate sheet was created for all occurrences within the Greater Antilles region and another separate sheet was made for all records relevant to the Lesser Antilles.

One sheet of occurrence data for the Greater Antilles and one for the Lesser Antilles were brought into ArcGIS Pro and point data were created from each table, using the “Display XY data” tool. Each set of occurrence records were exported to a new file geodatabase for all occurrence data processing and they were stored as point-based feature classes in a feature dataset, using a WGS 1984 geographic coordinate system.

With separate point data layers for Greater Antillean amazons and Lesser Antillean amazons, range polygons reflecting the spatial extent of each point layer were created. The Aggregate Points function, a Cartography tool takes an input of point data and will create a clustering polygon surrounding the input point layer with respect to an inputted aggregation distance. The resulting output will be a polygon feature class or shapefile (Aggregate Points (Cartography), Esri).

A separate polygon feature was created for the Greater and Lesser Antillean amazon point datasets, using the same 1500 km measurement derived from Klaassen (1996) as the aggregation distance. This was done to preserve continuity in the study. The resulting polygons simulate the hypothesized geographic range extents for amazon parrots in the Greater and Lesser Antilles, according to prehistoric and historic information, with respect to the previous forms of spatial analysis performed in this study.

Modern geographic range information for every bird species was obtained from BirdLife International's Birds of the World (2020) database. The dataset was a polygon feature class, in a file geodatabase and amazon species range records were queried based on genus and species and exported to a separate polygon feature class. The *Amazona* dataset was then separated by individual species, to create a separate range polygon for each Caribbean amazon species. While modern geographic range data for amazon parrots was included in this study from Birdlife International, modern geographic range data was used mainly as references and comparisons.

### **Geographic Parsimony**

Phylogenetic studies often turn to related plumage colors, in addition to geographic proximity, to reconstruct phylogenetic relationships among amazons (Kolchanova et al. 2021). The monophyletic status of Greater Antillean amazon parrots and records of molecular ages for divergence times (Kolchanova et al. 2021) permitted me to use eustatic sea level values derived from MIS periods of similar ages in order to provide geographic clarity to Greater Antillean amazon dispersal history and to offer a hypothesis for Lesser Antillean amazon history by using those same values as an estimation.

To assess previous molecular studies for Greater Antillean amazon parrots (Kolchanova et al. 2021) with the potential dispersion maps produced through Euclidean distance and

Network route mapping in this study, a maximum parsimony (MP) using geographically-binned characters was carried out in the Java-based program, Mesquite (version 3.51) for the Greater Antillean amazon group. After a simple tree cladogram was created for the Greater Antillean amazons, the parsimony analysis was created through character tracing, in order to coordinate the parsimony reconstruction of the ancestral states for these characters.

Each island-endemic species or subspecies was treated as its own distinct geographic population and a set of characters were determined to classify them by geography, in conjunction with the molecular phylogeny by Kolchanova et al. (2021) and the GIS results of this study. Characters included geographic location (each island was given a distinct character state, with the mainland species, *A. albifrons* serving as the outgroup with a character of “0” for the mainland), nearest island neighbor (closest island), and direction of dispersion: east versus west. The character of nearest neighbors was determined through geographic vicinity while the character of west-east dispersion was based on the direction of amazons dispersing eastward from Central America, with the character for east (“2”) being chosen for the two easternmost islands, Hispaniola and Puerto Rico. Table 4 lists all amazon species of the Greater Antilles and their associated geographic character values. Please see Figures 43-45 in the Results section for the character trees derived from Mesquite, for each individual character.

The paraphyly of Lesser Antillean amazons prevented this analysis in Mesquite from being run on the Lesser Antillean lineage. However, operations carried out using Network Analyst and raster Euclidean distance were used to produce to hypotheses of their dispersal history.

Table 4. Characters representing geographic attributes for each Greater Antillean amazon parrot. Only extant species/populations were used.

<b>Taxon/Character</b>	<b>Landmass: Island or Mainland</b>	<b>Nearest neighbor</b>	<b>Location/Direction of Dispersion: East or West</b>
<i>A. albifrons</i> (Central America) - A	0 (Mainland)	0 (Mainland)	0 (Mainland)
<i>A. agillis</i> (Jamaica) - B	1 (Jamaica)	1 (Jamaica-Caymans)	1 (West – Jamaica, Cuba, Cayman Islands, Bahamas)
<i>A. collaria</i> (Jamaica) - C	1 (Jamaica)	1 (Jamaica-Caymans)	1 (West – Jamaica, Cuba, Cayman Islands, Bahamas)
<i>A. l. leucocephala</i> (Cuba) - D	2 (Cuba)	2 (Cuba-Bahamas)	1 (West – Jamaica, Cuba, Cayman Islands, Bahamas)
<i>A. l. caymanensis</i> (Grand Cayman) - E	3 (Grand Cayman)	1 (Jamaica-Caymans)	1 (West – Jamaica, Cuba, Cayman Islands, Bahamas)
<i>A. l. hesterna</i> (Cayman Brac) - F	4 (Cayman Brac)	1 (Jamaica-Caymans)	1 (West – Jamaica, Cuba, Cayman Islands, Bahamas)
<i>A. l. bahamensis</i> (Bahamas) - G	5 (Bahamas)	2 (Cuba-Bahamas)	1 (West – Jamaica, Cuba, Cayman Islands, Bahamas)
<i>A. ventralis</i> (Hispaniola) - H	6 (Hispaniola)	3 (Hispaniola-Puerto Rico)	2 (East- Hispaniola and Puerto Rico)
<i>A. vittata</i> (Puerto Rico) - I	7 (Puerto Rico)	3 (Hispaniola-Puerto Rico)	2 (East- Hispaniola and Puerto Rico)

## RESULTS AND DISCUSSION

This study analyzed the biogeography of amazon parrots in the West Indies, utilizing the GIS functionality associated with network analysis, raster analysis, and feature class creation. In this study, the West Indies were split into two study areas: the Greater Antilles and the Lesser Antilles. This was to account for there being a distinct amazon parrot lineage in the Greater Antilles and one found in the Lesser Antilles (Russello & Amato 2004).

Operations in GIS resulted in network and feature datasets which modeled the timing of amazon parrot dispersal and evolution of single-island endemic species. Sea level fluctuations according to four MIS periods of the late Pliocene and Pleistocene were correlated to molecular-dated evolution times from Greater Antillean amazon evolution, and were used in this study to create inputs and outputs in the different analyses. Two other MIS periods representing the LGM and the early Holocene were used as well. Network datasets and Euclidean raster datasets were modified using two distance thresholds that served as models for the poor body of literature regarding the maximum potential flight distance for the *Amazona* genus. These GIS operations demonstrated how paleogeography of the Greater and Lesser Antilles had effects on amazon dispersal, specifically with respect to interisland distances.

Results for changes in the insular geography of the Greater and Lesser Antilles (total interisland distance total island area) and areas of total feasible flight regions according to processing the distance thresholds on the Euclidean distance rasters, are summarized in Table 5. Pure distance was the only variable to cost of travel measured in this study by creating routes using region connectivity and Network Analyst, and Euclidean distance raster creation, in Spatial Analyst.

Table 5. Results for total island area, interisland island network distance, interisland network distance according to the 500 km distance threshold, and the area of each flight region for the Greater and Lesser Antillean seascapes, by marine isotope stages (MIS) used in this study.

	Marine Isotope Stage (MIS)	Total Area (km <sup>2</sup> )	total network distance (km)	total network distance (500 query) (km)	Euclidean Distance (1500 km threshold) Region Area (km <sup>2</sup> )	Euclidean Distance (500 km threshold) Region Area (km <sup>2</sup> )	Mainland-Only Euclidean Distance (1500 km threshold) Region Area (km <sup>2</sup> )	Mainland-Only Euclidean Distance (500 km threshold) Region Area (km <sup>2</sup> )
Greater Antilles	MG6	174488.7	6850.5	6177.7	5643380	4894174	4087271	1694325
	M2	441855.7	3099.8	3099.8	5643380	5177943	4523169	2259082
	Mid-Piacenzian Warm period	173232.3	6684	6011.2	5643380	5007514	4087271	1694325
	MIS 16	444489.7	2712.8	2712.8	5643380	5103059	4606803	2351498
	MIS 2	449351.2	3142.4	2609.9	5643380	5251978	4613297	2373850
	MIS 1	435086.4	3422.2	3422.2	5643380	5078087	4484627	2135159
Lesser Antilles	MG6	13976.1	2483	2483	828200	828200	828200	521943
	M2	25905.5	1024.4	1024.4	828200	828200	828200	603994
	Mid-Piacenzian Warm period	10216.5	2038.8	2038.8	828200	828200	828200	500955
	MIS 16	25968.3	857.6	857.6	828200	828200	828200	592593
	MIS 2 (LGM)	25718	755.7	755.7	828200	828200	828200	618427
	MIS 1	19546.35	1231.4	1231.4	828200	828200	828200	547524

In the route maps produced using Network Analyst, specifically for the Greater Antilles, maps with specific routes (i.e., between Jamaica and Cuba) are zoomed in on to emphasize said route during a specific MIS period that is cross-referenced with molecular divergence times for specific Greater Antillean amazon species.

While the Caribbean region as a whole has a developing vertebrate fossil record specifically when it comes to birds, the only fossils identified as belonging to amazon parrots come from deposits that are Holocene or Pleistocene at the oldest (Olson 1982; Steadman et al. 2007; Steadman & Franklin 2015; Suárez 2021). Results of these network route and Euclidean distance maps support suitable routes of potential dispersal that would have had amazons settling on numerous islands, across the Greater and Lesser Antilles, by the time they appear in the vertebrate fossil record for the Caribbean.

### **Network Routes and Euclidean Distance, by Marine Isotope Stage (MIS): Greater Antilles**

In the Greater Antilles, Russello & Amato (2004) and later, Kolchanova et al. (2021) argued that Greater Antillean amazon parrots represent a stepping-stone dispersal pattern from Central America. Network routes produced in Network Analyst using connections between landmasses, based on most optimal distances were used to map out this pattern, in conjunction with Euclidean distance raster analysis.

#### MG6; Greater Antilles

For the first MIS period considered, MG6 (~3.6 – ~3.3 Ma), (De Schepper et al. 2013; Dumitru et al. 2021), global sea levels were estimated to be around 20 m higher than present. In the Greater Antilles, a total area of 174,488.70 km<sup>2</sup> was calculated for only landmasses representing islands during this time (Table 4). Kolchanova et al. (2021) had the clade

representing the five extant Greater Antillean amazons as splitting from a common ancestral taxon from Central America, *A. albifrons*, around 3.43 Ma. This would have been occurring during the MG6 period of the Late Pliocene.

Between Central America and Jamaica, running Optimal Region Connections produced an optimal distance pathway between the mainland and Jamaica of about 672.8 km. With respect to the two distance thresholds for amazon travel, this value meets the conditions for being under 1,500 km, using the body mass-flight potential graph of Pennycuick (1989) and later, Klaassen (1996). However, this route would be flagged as not an optimal route for the second distance threshold of 500 km, being almost 175 km greater (Figure 22).

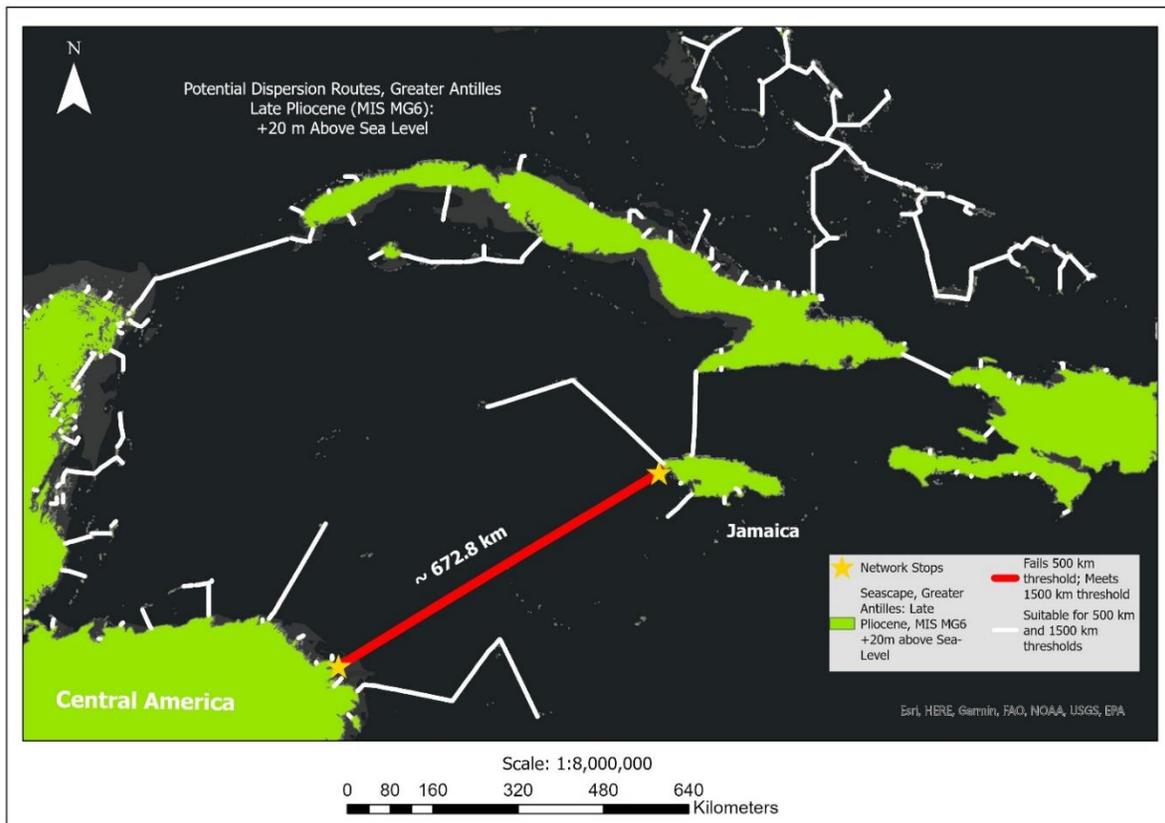


Figure 22. Network mapping results for the Greater Antilles, during marine isotope stage, MG6, during the late Pliocene. The route made between Central America and Jamaica for the Jamaican amazons meets the first distance threshold of 1500 km but not the second one of 500 km.

*A. agilis*, the Black-Billed Parrot, one of the two endemic species to Jamaica is the most phylogenetically distinct amazon from the other four Greater Antillean taxa, but it is still sister to *A. collaria*, the Yellow-Billed Parrot, the other parrot endemic to Jamaica (Kolchanova et al. 2021). Despite the network route map failing to meet the second distance threshold applied in this study, a distance of 672.8 km between Central America and Jamaica meets the main distance threshold utilized, offering a potential explanation for the origins of *A. agilis*. In comparison, this distance falls within the flight suitability region made from running Euclidean distance only from the mainland and applying the 1500 km threshold while it fell outside the second region produced from applying the 500 km threshold applied as well (Figure 23).

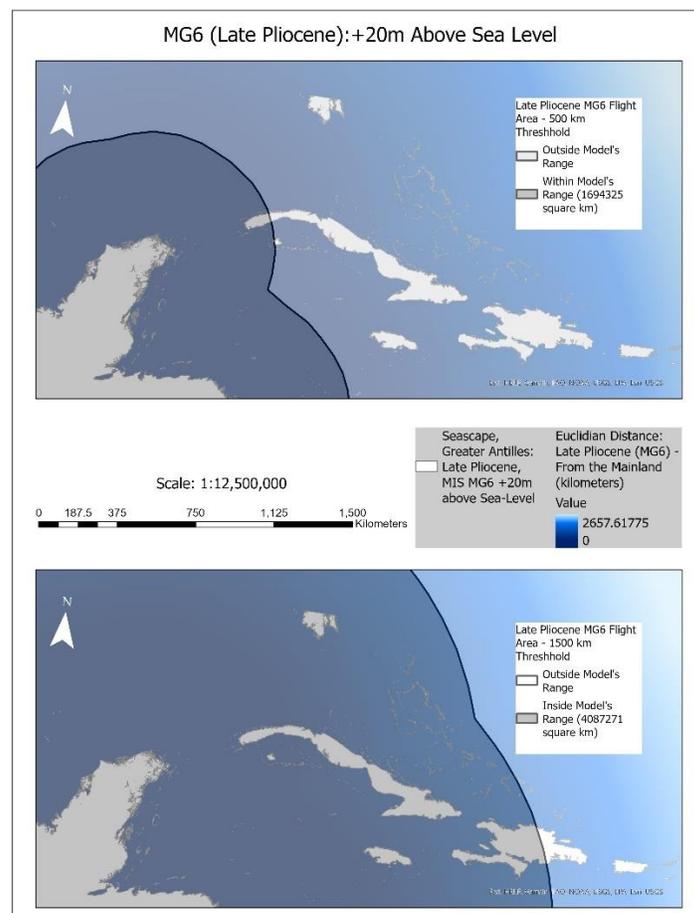


Figure 23. Euclidean distance mapping results of the MG6 marine isotope stage in the Greater Antilles, for the distance thresholds of 1500 km and 500 km, respectively. Under the first threshold, a larger potential flight region for amazons dispersing from the mainland was determined.

M2, Greater Antilles:

During the Late Pliocene, specifically the M2 MIS which was a short, intense episode of a glaciation with estimated sea level drops up to 65 m (De Schepper et al. 2013). Here, a route produced from the network dataset representing optimal travel potential between Central America and islands of the Greater Antilles (Figure 24).

