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Qualities of Successful Invasions: Examples from the Great American Biotic Interchange

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QUALITIES OF SUCCESSFUL INVASIONS: EXAMPLES FROM THE GREAT AMERICAN BIOTIC INTERCHANGE

by

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ABSTRACT

A good understanding of the past can shed light on the patterns observed and mechanisms at work in the present day. As the climate continues to change in the present, we can look to the past to help determine how organisms might react to large scale habitat shifts. The Great American Biotic Interchange (GABI) is a past biotic interchange that can offer a unique perspective on dispersal. It occurred roughly 3 million years ago (MYA) when the continents of North and South America were first joined by the formation of the Isthmus of Panama. By looking at the body masses and diet compositions of the organisms living on these continents at this time we can find some patterns determining which organisms are more likely to invade and which are not. This was done by collecting data from Carrillo et al. (2020), The Paleobiology Database, and PHYLACINE_1.2, and running various t-tests and regression analyses. Invader masses were found to be higher at the start of the GABI and decreased as time went on. Also, invader masses tended to be higher than non-invaders. Analyses on diet data support observations in the literature that North American carnivores were highly successful in South America.

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INTRODUCTION

A good understanding of the past can shed light on the patterns observed and mechanisms at work in the present day. With the current climate upheaval and human mediated transport organisms, and entire ecosystems, are on the move. The patterns of these dispersals are sometimes difficult to parse out due to the presence of humans around the globe. Therefore, studying past biotic interchanges of organisms can help to separate human influences from the underlying mechanisms. The Great American Biotic Interchange (GABI) is one such past interchange that offers a unique perspective on dispersal. The GABI marks a period of time in which the flora and fauna of North America and South America were exchanged. The height of this exchange is typically cited as being around 3 million years ago, with the earliest invaders making the journey at 9 MYA. Many factors contributed to the initiation of this interchange including large scale geologic processes and changes in climate conditions. The wealth of data available on the species, climate, and the geologic processes involved makes the GABI an ideal event to study.

Geologic Setting

One of the main factors contributing to the initiation of the GABI was the formation of a connection between South America and North America through the emergence of the Isthmus of Panama. The emergence of the isthmus was synchronous with the closure of the Central American Seaway (CAS). This process started when the Caribbean plate collided with the South American plate between 67 and 39 MYA (Coates and Stallard 2013; Montes et al. 2015). The collision marked the start of the formation of a volcanic arc in the Central American Seaway that would later be uplifted to become the

Isthmus of Panama. An archipelago had emerged from the waters around 12 MYA. By 10 MYA there were no deep-water connections (deeper than 200m) between the Pacific Ocean and the Caribbean Sea (Bacon et al. 2016). Shallow marine connections probably lasted for millions of years after but have been difficult to trace in the sediment records (Molnar 2008; Woodburne 2010; Woodburne et al. 2006; Bacon et al. 2015). The Isthmus had likely completely emerged by 3 MYA. In other words, by 3 MYA there was a whole and dry land bridge connecting South America and North America (Cody et al. 2010; Vermeij 1991; Coates and Stallard 2013; Marshall 1988).

Although there have been many studies done to clarify the timing of the closure of the Central American Seaway and the formation of the Isthmus of Panama, there is still a lot of uncertainty. There is evidence that there was a river system connecting South America and Panama starting between 13 and 15 MYA, indicating at least a partial emergence of the isthmus by that time (Montes et al. 2015). Others suggest that emergence did not start until around 6 MYA (Woodburne 2010). Equally muddy is the exact timing of when the new land bridge was completely dry. There may have been a series of flooding events as sea levels fluctuated around 6 MYA (Woodburne 2010; Bacon et al. 2016). Some have also suggested that the land bridge was actually in place