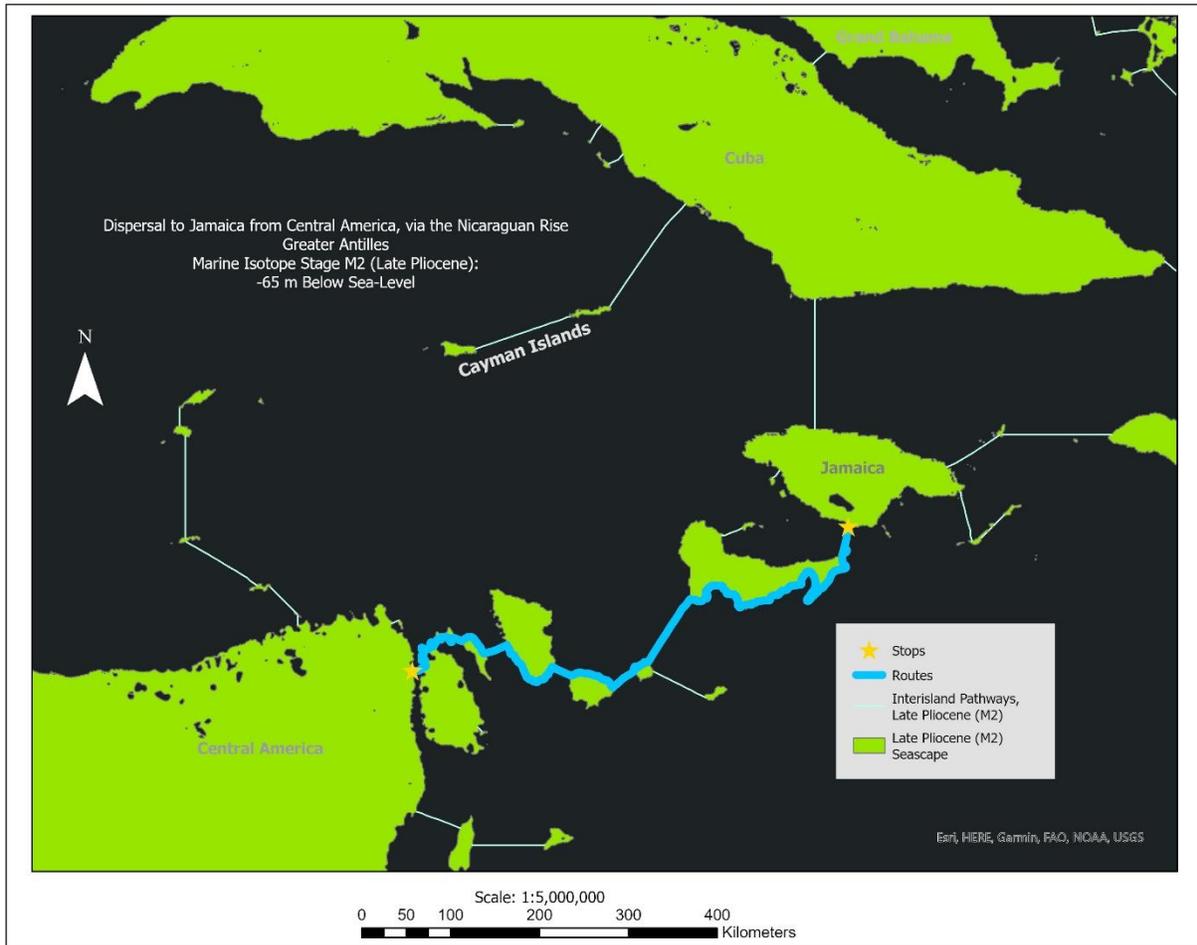


Figure 24. Network mapping results for the Greater Antilles, focused in on Jamaica. During marine isotope stage, M2, of the late Pliocene, a brief glaciation event with global sea levels estimated as low as -65 m, occurred. The route made between Central America and Jamaica for the Jamaican amazons here is facilitated by the exposure of the Nicaraguan Rise, from Central America. Several small islands exposed at lower sea levels likely helped facilitate for amazon parrots and perhaps other birds, to Jamaica.

The Nicaraguan Rise, a submerged suboceanic ridge extending from Central America (specifically Honduras and Nicaragua) has been exposed and inundated during different

fluctuations in global eustatic sea level (Sanchez et al. 2015). Kolchanova et al. (2021) postulated that the exposure of the Nicaraguan Rise facilitated dispersal of Central American amazon species, such as *A. albifrons*, which, phylogenetically is placed as the ancestral taxon to all Greater Antillean amazons. In their phylogenetic studies of Greater Antillean amazons, the emergent Nicaraguan Rise was pivotal in amazon dispersal to Jamaica. Additionally, prior to the ridge becoming submerged again, the time during the Late Pliocene represented by the M2 glaciation likely facilitated back and forth dispersal and exchange of genetic material between populations of amazons on the mainland and those on the island of Jamaica. The inundation after M2 period would lead to a breakage in the genetic link between *A. agilis* and *A. albifrons*.

Under the pretext that the Nicaraguan Rise not being inundated during the M2 period of the late Pliocene allowed for a shared gene pool between Central American and Jamaican amazons. This can be seen with Jamaica falling within the area for both maximum distance threshold flight regions, beginning from the mainland (Figure 25). Network routes along the Nicaraguan Rise indicate relatively to moderately easy dispersal between Central America and Jamaica.

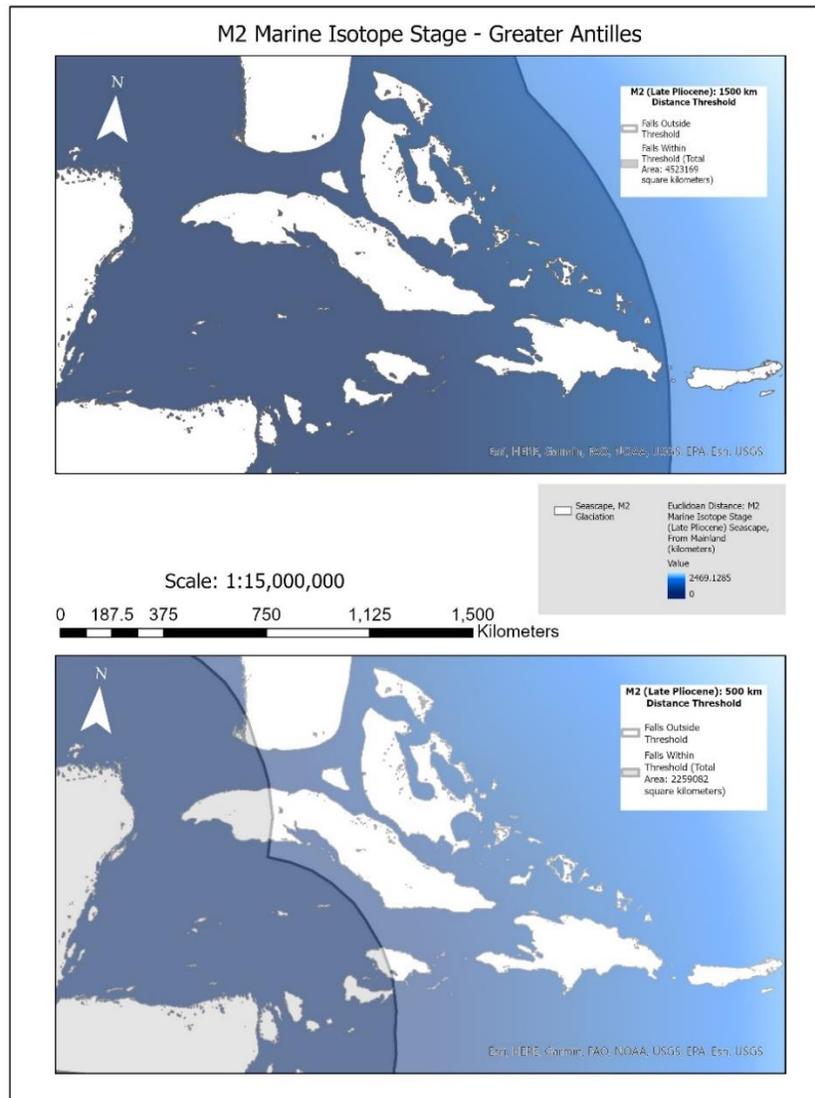


Figure 25. Euclidean distance mapping results for the Greater Antilles, during the M2 glaciation event of the late Pliocene. Results for each distance threshold agree with the network route produced which, emphasized the exposure of the Nicaraguan Rise from Central America creating greater mainland area, closer proximity to Jamaica, and intermittent islands exposed at lower sea levels to facilitate dispersion for amazon parrots.

### Greater Antilles mPWP:

The mid-Piacenzian Warm Period occurred immediately after the M2 glaciation event (3.25 – 2.9 Ma). With similar results to the MG6 network in terms of island distance and potential for interisland connectivity, the mPWP network dataset and routes made represented the late Pliocene when the Earth warmed after the brief M2 glaciation, warming in a rate most

similar to that observed today (De Schepper et al. 2013). Despite the network routes in this study for the mPWP in the Greater Antilles meeting the first distance threshold and not the second threshold, similar to the MG6 dataset, the difficulty in travel between Central America and Jamaica should still be noted (Figure 26).

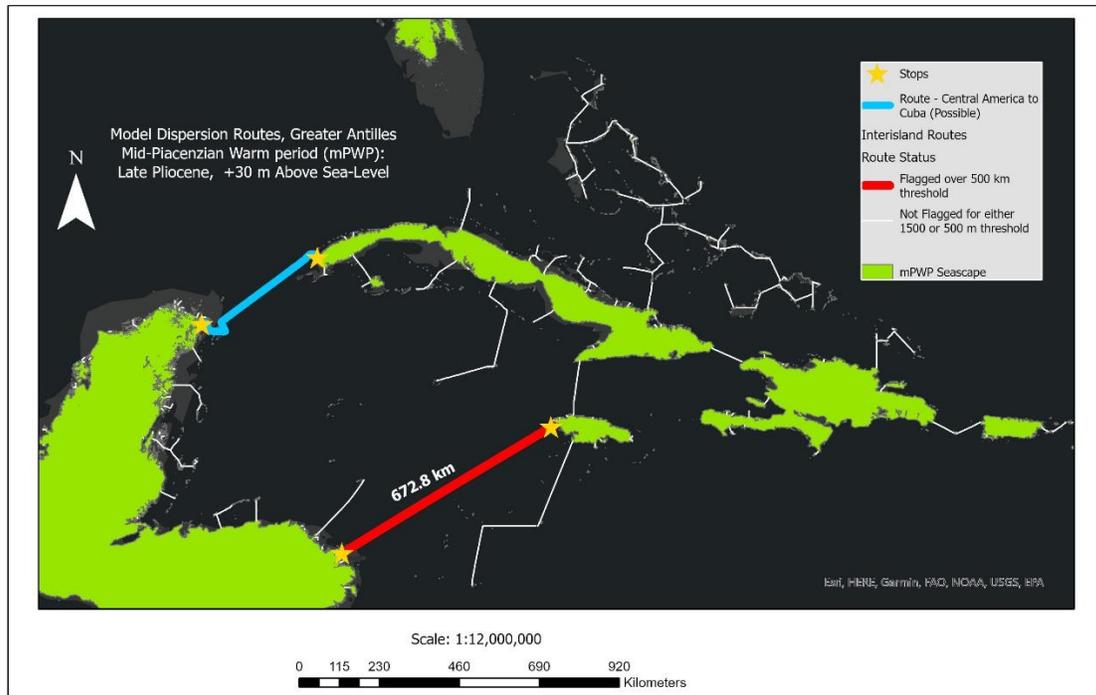


Figure 26. Network mapping results for the Greater Antilles, during the mid-Piacenzian Warm Period of the late Pliocene. The route made between Central America and Jamaica for the Jamaican amazons meets the first distance threshold of 1500 km but not the second one of 500 km as global sea levels were as high +30m higher than present.

Kolchanova et al. (2021) determined that the divergence between the two endemic amazon species of Jamaica potentially occurred during the mPWP. *A. collaria*, the Yellow-Billed Parrot, the second parrot endemic to Jamaica is phylogenetically closer to the other three Greater Antillean amazons, which lead to Kolchanova et al. (2021) to argue that *A. agilis* and *A. collaria* are derived from two separate colonization events to Jamaica at different times or they originated as two subpopulations of a same ancestral species on Jamaica that became two separate species.

Both endangered today, *A. agilis* and *A. collaria* both occur in mid-elevation limestone forests of Jamaica (Koenig 2001). *A. collaria* can also be found in more montane evergreen forests and *A. agilis* can be found there but in tropical lowland forests sometimes as well (Flieg & Sander 2016).

Kolchanova et al. (2021) really emphasized the presence or absence of the Nicaraguan Rise when discussing dispersion of Central American amazons to Jamaica. Similar to this study, theirs made use of minimal literature on the long-distance flight capabilities of amazon parrots as a whole. I am led to argue and concur with Kolchanova et al. (2021) that inundation of the Nicaraguan Rise due to rising sea levels of 20-30 m during the mPWP had an impact on gene flow between populations on Jamaica and Central America. Kolchanova et al. (2021) emphasized how there likely was genetic exchange between mainland *A. albifrons* and insular *A. agilis* up until the absence of optimal routes to Jamaica after the Nicaraguan Rise became inundated. Network routes produced for the M2 glaciation event depicted such optimal routes with several intermediate islands exposed along the Nicaraguan Rise and the resulting connections produced an optimal network route seen when running routes with the M2 network dataset.

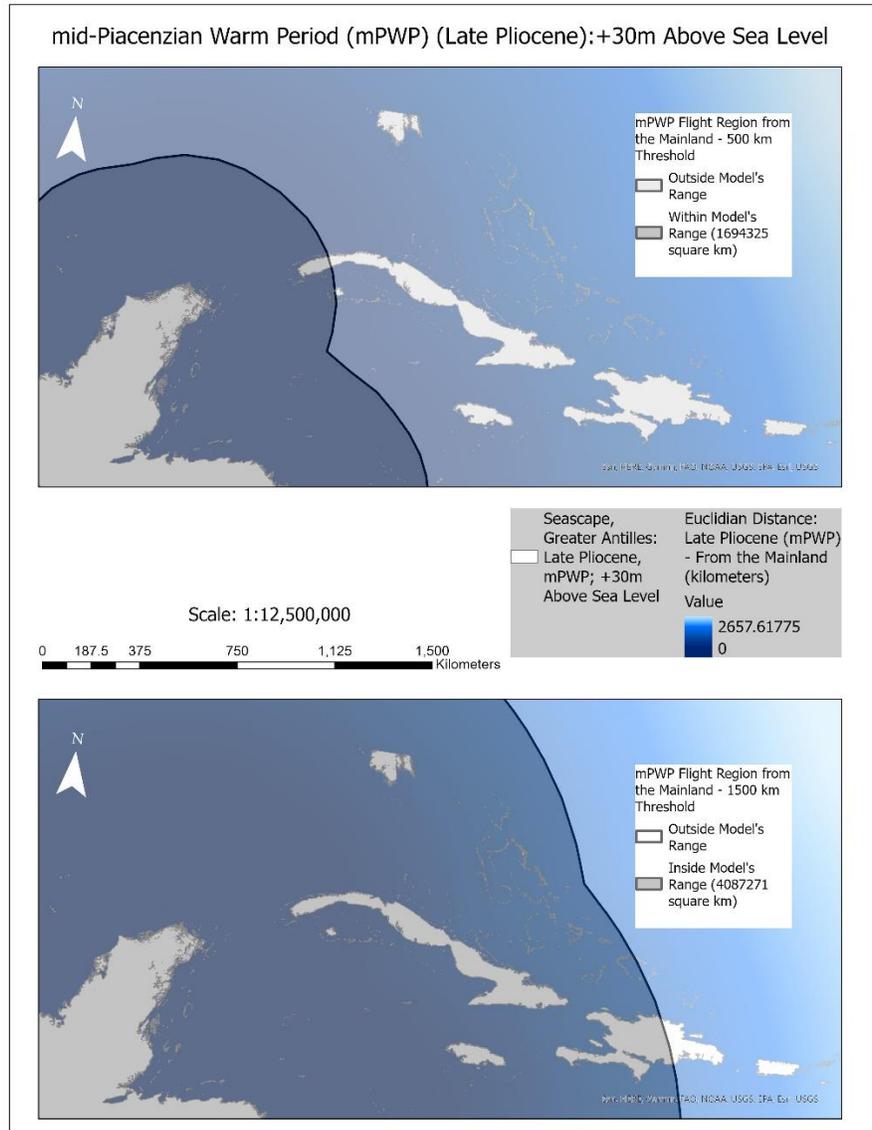


Figure 27. Euclidean distance mapping results for the Greater Antilles, during the mid-Piacenzian Warm Period of the late Pliocene. The islands of Jamaica, Cuba, and Hispaniola fall within the first distance threshold of 1500 km but not the second one of 500 km as global sea levels were as high +30m higher than present, indicating that dispersion was likely difficult and the divergence between mainland and Jamaican amazons described by Kolchanova et al. (2021) may have occurred during this time.

I argue that established, now isolated populations of that *A. albifrons*-*A. agilis* relationship described by Kolchanova et al. (2021) led to the origin of the second Jamaican amazon, *A. collaria*, likely around the mPWP which likely then began colonizing other islands in the Greater Antilles, starting with Cuba.

### MIS 16, Greater Antilles:

The Hispaniolan Parrot, *A. ventralis*, and the Puerto Rican Parrot, *A. vittata*, have been resolved as being sister to the Cuban Parrot, otherwise known as the Rose-Throated Amazon (*A. leucocephala*) (Russello & Amato 2004; Kolchanova et al. 2021). Studying Greater Antillean amazons, Kolchanova et al. (2021) determined that amazons reached Puerto Rico by 0.67 Ma, during the late Pliocene (Ionian). Lack (1976) had *A. ventralis* and *A. vittata* sharing a common ancestor with *A. leucocephala* as well.

MIS 16 is a major glacial stage, also grouped with the Donian Glaciation, occurred during the Middle Pleistocene, 0.5 – 0.8 Ma (Hughes & Gibbard 2018). This marine isotope stage, representing one of the last ten 100 ka glacial cycles in which eustatic sea levels fluctuated by 100 m, was used for mapping routes in the Greater Antilles for amazon species found on Cuba, Hispaniola, and Jamaica by applying a value of 100 for -100 m below sea level, to model bathymetry.

Routes going from Cuba to Hispaniola and Jamaica and creating Euclidean distance rasters for this seascape helped illustrate feasibility for amazon parrot travel throughout this part of the Greater Antilles (Figures 28 and 29). Traveling to Hispaniola from Cuba or island-hopping from Cuba to Hispaniola and then to Puerto Rico, would not have been an issue under either of the two distance thresholds. The 1500 km threshold yielded a region with an area of 5,643,380 km<sup>2</sup>, the same as the area of the region for all previous seascapes while a suitability area of 5,103,059 km<sup>2</sup> (Table). When taking the mainland into consideration, an amazon parrot taking off from Central America would have been capable of traveling a region with an area of 4,606,803 km<sup>2</sup>, under the 1500 km distance threshold, and for the 500 km distance threshold, this would have been an area of 2,351,498 km<sup>2</sup> (Table 4).

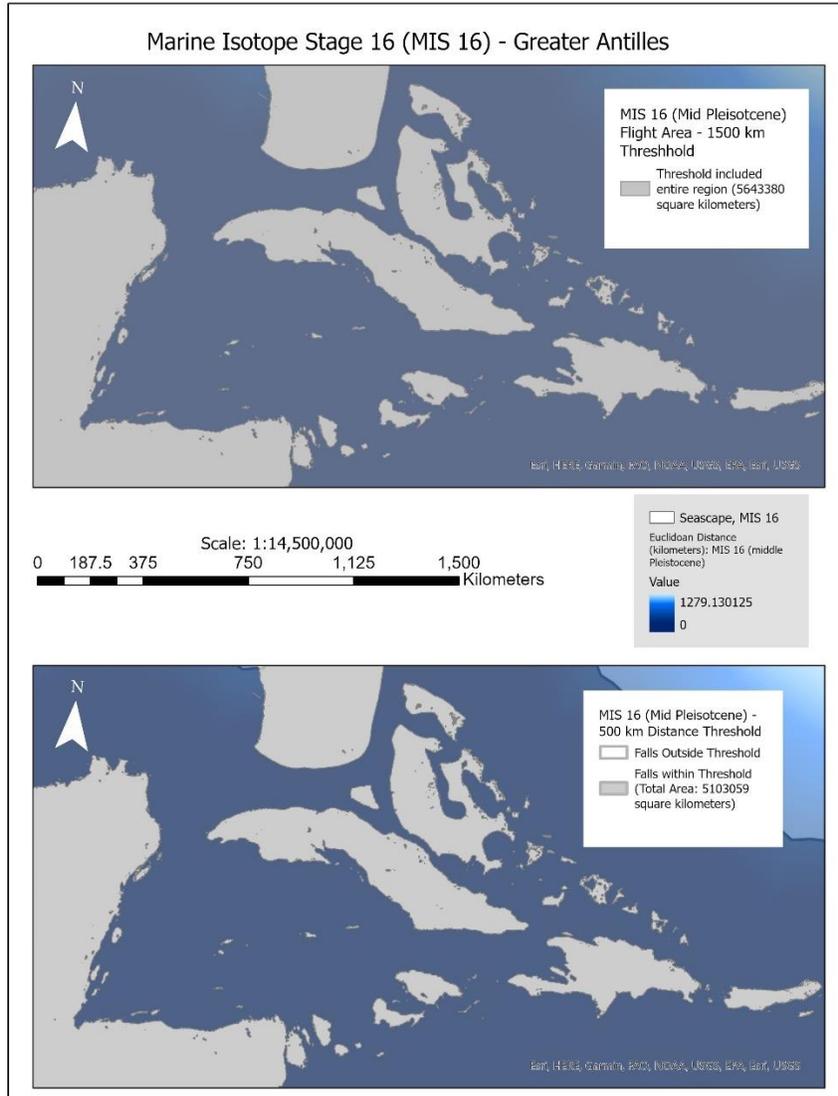


Figure 28. Euclidean distance mapping results for the Greater Antilles, during MIS 16 (middle Pleistocene). Island-hopping from Jamaica and Cuba, to Hispaniola and Puerto Rico occurred during this period for amazons, according to Kolchanova et al. (2021). Across the entire Greater Antilles during this time, sea levels were 100 m below present, likely facilitating easier dispersion between different islands.



Figure 29. Network route mapping results for the Greater Antilles, during MIS 16 (middle Pleistocene). The first route represents dispersion from Jamaica to Cuba and second reflects a dispersal event from Cuba to Hispaniola and Jamaica. During this part of the middle Pleistocene, sea levels were 100 m below present, likely facilitating easier dispersion between different islands.

The Hispaniolan parrot, *A. ventralis* has been found in extensive vertebrate fossil assemblages both prehistoric and historic from Hispaniola, associated with other fossil and subfossil landbirds, some extant and some extinct, with *A. ventralis* still being found on Hispaniola today. Similar habitats to the Pleistocene Bahamas, when the Caribbean was cooler and drier (Steadman & Franklin 2015) were seen on Hispaniola. For instance, fossils of *A. ventralis* have been associated with humid broadleaf forests and pine forests (Steadman & Takano 2013).

The Puerto Rican Parrot, *A. vittata*, is native to Puerto Rico but was also once found on Culebra (Snyder et al. 1987; Williams & Steadman 2001), and Late Quaternary remains reported from Antigua and Barbuda were identified as *A. vittata* by Pregill et al. (1994) but this diagnosis is debated.

The close distance between Puerto Rico and Culebra during periods of lower sea level (such as MIS 16), similar to the close distance between Cuba and the Bahamas, potentially offers a reason for why there is a subspecies found on an island very close to the larger island (Puerto Rico). Rising sea levels after the LGM, most likely would have separated populations of *A. vittata*. With this in consideration, a large island subject to significant eustatic sea level rise could become split into multiple islands, with endemic taxa either diverging into new species or subspecies. In the case of the complex phytogeography of the Galápagos Islands, lava lizards (*Microlophus spp.*) arrived in the Galápagos archipelago via passive dispersal, similar to tortoises, but eustatic sea level changes caused localized vicariant events, isolating populations of *Microlophus spp.*, leading to divergences in new subspecies or new species (Geist et al. 2014).

#### LGM: Greater Antilles

While *A. ventralis* and *A. vittata* have been distinctly grouped as being sister *A. leucocephala* (Kolchanova et al. 2021), *A. leucocephala* has been found to have five distinct subspecies (Forshaw 2006). *A. leucocephala* is the only amazon in the Caribbean found on multiple islands, being found in Cuba, the Cayman Islands, and parts of the Bahamas, with it being once more widespread across the Bahaman Archipelago, reaching the Turks and Caicos Islands (Williams & Steadman 2001).

For GIS network and Euclidean distance operations, a value of -130 for -130m below sea-level (Spratt & Lisiecki 2016) was used in modifying bathymetric raster data to model the LGM. The Great Bahama Bank, Cal Say Bank, and Little Bahama Bank were exposed above sea level with Great Bahama being as close as 19 km from Cuba (Figures 30 and 31), making dispersal from Cuba to the Bahamas for amazon parrots likely very feasible. Throughout the

Cenozoic, Cuba's close distance to the Bahamas and the Caymans likely promoted dispersal and genetic exchange between separate populations of amazons.

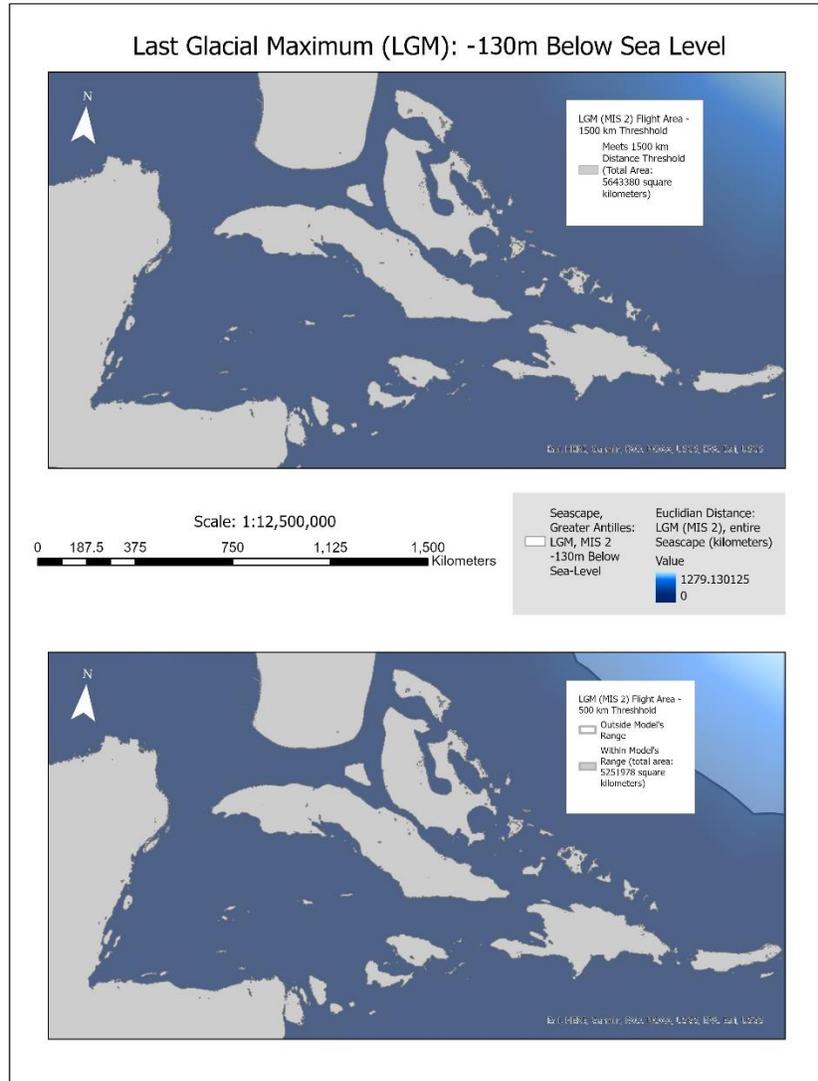


Figure 30. Euclidean distance mapping results for the Greater Antilles, during MIS 2, the Last Glacial Maximum. Global sea levels were as low as -130m during the LGM. Molecularly speaking, each island endemic amazon in the Greater Antilles diverged prior to the LGM (Kolchanova et al. (2021).

For the LGM, a route map was made for potential amazon parrot routes between Cuba, the Bahaman Archipelago (the Bahamas and the Turks and Caicos Islands), and the Cayman Islands (Figure ). Routes beginning in Cuba and traveling to the Cayman Islands and the entirety of the Bahamas, including the Turks and Caicos likely explain the fossil distributions of

*Amazona* across these islands, specifically throughout the Bahamas, as these have been identified at the species-level, as *A. leucocephala* (Steadman et al. 1984; Williams & Steadman 2001).

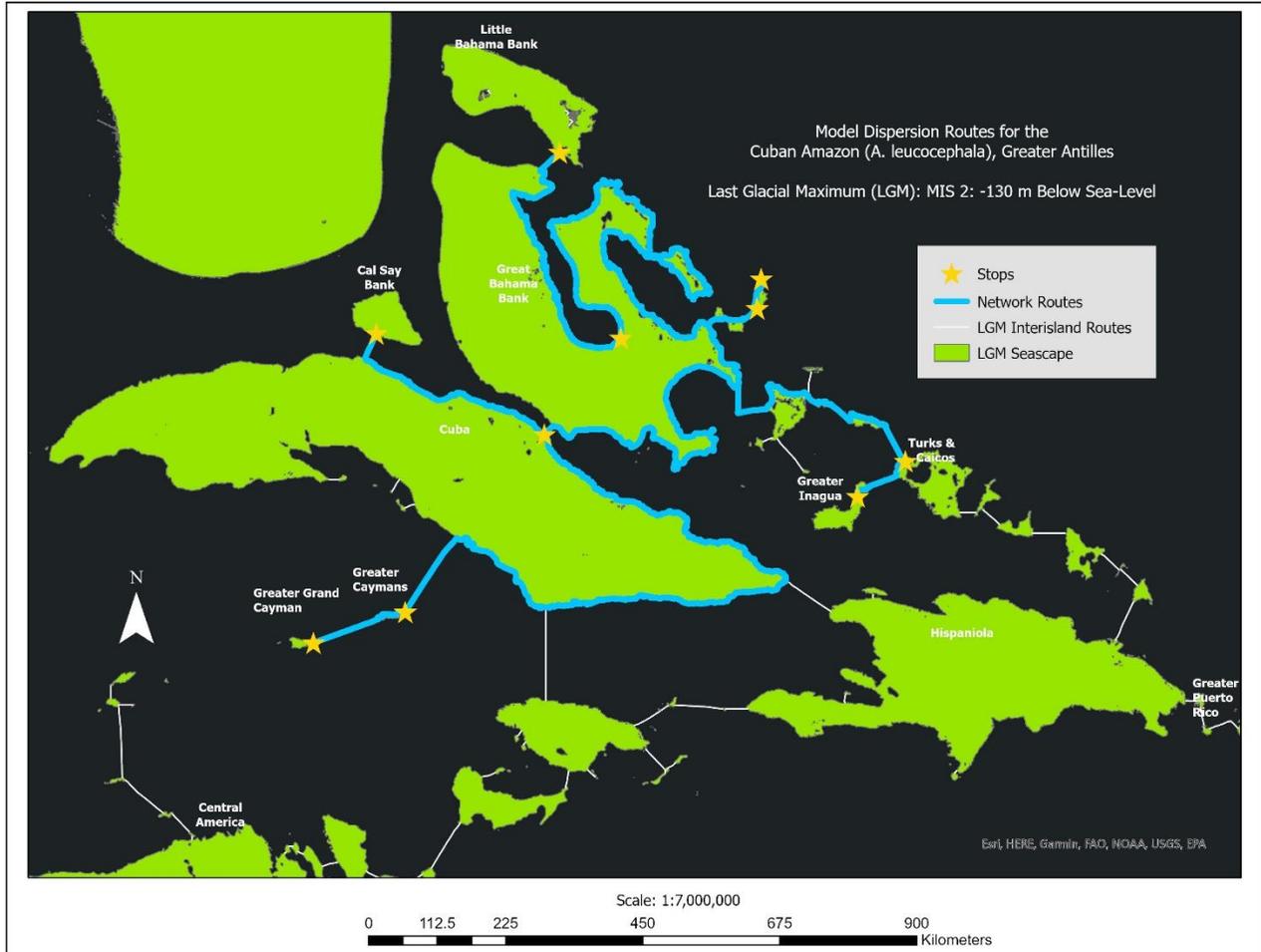


Figure 31. Routes of dispersion from Cuba to the Cayman Islands, Bahamas, and the Turks and Caicos Islands during the LGM. The Cuban amazon (*A. leucocephala*) is the only amazon found on multiple islands today. During the LGM, this species likely traveled between Cuba, the Cayman Islands, the Bahamas, and the Turks and Caicos Islands, establishing distinct subspecies. Islands with low elevations including the Bahamas, likely offered optimal habitat for amazons during the LGM as their fossils have been reported numerous Bahaman islands and the Turks and Caicos Islands, where they are extirpated today (Williams & Steadman 2001).

Using a value of -130 for modifying bathymetry, the LGM had the greatest total island area for all size MIS periods used for the Greater Antilles, at 444,489.70 km<sup>2</sup> (Table 4). Despite endemic amazon parrots of the Caribbean likely reaching their respective islands prior to the LGM, according to molecular dating (Kolchanova et al. 2021), the significant area exposed

during record low sea level during the last ice age, likely facilitated significant migration of vertebrates throughout the Greater Antilles, including mammals and birds. This can be seen in modeling island biogeography in GIS to assess connectivity, such is the case with a study by Robles (2013) for the Philippines, built on the concept of islands joined together during sea level lows of the Pleistocene, coined “Pleistocene aggregate island complexes, or PAICs by Heaney (1986).

#### MIS 1 (early Holocene), Greater Antilles

40m above sea-level network and Euclidean distance datasets, for MIS 1, the early Holocene was the MIS period used in this study. The Caribbean experienced significant sea level rise following the end of the LGM. During the early Holocene, sea levels had risen considerably but they were still around 40 m above present (Steadman & Franklin 2015). Despite closer distances between islands than today that likely promoted dispersion among terrestrial vertebrate taxa, the Caribbean only had a total island area of 435086.4 km<sup>2</sup> during the Holocene (Table 4), significantly lower than periods of even lower sea level like LGM or MIS 16. Regardless, Euclidean distance maps produced for the early Holocene MIS Greater Antillean seascape showed that for each distance query, dispersion throughout the Greater Antilles was highly feasible (Figure 32).

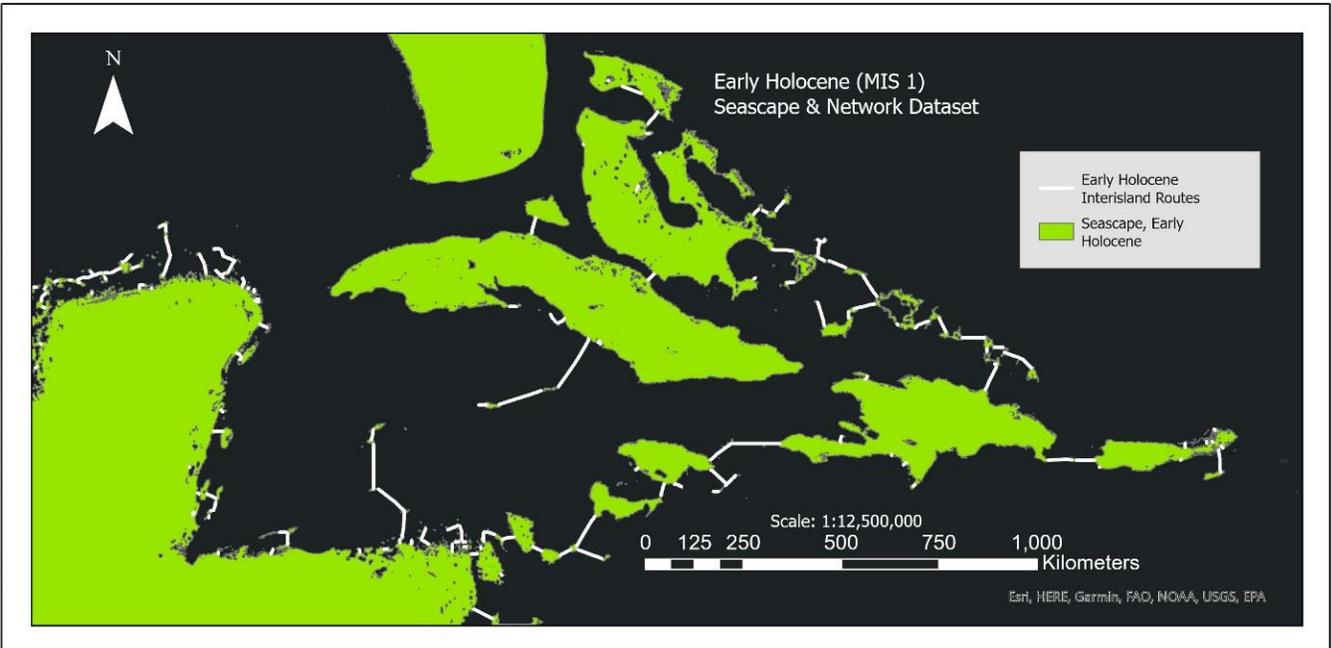


Figure 32. Network dataset for the Greater Antilles, during the early Holocene. Sea levels were still as low as -40m, reflecting higher and more optimal dispersion between islands for amazon parrots, specifically *A. leucocephala*, between Cuba, the Bahamas, the Turks and Caicos Islands, and the Cayman Islands.

During the early Holocene and prior to the arrival of humans to numerous islands in the Greater Antilles like the Bahamas, Steadman & Franklin (2015) determined that certain landbirds were likely wiped out by climate change and not the arrival of people. Sea level rise for low-lying islands such as the Bahamas may have contributed to the range contraction for the Rose-Throated Amazon (Cuban Amazon) subspecies, *Amazona l. bahamensis*, found in the Bahamas today only on Abaco and Inagua. In a similar study for sea-level rise and landbirds in the Bahamas, Steadman & Franklin (2017) determined that sea level rise after the LGM, including highs of +5 to +20 m during MIS 11 likely contributed to the extirpation of eastern bluebirds (*Sialia sialis*) and Hispaniolan crossbills (*Loxia megalaga*) from the island of Abaco, in the Bahamas.

## **Network Routes and Euclidean Distance, by Marine Isotope Stage (MIS): Lesser Antilles**

The phylogenetic and evolutionary history of Lesser Antillean amazons is not as well-known and established as the Greater Antillean amazon group. Amazon parrots in the Lesser Antilles are a paraphyletic group and likely the result of more than one colonization event, from northern South America (Russello & Amato 2004). Due to the uncertainty with the evolution of insular amazons in the Lesser Antilles, results reported here for the Euclidean distance and network maps for the Lesser Antilles are based on estimations with optimal routes in terms of minimal distance to travel and estimated island areas are reported. The fossil distribution map for Lesser Antillean amazons, like its Greater Antillean counterpart, helps shed light on the prehistoric and historic distribution of amazons in this region of the West Indies.

### MG6, Lesser Antilles:

At 20 m higher than present during MG6 (~3.6 – ~3.3 Ma), (De Schepper et al. 2013; Dumitru et al. 2021), modification to bathymetry of the Lesser Antilles produced a total island area of 13,976.1 km<sup>2</sup> and with that, a total interisland network route distance of 2,483 km from the mainland across all islands in the chain (Table 4), while individual interisland route distances met each of the two distance thresholds (Figure 33).

In the Euclidean distance operations, the entire Lesser Antillean seascape for the Lesser Antilles during the MG6 stage produced a suitable flight region area of 828200 km<sup>2</sup>, for the 1500 and 500 km thresholds. Meanwhile, for the distance thresholds for beginning only from the mainland, the entire seascape met criteria for the 1,500 km while the flight region produced for the 500 km threshold on the mainland Euclidean distance raster produced an area of only 521943 km<sup>2</sup>, with this optimal region terminating close to the island of Dominica (Figure 34). There are

two endemic species of amazon from Dominica (Flieg & Sander 2016). Results for the Euclidean distance analysis for starting from the mainland demonstrated that beginning from the mainland and flying non-stop, amazons perhaps would have been only capable of making it to Dominica. However, a bird flying from the mainland would have likely had to stop at some point as long-distance migration can be energy costly (Concepcion et al. 2020).

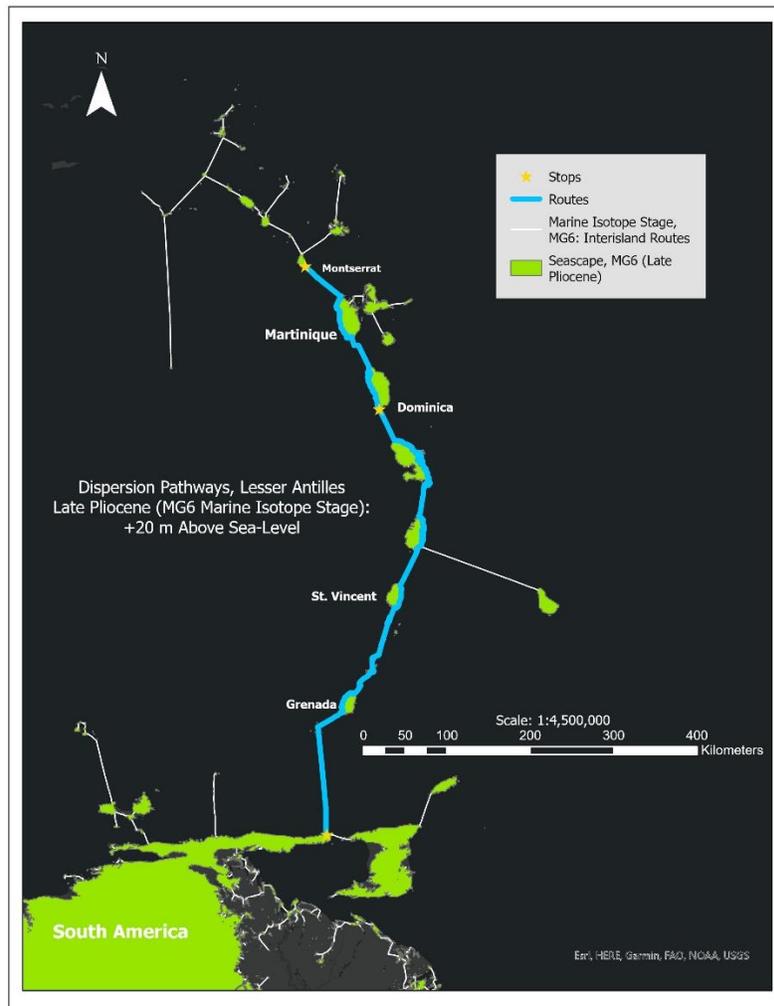


Figure 33. Potential island-hopping route for amazon parrots from northern South America, to different islands in the Lesser Antilles during the MG6 marine isotope stage for the late Pliocene.

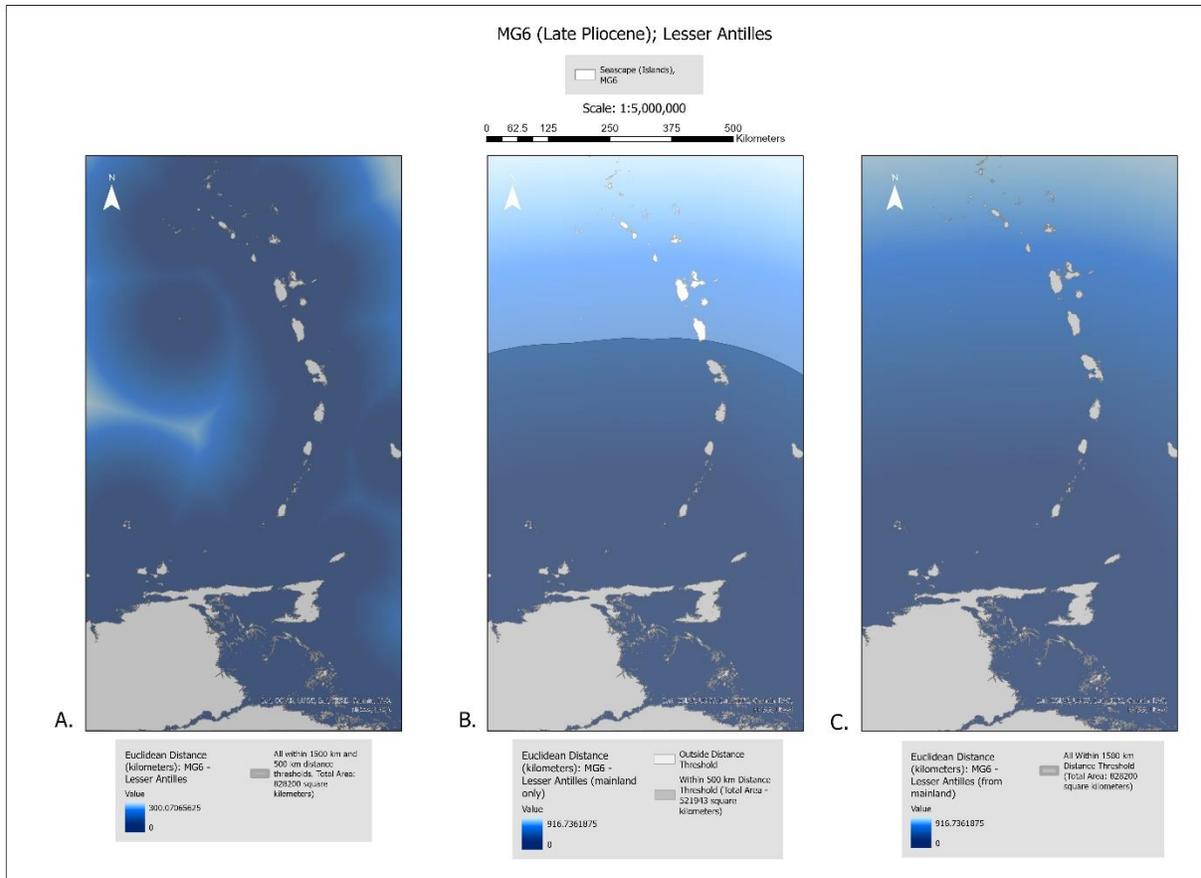


Figure 34. Euclidean distance results for the Lesser Antilles during the MG6 isotope period. Sea levels were 20m higher than present, making dispersion from mainland South America likely somewhat difficult. At +20m above sea level, islands such as Grenada were more cut off from South America.

### M2, Lesser Antilles:

Following the MG6 stage of the late Pliocene, the glacial episode reflected by M2 produced an estimated lowering of global sea levels of up to 65 m. In the Lesser Antilles, a total island area of 25905.5 km<sup>2</sup> was produced in modeling bathymetry for this MIS period. This seascape also had a total interisland network route distance of 1024.4 km (Table 4).

According to flight region maps produced for the M2 Lesser Antillean seascape, dispersion for amazon parrots was highly feasible at sea levels as low as 65 m below present, as

the entire seascape's Euclidean distance dataset met both query distance criteria (Figures 35 and 36).

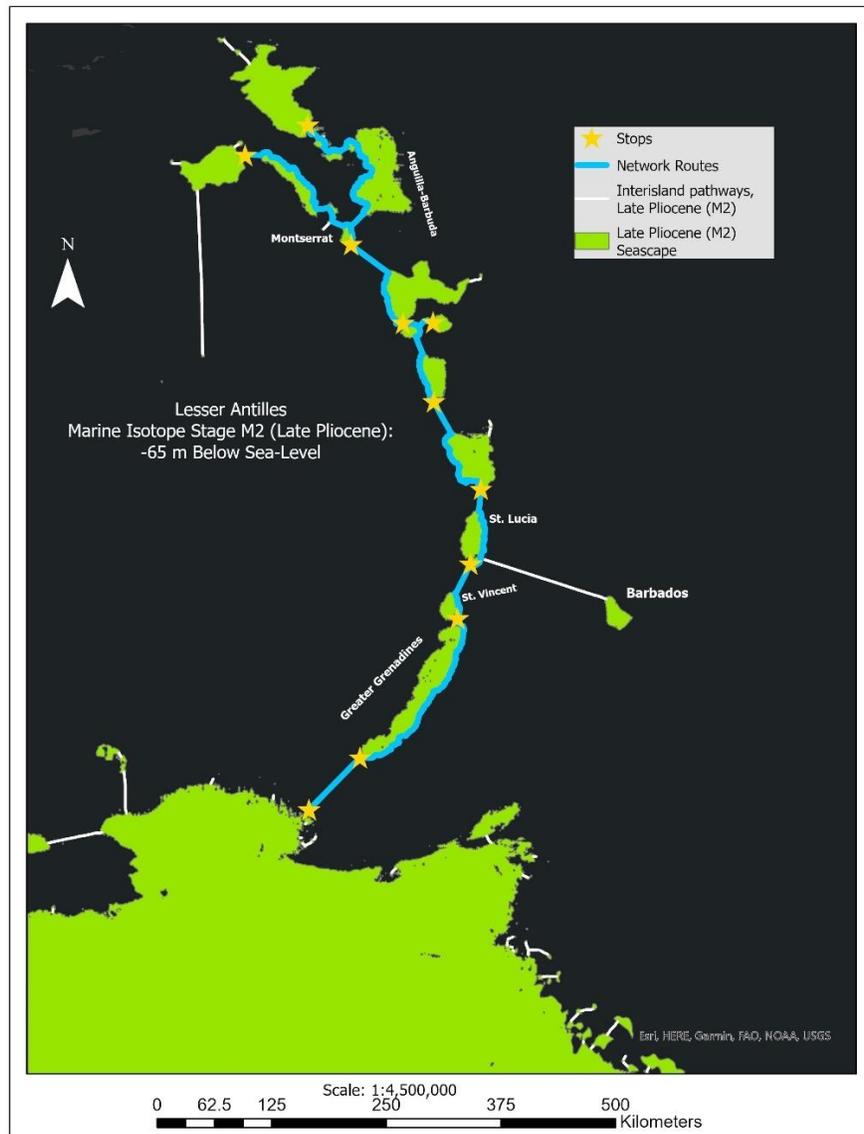


Figure 35. Hypothesized island-hopping route for amazon parrots from northern South America, to different islands in the Lesser Antilles during the M2 glaciation event with sea levels as low as -65m. Grenada and the Grenadines were a singular landmass, potentially supporting a population of island-hopping amazons.

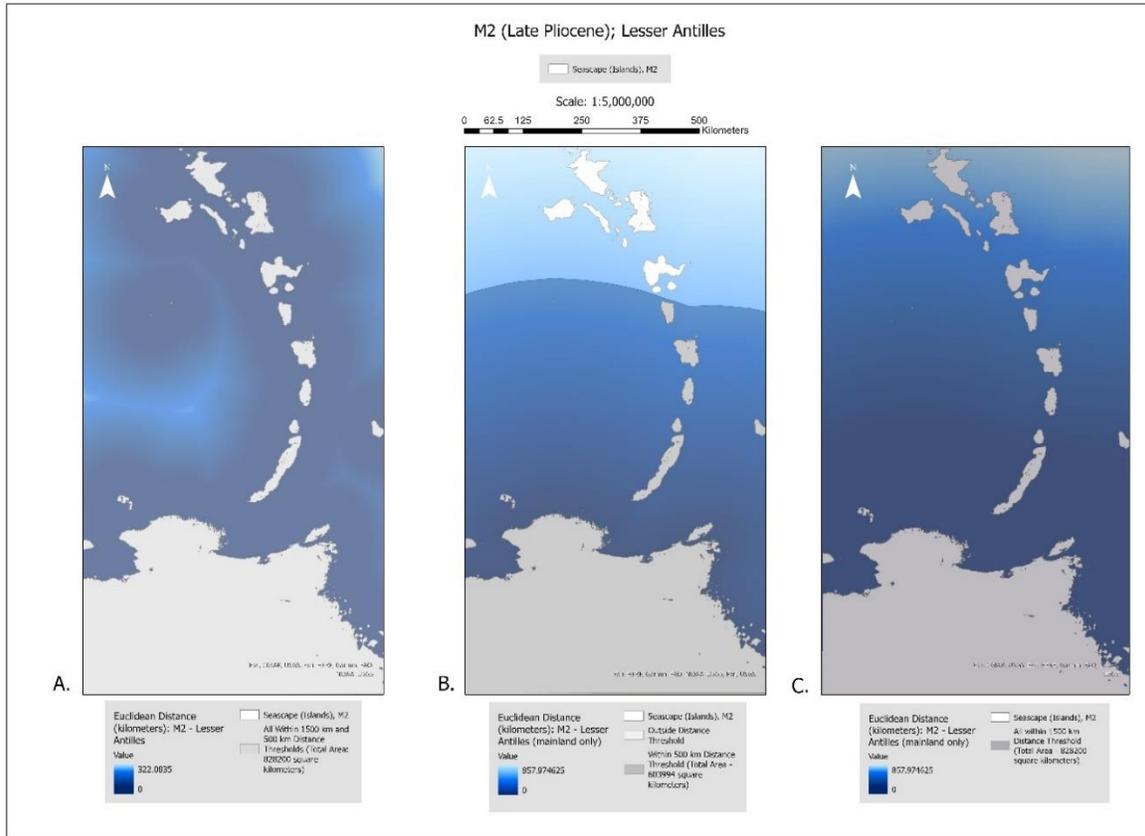


Figure 36. Euclidean distance mapping results for travel between different islands in the Lesser Antilles, during the M2 glaciation event of the late Pliocene. The raster met both distance thresholds of 1500 km and 500 km, respectively.

Dispersing from the mainland, similar to the MG6 Euclidean results, an amazon on the 500 km distance threshold would have potentially reached Dominica versus making it across the entire Lesser Antilles under the 1500 km threshold. The two amazon parrots that are endemic to Dominica may be descended from a mainland ancestor or perhaps an ancestor traveling from an island close to Dominica, like Martinique as there is an undescribed extinct species of amazon from this island, according to Williams & Steadman (2001).

#### Mid-Piacenzian Warm Period (mPWP), Lesser Antilles

Much like the seascape of the Greater Antilles during the mid-Piacenzian Warm Period, this MIS produced the least amount of total island area and greatest interisland distances of

10216.5 km<sup>2</sup> and 2038.8 km, respectively (Table 4) as sea levels were 30 m above present.

Euclidean distance and network route mapping indicated that this MIS period chosen for the study produced the most difficult routes of travel, in terms of interisland distance and distance of the island of Grenada from South America (Figures 37 and 38). Travel between islands in the Lesser Antilles during this period would have been the most difficult for amazons (of the six MIS periods used). In addition, previous colonists to islands in the Lesser Antilles perhaps could have become isolated at this time, due to being products of an amazon dispersal event at lower sea levels in the Lesser Antilles.

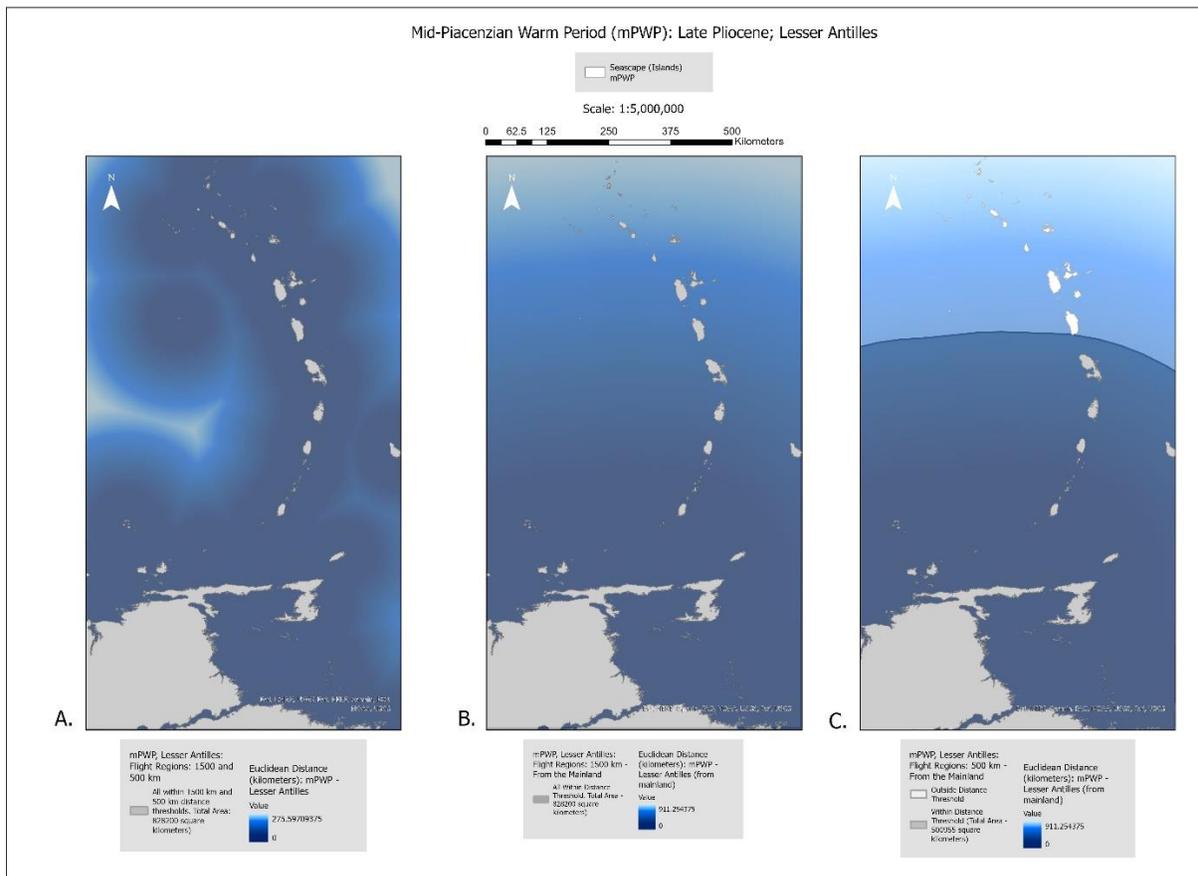


Figure 37. Euclidean distance mapping results for the Lesser Antilles, during the mid-Piacenzian Warm Period of the late Pliocene. The raster representing the entire seascape met both distance thresholds of 1500 km and 500 km, respectively. For potential travel from mainland South America, conditional statements for the second Euclidean raster determined that dispersal from the mainland under the 1500 km threshold was possible but not for the 500 km threshold, as the suitable flight region produced terminated at the island of Dominica.

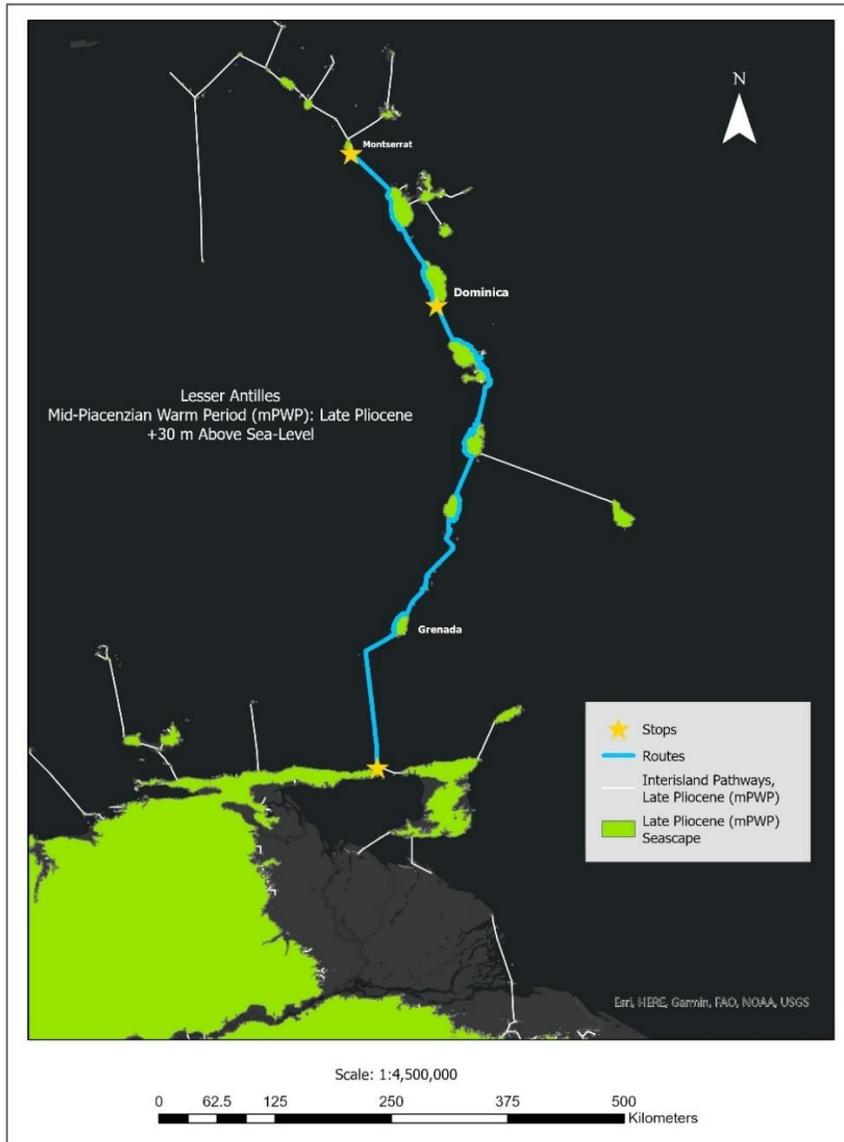


Figure 38. Potential island-hopping route for amazon parrots from northern South America, to different islands in the Lesser Antilles during the mid-Piacenzian Warm Period, for the late Pliocene. With sea levels as high +30m above present, this MIS period of the six in this study indicated the most difficulty of travel, in terms of interisland distance for amazon parrots.

### MIS 16, Lesser Antilles

During the middle Pleistocene, sea levels, 100 m below present facilitated optimal dispersal for amazons across the Lesser Antilles. The MIS 16 seascape for the Lesser Antilles had a total island area of 25968.3 km<sup>2</sup> and a total interisland route distance of 857.6 km (Table 4). Dispersion between islands during MIS 16 was highly feasible according to both Euclidean

distance thresholds (Figure 35). While the entire seascape met the 1500 km distance criteria, the 500 km condition for the Euclidean distance raster based solely on the mainland produced an optimal flight region with a total area of 592593 km<sup>2</sup> that reached just south of the island of Guadalupe for potential dispersion directly from the mainland. In Figure 36, the routes from running network routes for MIS 16 in the Lesser Antilles are shown as well, with a stop just south of the Guadalupe include as well.

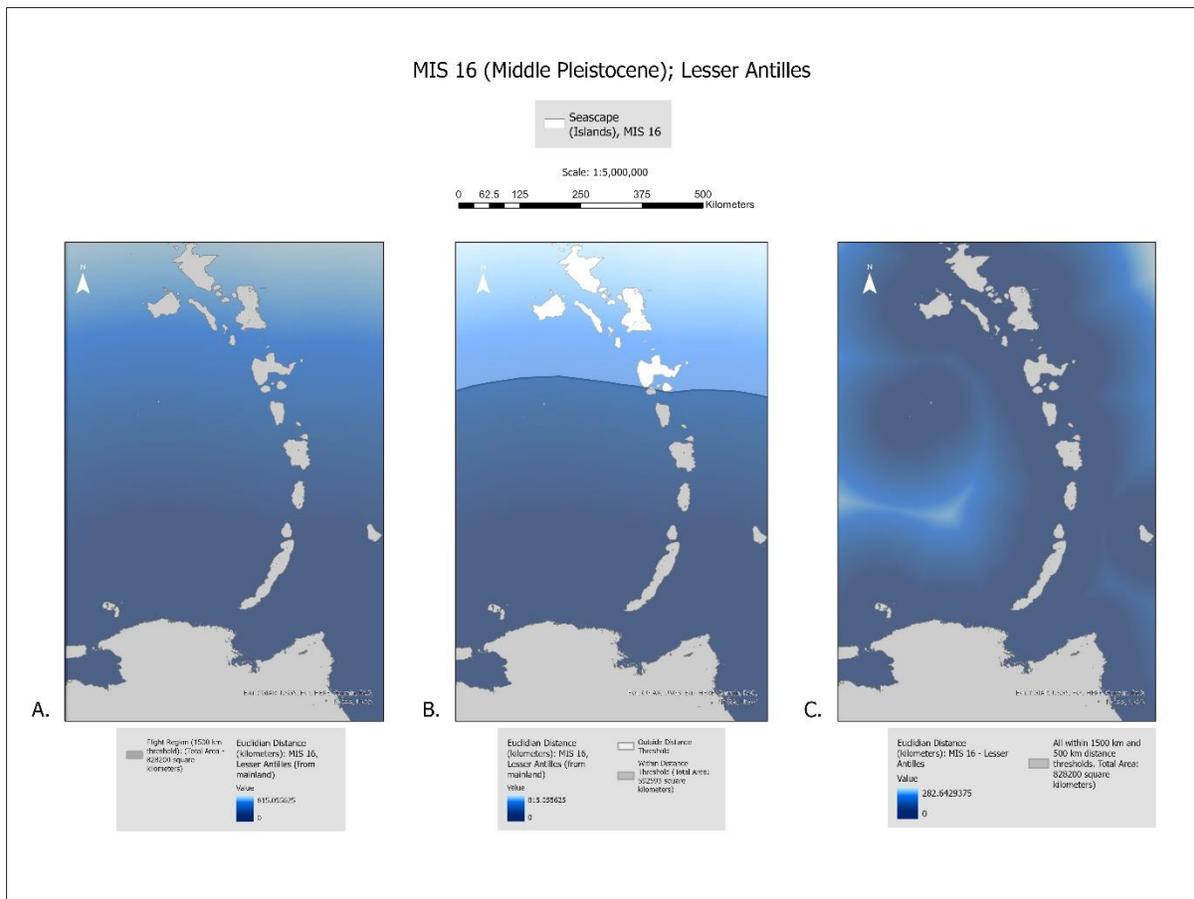


Figure 39. Euclidean distance mapping results for the Lesser Antilles, during the mid-Piacenzian Warm Period of the late Pliocene. The raster representing the entire seascape met both distance thresholds of 1500 km and 500 km, respectively. For potential travel from mainland South America, conditional statements for the second Euclidean raster determined that dispersal from the mainland under the 1500 km threshold was possible but not for the 500 km threshold, as the suitable flight region produced terminated close to the island of Guadalupe.



Figure 40. Hypothesized island-hopping route for amazon parrots from northern South America, to different islands in the Lesser Antilles during the middle Pleistocene (MIS 16) when sea levels were -100m below present. Grenada and the Grenadines were a singular landmass, as were Antigua and Barbuda, potentially supporting a population of island-hopping amazons.

### MIS 2 (LGM), Lesser Antilles

Using a value of -130 m for modeling bathymetry for the LGM (Spratt & Lisiecki 2016), produced the most optimal routes and connectivity for the Lesser Antilles (Figure 42). Islands such as Grenada and Antigua had nearly the area they have today, opening potential habitat for

amazons during the end of the end of the Pleistocene and permitting suitable areas of dispersion. According to the modeled bathymetry produced, the Lesser Antilles had a total island area of 25718 km<sup>2</sup> and the lowest total interisland distance sum of 755.7 km (Table 4).

For the entire seascape, the islands and mainland all fell within the optimal flight regions for the 500 km and 1,500 km thresholds, as did the entire Euclidean distance raster starting from the mainland, using the 1,500 km threshold (Table 4). Using the 500 km threshold on the mainland Euclidean distance raster for the LGM, only an area of 618427 km<sup>2</sup>, up to Guadalupe was produced (Figures 41).

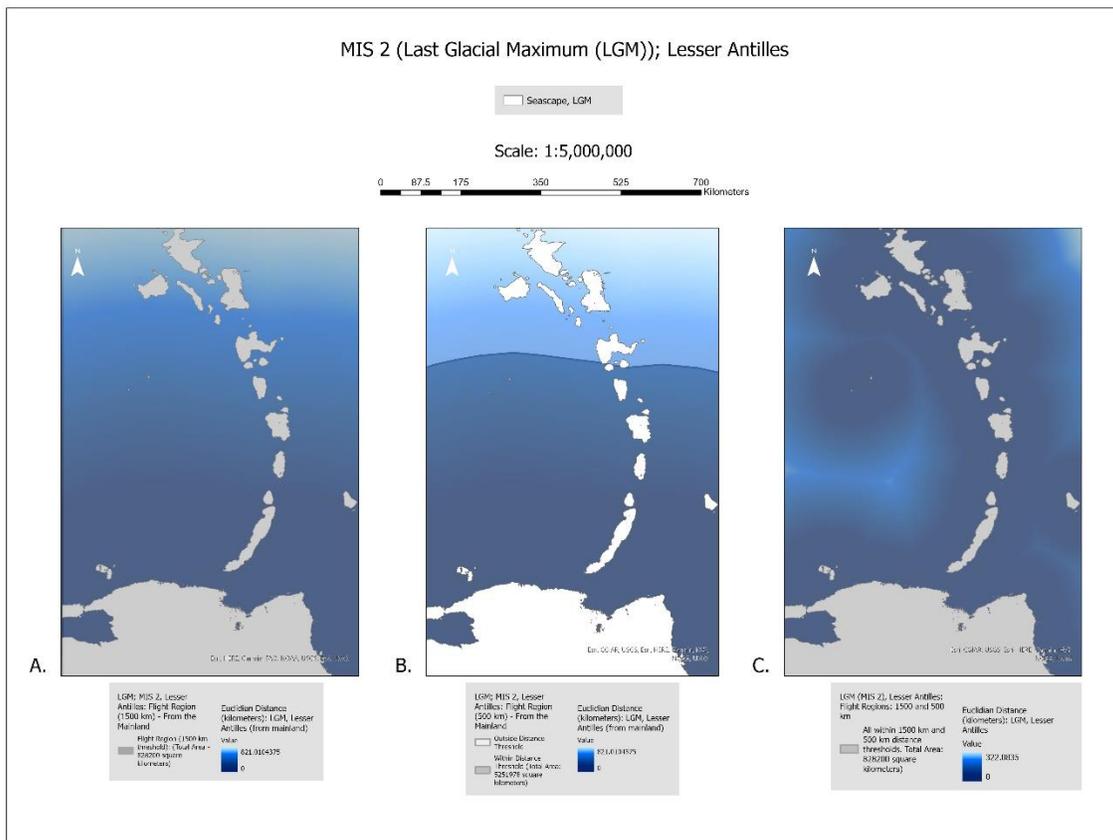


Figure 41. Euclidean distance results for the Lesser Antilles, during the LGM (MIS 2). The raster representing the entire seascape met both distance thresholds of 1500 km and 500 km, respectively. For potential travel from mainland South America, conditional statements for the second Euclidean raster determined that dispersal from the mainland under the 1500 km threshold was possible. Similar to the results for the Lesser Antilles during MIS 16 (-100m below sea level), the suitable flight region for the 500 km threshold here terminated at the island of Guadalupe.

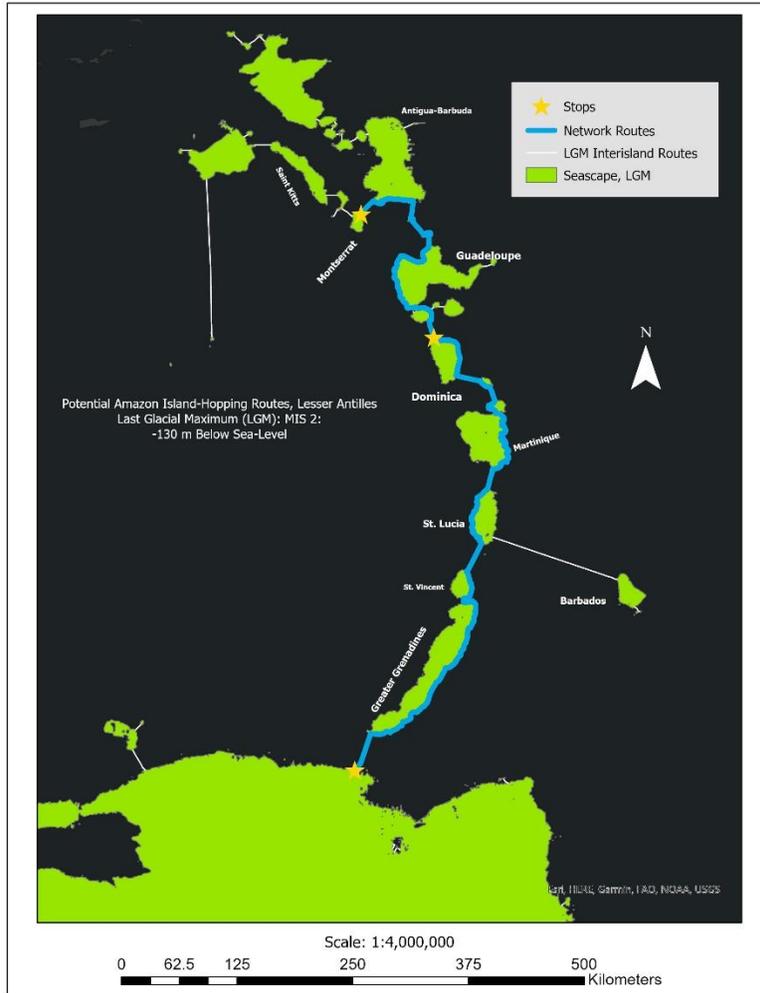


Figure 42. Network routes for the Lesser Antilles, during the LGM (MIS 2). For the Lesser Antilles, this network produced the most optimal dispersion routes, in terms of interisland distance and island area.

### MIS 1 (early Holocene), Lesser Antilles

As sea levels fell during the early Holocene, a seascape with sea levels 40 m below present produced a total island area of 19546.35 km<sup>2</sup> and a total network interisland distance sum of 1231.4 km (Table 4). The network dataset for the early Holocene is presented with its associated seascape, in Figure 43.

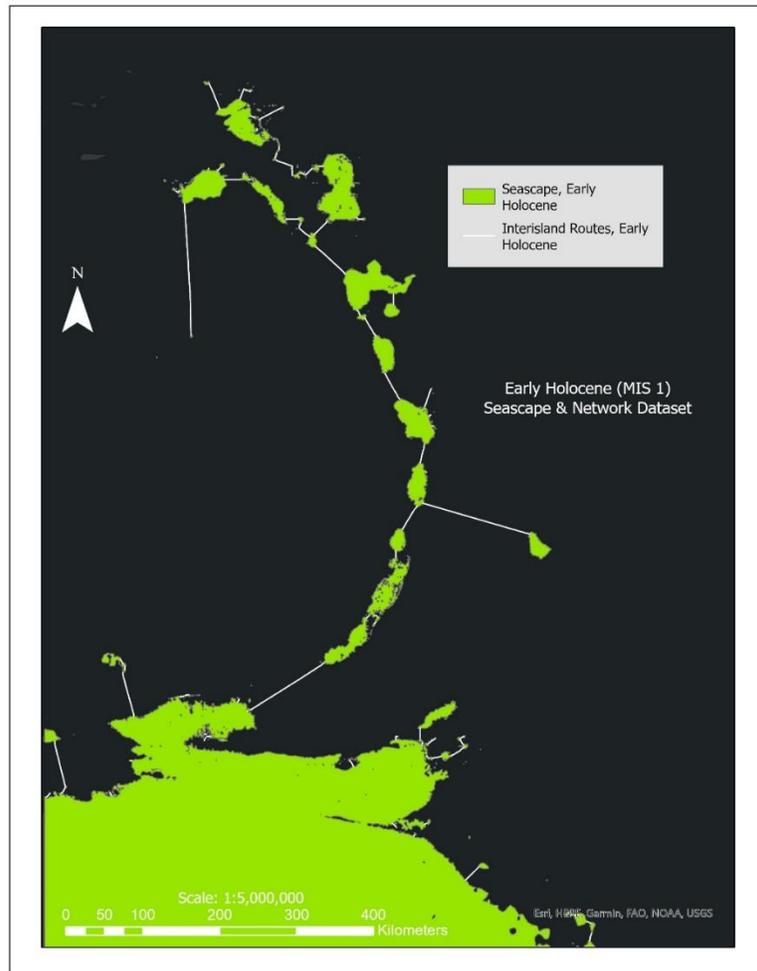


Figure 43. Network dataset for the Lesser Antilles, during the early Holocene. Sea levels were still as low as -40m, reflecting higher and more optimal dispersion between islands for amazon parrots, such as between Grenada and St. Vincent and the Grenadines. Ultimately, the phylogenetic knowledge for the evolutionary history for Lesser Antillean amazons is poorly known and thus, island-hopping during the early Holocene is up for speculation.

Despite several islands in the Lesser Antilles being volcanic in nature, rising sea levels following the LGM reduced island connectivity and increased interisland distance. This may have had localized effects on biota for certain islands, as seen in the Bahamas with several landbird species becoming extirpated from low-elevation islands in the Bahamas due to sea level rise (Steadman & Franklin 2017). Despite sea level rise after the LGM, according to bathymetric model estimates and Euclidean distance modeling for this seascape, dispersion for amazons was still feasible, under the two distance thresholds, much like all of the previous MIS periods for the

Lesser Antilles. However, with the 500 km threshold and starting at the mainland, an amazon under this threshold would have been capable of making it only as far as Dominica without stopping (Figure 44).

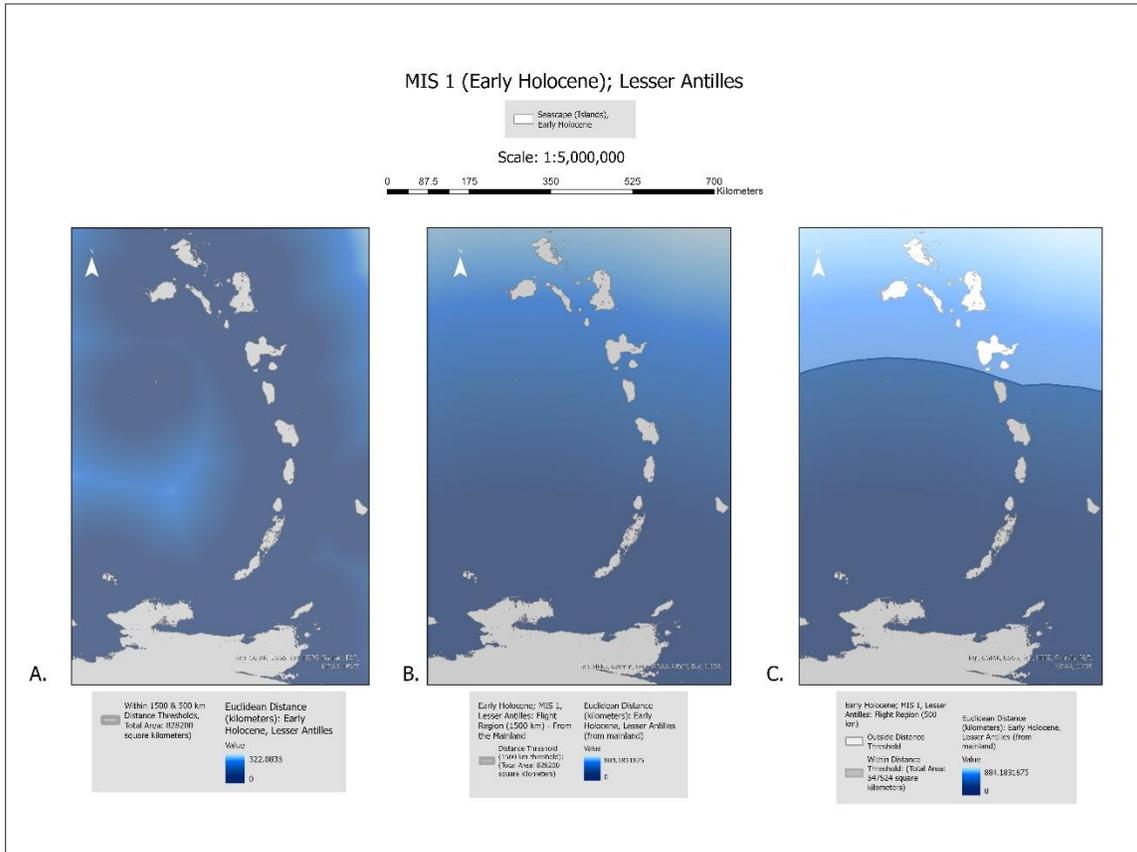


Figure 44. Euclidean distance representing the Lesser Antilles during the early Holocene. With sea levels as low -40m, dispersion was still highly feasible from the mainland as the entire raster meets the 1500 km distance threshold while the 500 km threshold only produced a region that reaches just north of the island, Dominica.

### Hypothesis for Lesser Antillean Amazon Dispersion

Maps of network routes and Euclidean distance-based flight regions led me to argue that amazon parrots colonized the Lesser Antilles during periods of glacially-lowered sea level like M2 in the late Pliocene, MIS 16, or the LGM. Lower sea levels exposing greater land area may connect nearby islands together, creating singular islands (Heaney 1986), decreasing the distance

separating islands or decreasing the distance from the mainland, and leading to many dispersal events from the mainland at lower sea levels (Mead et al. 2002; Oliveros & Moyle 2010).

However, due to Lesser Antillean amazons being a paraphyletic group (Russello & Amato 2004) and several, now extinct taxa whose taxonomic affinity is somewhat debated (Williams & Steadman 2001), the biogeography of Lesser Antillean amazon parrots may need further work.

Based on using molecular ages for Greater Antillean amazons (Kolchanova et al. 2021) in temporal conjunction with different MIS periods being used as an estimation for Lesser Antillean amazon parrot evolution, I present here a hypothesis on Lesser Antillean amazon evolutionary history but argue as well that more phylogenetic studies on Lesser Antillean amazons are needed. If extinct Lesser Antillean amazons such as the Grenada Parrot (Butler 1992) or the extinct amazon from Martinique (Williams & Steadman 2001) were still extant, perhaps a stronger phylogenetic conclusion would be reached. Using sea-level values for the Pliocene, Pleistocene, and early Holocene to estimate potential routes of dispersal with respect to geologic time likely only tell part of the story. Suitability in travel between islands of the Lesser Antilles and mainland South America led to me agree with Russello & Amato (2004) that amazon parrots of the Lesser Antilles might be the result of more than one dispersal event from South America.

### **Fossil Maps**

Location data representing both prehistoric and historic records of Greater Antillean amazons was compiled from the PBDB, iDigBio, and primary literature (see Figures 20-21). After running the Aggregate Points tool, polygon feature classes representing the historic and prehistoric range for Greater and Lesser Antillean amazons was created. Overlaying polygon feature data for modern ranges of extant amazons in the West Indies, the fossil-historic range estimation was indicative of amazons being common across the West Indies, concurring with

Williams & Steadman (2001) before certain island endemic species, specifically in the Lesser Antilles became extinct while certain populations (subspecies) of *A. leucocophala* became extirpated from some but not every island in the Bahamas and the Cayman Islands, in the Greater Antilles.

### Fossil Map - Greater Antilles

As demonstrated above with the network route and Euclidean distance mapping in the Greater Antilles, amazon parrots likely island-hopped during periods of lower sea level. Molecular divergence times from phylogenetic work by Kolchanova et al. (2021) matched to the temporal range for specific MIS eustatic sea level values for the late Pliocene and middle Pleistocene help support that amazon parrots reached a wide distribution in the Greater Antilles. 3.47 Ma (roughly during the MG6 isotope period of the late Pliocene), Central American amazons began to disperse to Jamaica, with perhaps other colonization events during the M2 glaciation (~ 3.3 Ma). Amazons ultimately reached Puerto Rico by 0.67 Ma, which roughly occurred prior to the MIS 16 period during the middle Pleistocene. With this in consideration, Pleistocene and Holocene fossil records for Greater Antillean amazons (data herein) indicate that islands of the Greater Antilles had amazon parrots by the middle Pleistocene at the earliest. To add further context to this, the prehistoric-historic range polygon of *Amazona* in the Greater Antilles was overlain with the modern geographic range data for *Amazona* in the region (Figure 45).

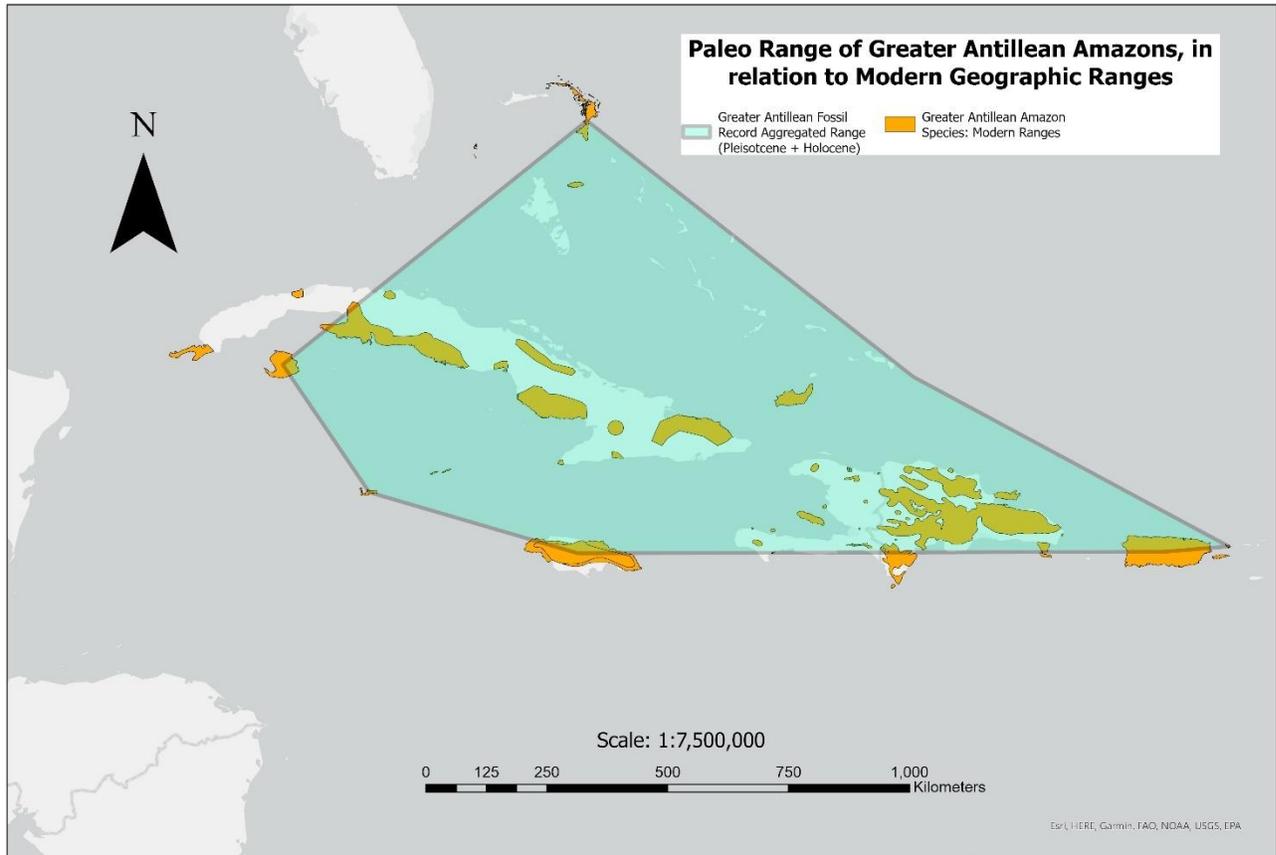


Figure 45. Modern geographic range of the amazon parrot genus across the Greater Antilles, representing five extant species, with the spatial extent of the Greater Antillean amazon fossil record. Modern occurrences on Cuba, the Bahamas, and the Cayman Islands represent the different subspecies of *A. leucocephala*. The fossil record suggests that amazons were more widespread prior to the arrival of humans to the Greater Antilles.

Due to the incomplete fossil record and the data used to derive the paleo range polygon coming from point data, the entire Greater Antilles is not covered. For instance, according to Kolchanova et al. (2021) and network and Euclidean distance maps for the late Pliocene M2 Greater Antilles, amazons from Central America island-hopped exposed islands of the Nicaraguan Rise, at lower sea levels, in between Central America and Jamaica. With these intermediate islands submerged due to the inundation of the Nicaraguan Rise any fossil record for *Amazona* includes these now submerged islands, which in turn would represent *A. albifrons* or intermediate species that island-hopped to Jamaica, as argued by Russello & Amato (2004) and Kolchanova et al. (2021).

Williams & Steadman (2001) argued that each island in the Greater Antilles had endemic psittacid species. From constructing total paleo range data using fossil and archaeological occurrence information, I agree that amazon parrots had a largely similar distribution in the Greater Antilles to today.

Synthesizing Bahaman fossil records (Williams & Steadman 2001; Steadman et al. 2007) with other prehistoric occurrence data and using route mapping in Network Analyst, *A. leucocephala* certainty occurred on other islands besides Cuba as the species does today. However, my network mapping and range reconstruction affirm prior studies that this parrot has experienced significant extirpation from numerous islands in the Bahamas, including the Turks and Caicos Islands. Optimal times of dispersion based on low sea levels during the middle Pleistocene or even the LGM lead me to argue that amazons from Cuba readily colonized the Cayman Islands, and the Bahamas, ultimately reaching the Turks and Caicos Islands, prior to human arrival and impact and the accumulation of bird fossils, among other terrestrial vertebrate remains in cave deposits and archaeological sites. Other amazon species, based on route and Euclidean distance mapping, reached islands in the Greater Antilles most likely prior to human arrival as well as ages for fossil data utilized in aggregating the paleo range map were Pleistocene and Holocene in age.

#### Fossil Map – Lesser Antilles

Occurrence data (see Figure 21) for Lesser Antillean amazons used in creating an aggregated polygon representing the total former geographic range of amazons in this part of the West Indies included records for the modern Lesser Antillean amazons and fossil and historic information on known and undescribed Lesser Antillean amazon species.

Today, amazons are represented in the Lesser Antilles by *A. guildingii* (St. Vincent), *A. imperialis* (Dominica), *A. arausiaca* (Dominica), and *A. versicolor* (St. Lucia) (Williams & Steadman 2001; Russello & Amato 2004) (Figure 3). Inferred species reported from sparse fossil data and historical observations, such as the Guadeloupe parrot (†*A. violacea*) of Guadeloupe and neighboring Marie Galante (Greenway 1958), Martinique (Martinique parrot; †*A. martinicana*) (Rothschild 1907), Montserrat (Montserrat parrot; †*Amazona* undescribed sp.) (Reis & Steadman 1999), and Grenada (Grenada parrot; †*Amazona* undescribed sp.) (du Tertre 1667; Snyder et al. 1987; Butler 1992) were included for creating the estimated former Lesser Antillean geographic range of amazons as well. Figure 46 depicts a map with the estimated geographic range of amazon parrots during prehistoric and historic times by running the Aggregate Points tool in ArcGIS Pro on Lesser Antillean amazon data. This polygon overlays the modern geographic range data for amazon parrots in the Lesser Antilles, which includes four species, two of which are endemic to Dominica.

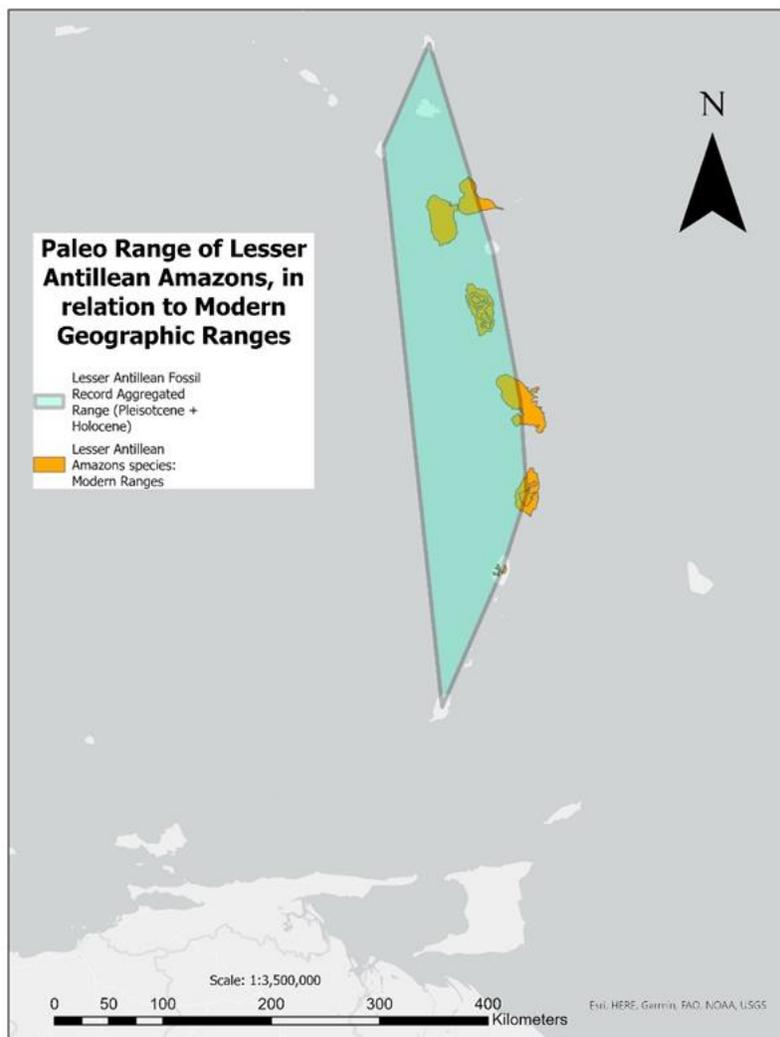


Figure 46. Modern geographic range of the amazon parrot genus across the Lesser Antilles, which represents four extant species, with the spatial extent of the Lesser Antillean amazon fossil record. The fossil record suggests that amazons were more widespread prior to the arrival of humans to the Lesser Antilles.

Ages of amazon fossils found in the Lesser Antilles (the oldest being early Holocene from Montserrat) line up well with the MIS ages used to make dispersion maps to align with molecular dates for Greater Antillean amazon diversification from Kolchanova et al. (2021), used here for the Lesser Antillean amazons as estimates.

If island-hopping occurred for Lesser Antillean amazon parrots, colonists from northern South America may have begun colonizing nearby islands during the M2 stage of the late

Pliocene, when sea levels were as low as -65m (De Schepper et al. 2013), using the molecular dates for Greater Antillean amazon diversification from Kolchanova et al. (2021). It is very possible that amazon parrots began colonizing the Lesser Antilles earlier than that.

As Lesser Antillean amazons represent a paraphyletic group (Russello & Amato 2004), colonization of the Lesser Antilles by amazon parrots may have occurred with multiple dispersion events by multiple lineages.

Clark (1905) argued that the record of amazons for the northern Lesser Antilles is non-existent. However, material (coracoid, two humeri, femur, and ulna) for a small, undescribed *Amazona* species was recovered from the Trants archaeological site on Montserrat (Reis & Steadman 1999) and *Amazona* material from Barbuda and Antigua identified as possibly being *A. vittata* (based off of a rostrum) (Steadman et al. 1984) demonstrates that amazons reached further north in the Lesser Antilles than Clark (1905) projected. However, no evidence of amazon parrots or other Psittaciformes on Saint Kitts and Nevis, St. Croix, or the small islands in between there and the Virgin Islands has been found (Clark 1905).

Route maps produced for each of the six MIS periods considered in this study support the potential for amazon parrot travel to the northernmost Lesser Antilles. Meanwhile, the Euclidean distance maps, queried to the two flight ranges support this dispersion but the birds likely would have made stops before reaching Saint Kitts and Nevis.

### **Geographic Parsimony: Greater Antillean Amazons & Further Work for Lesser Amazons**

Characters based on geographic dispersal history was carried out for the Greater Antillean amazon lineage in order to assess my study's GIS results for modeling dispersion and evolution for this lineage. An MP analysis, this geographic parsimony analysis was based off of the Greater

Antillean amazon parrot phylogenetic tree from Kolchanova et al. (2021) (Figure 1 herein).

Figures 43 – 45 are the trees derived from Mesquite, for each individual character and each taxon is given a corresponding letter in the tree: A = *A. albifrons* (Central America), B = *A. agilis* (Jamaica), C = *A. collaria* (Jamaica), D = *A. l. leucocephala* (Cuba), E = *A. l. caymenensis* (Grand Cayman), F = *A. l. hesterna* (Cayman Brac), G = *A. l. bahamensis* (Bahamas), H = *A. ventralis* (Hispaniola), and I = *A. vittata* (Puerto Rico).

This part of my analysis using characters based on island geography was consistent with the molecular study carried out for Kolchanova et al. (2021) for Greater Antillean amazons. For instance, the trees have the mainland species, *A. albifrons* as the outgroup which stayed consistent for all three characters. *A. agilis* and *A. collaria* represent separate but sister lineages while all other Greater Antillean amazons (*A. leucocephala*, *A. ventralis*, and *A. vittata*) are all sister to *A. collaria*.

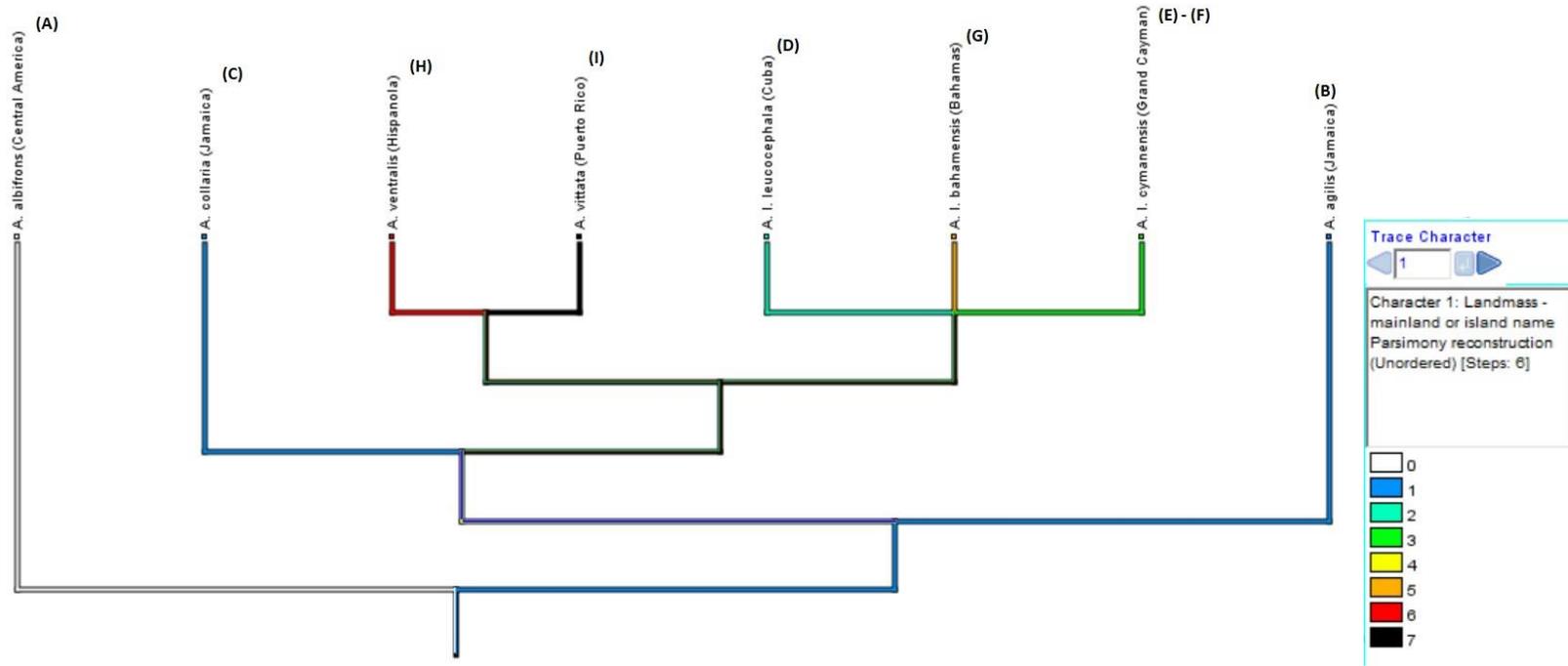


Figure 47. Mesquite Tree and its associated legend for the first geographic character: landmass locations. In the tree, “0” represents the mainland (the ancestral state), “1” indicates Jamaica for the two species endemic to Jamaica, *A. agillis* and *A. collaria*, “2” for the Cuban Amazon (*A. leucocephala*), “3”, “4”, and “5” are all distinct populations for the recognized subspecies of *A. leucocephala* spread out across the Cayman Islands and the Bahamas, while “6” and “7” represent *A. ventralis* and *A. vittata* of Hispaniola and Puerto Rico, respectively.

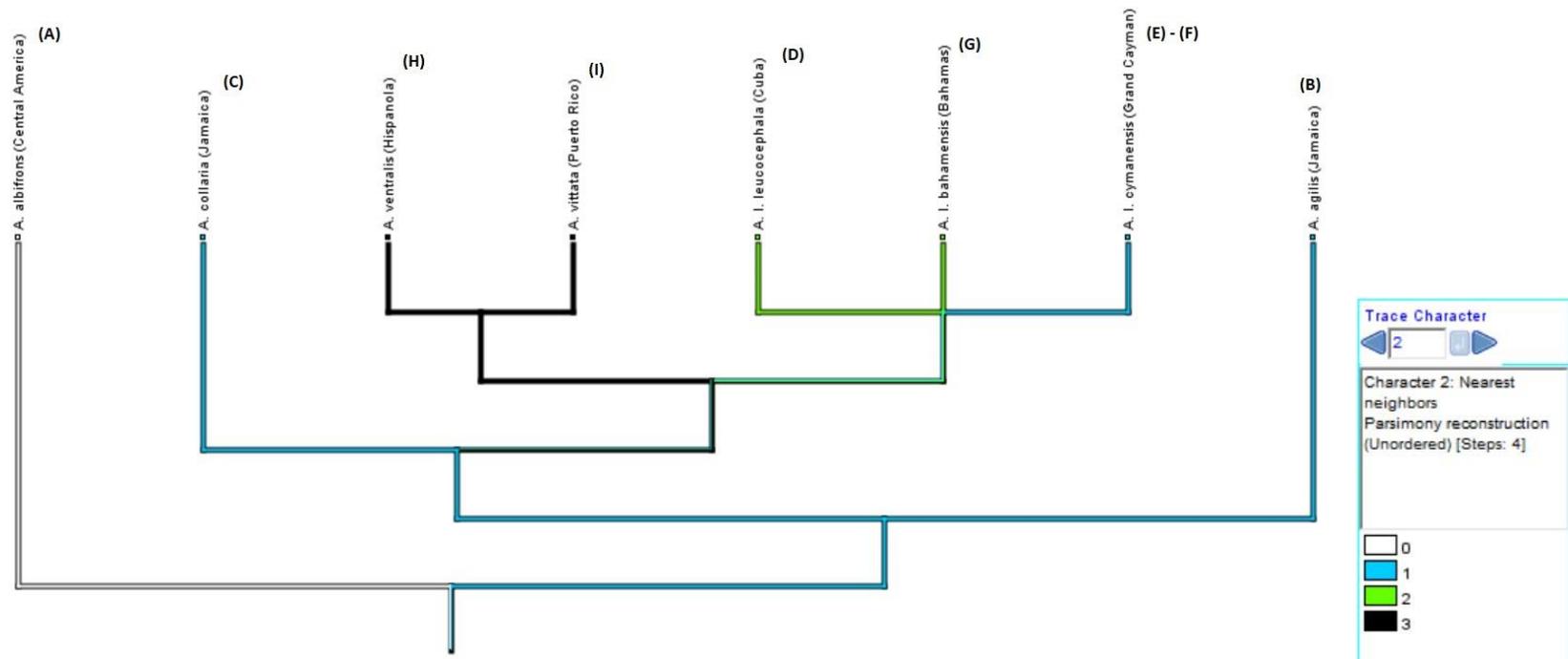


Figure 48. Mesquite Tree and its corresponding legend, based on the second geographic character: nearest neighbor. Here, “0” indicates mainland, “1” indicates close proximity between Jamaica and the Cayman Islands, “2” for Cuba and the Bahamas and the Cayman Islands, and “3” for Hispaniola and Puerto Rico which have the two most derived taxa, *A. ventralis* and *A. vittata*.

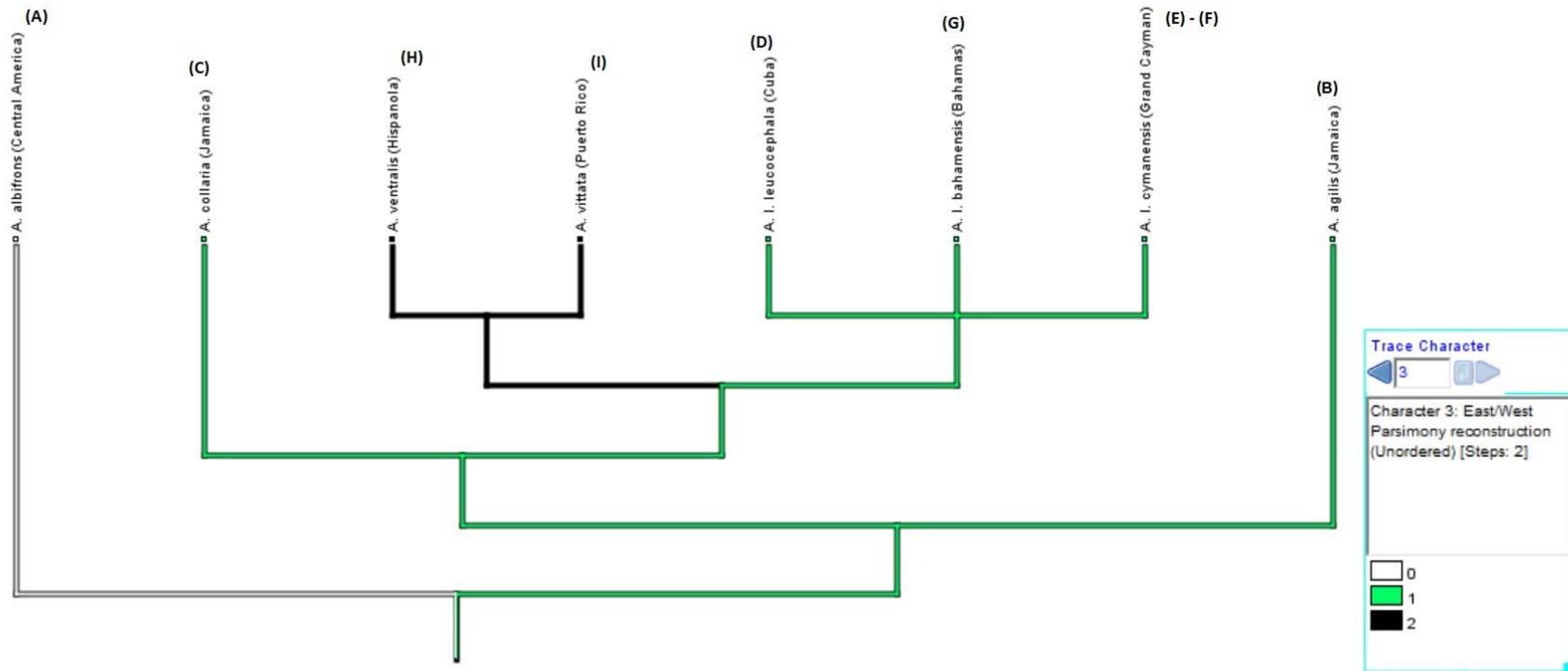


Figure 49. Mesquite Tree and its corresponding legend, based on the third geographic character: West to East dispersion. Amazons in the Greater Antilles are descended from Central American ancestors who moved in a west-east pattern. Here, “0” indicates mainland (ancestral), “1” indicates a location west of more derived taxa, and “2” represents those easternmost species, *A. ventralis* and *A. vittata*, specifically, which are the most derived.

For *A. leucocephala*, Kolchanova et al. (2021) did not go to the subspecies level but this study did, treating each island subspecies from Cuba, the Bahamas, and the Cayman Islands as separate populations with different characters based on location, nearest island neighbor, and direction of dispersal. Here, the *A. leucocephala* species complex is resolved as a polytomy based on the layout of the matrix but Kolchanova et al. (2021) were confident in *A. leucocephala* evolving first on Cuba. Despite the polytomy for the four *A. leucocephala* subspecies, my trees still illustrate the connection between the four distinct subspecies. My results from my route and Euclidian distance mapping led me to the same conclusion as Kolchanova et al. (2021), that there were multiple dispersion events and gene flow between Cuba, the Cayman Islands, and the Bahamas, specifically during periods of lower sea level. Fossil records representing extirpated populations (Williams & Steadman 2001), modern records of extant populations from the Bahamas and the Cayman Islands in addition to those on Cuba (Flieg & Sander 2016), and my GIS results in my study lead me to conclude that this animal was and is still widespread in the Greater Antilles.

The geographic characters used in my matrix agree with the molecular analysis carried out by Kolchanova et al. (2021). The trees based on each character produced can be interpreted with the results of this study's geospatial analysis. Dispersion events to Jamaica based on these trees (Figures 47-49) could be visualized in my Euclidean distance and Network maps that indicated degrees of dispersal feasibility based on the two distance thresholds of 1,500 and 500 km, to create optimal flight regions. With this in consideration, dispersion events to Jamaica were likely associated with the drowning or exposure of the Nicaraguan Rise, depending on eustatic sea level. From there, dispersion to Cuba occurred, with potential colonization events to the Caymans and the Bahamas, or they occurred later when sea levels were lower, during the LGM

perhaps. Regardless, the sea level mapping, specifically for the LGM and MIS 16 for the Greater Antilles, when focused in on Cuba and surrounding islands represent high feasibility for Cuban Amazons to disperse from Cuba to the nearby Cayman Islands, the Bahamas and the Turks and Caicos Islands (Figure 47). Today, populations still persisting on Cuba, Cayman Brac, Grand Cayman, and Abaco in the Bahamas represent what was once likely a larger distribution, according to my network routes of travel from Cuba and the Greater Antillean amazon fossil-modern amazon range map.

The trees made in Mesquite also demonstrate that dispersion from Cuba, not Jamaica occurred to Hispaniola, followed by Puerto Rico for *Amazona*, based on the characters for dispersion, moving west to east, with Puerto Rico being the easternmost island in the Greater Antilles (Figure 49). Euclidean and route mapping in GIS agreed with these results as well. I hope that my work herein can help future researchers visualize the evolutionary history of Greater Antillean amazon parrots, from the perspective of geography, using GIS and checking those results with a parsimony analysis based on geography.

Lesser Antillean amazons are a paraphyletic group whose members are not one another's closest living relative. Russello & Amato (2004) inferred that amazon parrots of the Lesser Antilles likely represent more than one dispersal event to the archipelago from South America. Network route and Euclidean distance maps produced for all six MIS periods for the Lesser Antilles lead me to argue that dispersion from South America across the Lesser Antilles was highly feasible, regardless of sea level changes in the region, based on the estimated maximum flight distance ranges used for modeling. The feasibility for travel according to the cartographic results in this study lead me to concur with Russello & Amato (2004) that Lesser Antillean amazons represent more than one episode of overwater dispersal.

## CONCLUSION

### Summary

The objective of this study was to map out potential routes of dispersal for insular amazon parrot species of the West Indies, from the timing of their evolution in relation to sea-level fluctuations according to MIS periods of the late Pliocene and Pleistocene, as well as the Holocene. Using sea level values, interisland distances were determined for islands of the Greater Antilles and the Lesser Antilles and travel potential was determined for the birds across the six chosen MIS periods, using Network Analysis and raster Euclidean distance analysis in ArcGIS Pro.

Utilizing the methodology of modifying bathymetric datasets in GIS to look at sea level fluctuations, this study took a new approach compared to previous studies using GIS to model biotic dispersion according to sea level change (Robles 2013; Kealy et al. 2018) in utilizing the Network Analyst function and Euclidean distance raster analysis in ArcGIS Pro. As put forward by Webster et al. (2016), distance holds some of the greatest potential amongst variables for influencing spatial and temporal patterns in natural or social landscapes/environments. In this study's case, changes in interisland distance and distance from the mainland would have had an effect on the potential long-distance flight behavior for amazon parrots.

Networks can be viewed as spatial networks that facilitate movement of people or animals (Prima et al. 2018). Creating network datasets from connecting landmasses with modified coastlines and areas according to different sea level values derived from MIS periods resulted in a successful demonstration of Network Analyst in ArcGIS Pro. Meanwhile, optimal flight regions, derived from Euclidean distance analysis verified the Network results of each MIS period. Distance values corresponding to non-suitable values (specifically not meeting my

distance thresholds of 1,500 and 500 km) were excluded from networks and in the Euclidean distance results, would fall outside the optimal dispersal regions.

The flight distance thresholds, 1,500 km for a maximum and 500 km, as a minimum and control, served as estimations. The results of this study helped illustrate geography of Greater Antillean amazon dispersal and evolutionary history, and offered a hypothesis for multiple colonization events in the Lesser Antilles, with respect to lower sea level, for Lesser Antillean amazons. However, I hope that these estimations for long-distance amazon parrot flight potential help drive further research on long-distance flight behavior for the *Amazona* genus.

These dispersion pathways, when put in the context of known MIS periods and the added information of molecular information for evolution of the Greater Antillean amazon lineage helped to better illustrate evolution and dispersal of amazon parrots in the Greater Antilles. Results of this study, in conjunction with determining flight distance potential using regions derived from Euclidean distance raster processing help to better inform the current understanding of evolution of different endemic amazon species in the Greater and Lesser Antilles.

In using different glacially influenced eustatic sea level values in this study, as area increased, the inverse happened with total interisland network distance. An increase in island area due to lower sea levels would decrease the distance from one island to another or the distance from an island to the mainland. Modeling changes in island geography over time in GIS helped confirm previous studies postulating that island physiography changes with respect to eustatic sea level and time (Steadman 2006; Fernández-Palacios et al. 2016).

## **GIS Limitations and Future Research**

A Euclidean distance raster dataset only has distance values (Wade & Sommer 2016). Thus, similar to running Network Analysis for determining routes along network datasets of each MIS seascape, distance was the only variable considered. In other raster operations, such as cost path analysis, distance and other parameters denoted in raster datasets that can be reclassified by different cost factors and values, can be combined to form “cost rasters” that an optimal pathway of least resistance or “cost” can be determined (Graham 2001). While cost path analysis could have been used here, Euclidean distance was utilized but one way in which this study could be improved could be the addition of other, secondary cost parameters, in the form of raster datasets, like precipitation, to determine routes of travel for amazon parrots throughout the Caribbean.

Variation in climate, especially in the Tropics, will produce higher habitat diversity. On islands, this in turn will increase an island’s species richness which, also increases with island area (Whittaker et al. 2008). Saupe et al. (2019) determined that higher spatiotemporal variation in precipitation closer to the Equator works as a significant driving force behind speciation as the bird diversity will increase closer to the Equator. If this study were to be improved, perhaps paleoclimatic raster data at temporal resolutions close to the MIS periods considered in this study could be utilized as cost variables where perhaps higher precipitation variation denoting greater habitat diversity could be reclassified as low-cost areas to travel on a cost surface raster for the parrots as they island hop in a cost path analysis model that would consider both climate and distance as costs to travel.

Another variable that could have potentially affected amazon parrot dispersion in the Greater and Lesser Antilles would be wind, specifically prevailing winds. The prevailing winds in a region where an island or group of islands is located can have effects on dispersal,

facilitating immigration or acting as a deterrent. For instance, in their estimates of gene flow across islands of Fiji for the Fiji bush-warbler (*Horornis ruficapilla*), Gyllenhaal et al. (2020) found that the prevailing easterly winds of Fiji could offer a potential explanation for this bird exhibiting less gene flow between the islands of Viti Levu east to Vanua Levu. In another, albeit more extreme case of winds influencing dispersal, a hurricane's prevailing winds carried green iguanas (*Iguana iguana*) on vegetation masses across the Caribbean Sea, before the iguanas made it to the island of Anguilla by a case of chance jump dispersal, otherwise known as a "sweepstakes route" (Censky et al. 1998).

Wind-related data for the Pliocene and Pleistocene could improve this study, and potentially explain the presences of amazons on some islands. While not migrating long distances, amazons will travel in flocks (Snyder et al. 1987). The addition of climatic variables such as precipitation patterns and prevailing winds at temporal resolutions matching the selected MIS periods to impact amazon flight and create cost surface rasters that included interisland and mainland distances could be another route of analysis this study or similar, future ones could take.

This study can be used as a platform to consider utilizing network analyst in future geospatial studies looking at island biogeography, treating islands and routes between them as spatial networks. Other researchers may use other MIS and sea level values but this study argued that suitable network datasets representing seascapes from deep time can be used in geospatial network operations that consider island biogeography. As discussed in the previous section, utilizing other variables such as paleoclimatic factors like wind, if it were available, or even a simpler variable with better availability like temperature or precipitation, as part of a cost distance analysis or suitability study would be one way to improve this study. Determining

bioclimatic variables with timestamps line up with the MIS's used in this study would be the first step of course.

The rising and lowering of sea levels had dramatic effects on the physiography of the Caribbean. Similar to other regions of islands such as the Philippines (Heaney 1986; Robles 2013) or the Wallacean Archipelago (Lohman et al. 2011; Kealy et al. 2018), distribution and connectivity of islands based on past sea level history is an important factor in understanding the biogeography of the Caribbean.

### **Greater Antilles**

Utilizing different sea level values derived from MIS periods to create modified seascapes of the Greater Antilles in order to model amazon parrot dispersion from mainland Central America helped to better illustrate inferences of island-hopping for this monophyletic group of amazon parrots.

Puerto Rico today is the farthest and westernmost island from Central America in the Greater Antilles with an amazon parrot species, the Puerto Rican Parrot (Snyder et al. 1987). According to Williams & Steadman (2001), the nearby island of Culebra once had an extinct subspecies of Puerto Rican Parrot (*A. v. gracilipes*). With the results from both Network and Euclidean distance mapping based on distance thresholds one (1,500 km) determined from Pennycuik (1989) and the other (500 km) used as a control to account for uncertainty, amazons dispersing across the Caribbean, all the way out to Puerto Rico, was highly feasible, especially at periods of lower sea level that also roughly match molecular divergence times determined through phylogenetic for thus lineage. For instance, Kolchanova et al. (2021)'s assessment of the sister relationship between *A. ventralis* of Hispaniola and *A. vittata* of Puerto Rico and their divergence time of ~ 0.67 Ma could be roughly matched with a period lower sea level (-100 m)

during MIS 16 (625 – 636 Ma), one of several 100 ka glacial cycles, during the middle Pleistocene. Meanwhile, due to the uncertainty in total flight distance potential for *Amazona*, periods of higher sea level such as the mPWP produced dispersion and pathway results that indicate dispersion from the mainland for amazons and the evolution of *A. agilis* and *A. collaria* on Jamaica likely was influenced by the inundation or exposure of the Nicaraguan Rise, between Central America and Jamaica, between the MG6 and M2 MIS periods. Previous studies such as Kolchanova et al. (2021) have made this inference for the Greater Antillean lineage and this study here verifies these previous ideas through using modified bathymetric raster data to consider changes in Caribbean geography and map out pathways using Network and Euclidean distance methods.

Applying a geographic perspective to a new parsimony matrix and tree for Greater Antillean amazons to compliment the molecular-based study by Kolchanova et al. (2021) by creating characters based on geography such as individual islands (for separate populations) and direction of dispersion, specifically west-to-east, lined up with this previous study and my own study's mapping of dispersion potential using network and Euclidean models designed from modified bathymetric raster datasets.

### **Lesser Antilles**

Dominica today is the farthest and northernmost island from South America in the Lesser Antilles with amazon parrots, with two endemic species (Forshaw 2006). Prehistorically, this was not the case because north of Dominica, the islands of Guadalupe and Montserrat once had populations of undescribed amazon species, according to fossils from archaeological sites. In addition, the islands of Antigua and Barbuda have yielded fossil remains representing extinct, undescribed species as well (Williams & Steadman 2001).

Using distance thresholds of 1500 km (Pennycuick 1989) and 500 km for potential dispersion according to Euclidean distance raster mapping and creation of network routes across the archipelago, amazons were capable of dispersing across the Lesser Antilles, based on the suitability of interisland distances, regardless of the modifications to eustatic sea level modeled in ArcGIS Pro herein. Based on these results, I agree with Williams & Steadman (2001) that many, if not all islands in the Lesser Antilles, at one point, had an endemic amazon species. However, given that the evolutionary history of Lesser Antillean amazons is still being developed and phylogenetically, Lesser Antillean amazons comprise a paraphyletic group and are not one another's closest living relative (Russello & Amato 2004), more phylogenetic work is needed for this lineage. To further complicate this, my Euclidean distance and network route mapping across the six MIS periods chosen for this study demonstrate that overwater dispersal from South America to the Lesser Antilles was highly suitable. These results may help explain the inference of Russello & Amato (2004) that Lesser Antillean amazons represent more than one colonization event across this chain of islands.

Using results from this study and those from Russello & Amato (2004), a parsimony matrix and tree were not produced for the Lesser Antillean amazons as they represent a paraphyletic group. Including undescribed fossil amazon taxa (Reis & Steadman 1999; Williams & Steadman 2001) was not an option as there is no molecular or morphologic phylogeny to use a basis for a matrix using geographic binning.

The decline in global biodiversity during the Holocene has handicapped a comprehensive understanding of pre-human biodiversity and biogeography and this is especially evident on islands (Oswald et al. 2021). The early Holocene or pre-Holocene fossil records from islands help paleontologists and biogeographers paint pictures of islands that supported higher amounts

of biodiversity before human impact. Among vertebrate taxa impacted the most by humans on islands, are birds (Steadman 1995). I concur with Williams & Steadman (2001) and infer, based on my determining potentially suitable times and pathways of dispersion for amazons in the Greater and Lesser Antilles, through GIS, that islands of both of these subregions of the West Indies each had distinct, endemic species of amazon parrots, that if not for a combination of climate change and human impact, would likely be still around today.

Given the dramatic climate changes during the Late Pliocene such as the mPWP or the M2 glaciation, events leading up to the Pleistocene glacial cycles and their resulting influence on eustatic sea level likely impacted distributions and dispersal of insular biotas as well. Molecular dating of migrations and diversification of amazon parrots has been correlated to known climatic and geologic events over the last five million years (Silva et al. 2014). Using molecular data, current phylogenies for Caribbean amazons and their divergence timing being linked to sea level rise and fall (Kolchanova et al. 2021) are a prime example of studying the influence of eustatic sea level on the biogeography of taxa. Retracing the evolution and dispersal history of insular taxa such as birds like amazon parrots of the Greater and Lesser Antilles using sea level changes helps to paint the picture that the biota we see on islands today are a fraction of what they sometimes once were, prior to the impacts of climate change and anthropogenic extinctions.

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Signature: Christopher James Kingwill 

Date: May 5th, 2023