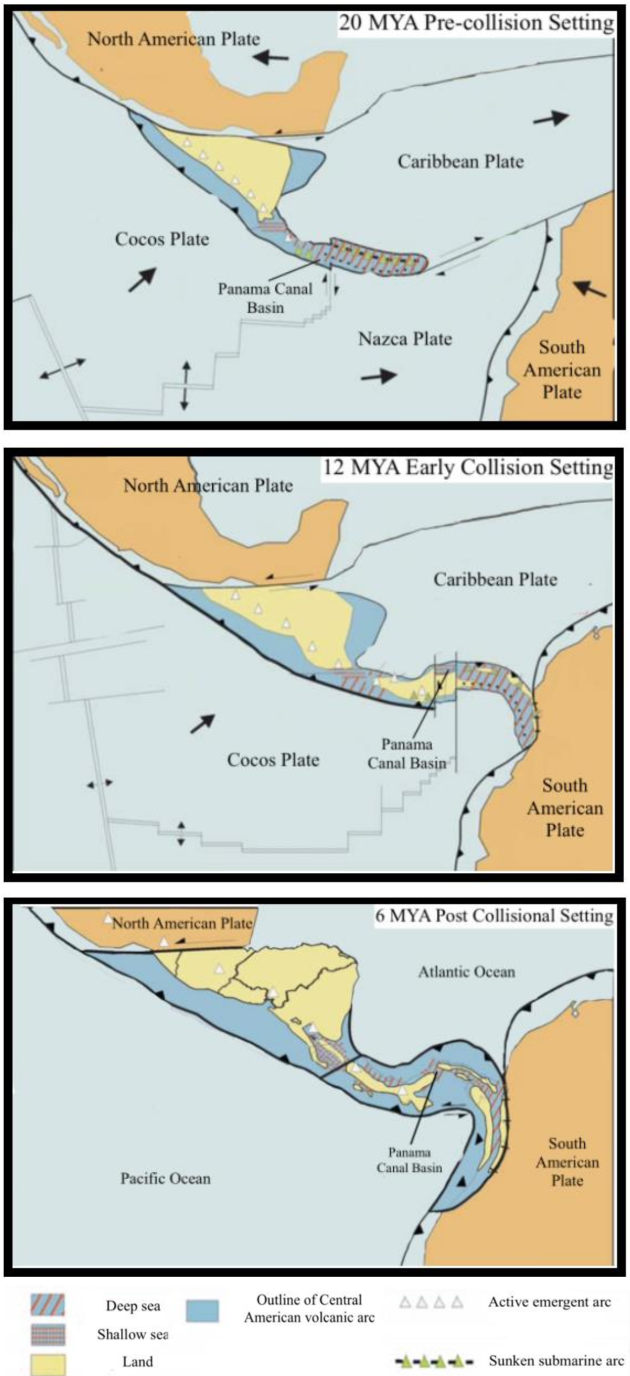


Figure 2. Map of the closure of the Isthmus of Panama showing one model of land mass positions at 20 MYA, 12 MYA, and 6 MYA. Figure adapted from Coates et al. (2004).

millions of years before the current scientific consensus of 3 MYA (Bacon et al. 2016; Coates and Stallard 2013).

The result of the complete emergence of the Isthmus and the closure of the CAS was the end of what has been called South America's "splendid isolation." It has been estimated that South America remained unconnected to any other continent for around 50 million years. While some dispute the duration of South Americas isolation, most agree that it contributed significantly to shaping the faunal assemblage present at the start of the GABI (Erkens 2015; Leigh et al. 2013; Webb 2006; Domingo et al. 2020).

Climatic Setting

The timing of the closure of the CAS has been linked to several changes in earth's climate system. One of which is the reorganization of global ocean circulation around 3.2 MYA (Bacon et al. 2015; Montes at al. 2015; Webb 2006). Around this time there was an intensification of North Atlantic thermohaline circulation, possibly due to the elimination of a mid-latitude oceanic connection between the Pacific and Atlantic Oceans through the CAS (Bartoli et al. 2005; Domingo et al; 2020). One theory suggests that the pre-closure connection between oceans allowed for colder, less salty Pacific waters to enter the Atlantic and dilute the poleward transport of salt. When the CAS closed, the waters moving poleward in the Atlantic remained saltier and warmer. This created a larger density difference in water masses, and enhanced global thermohaline circulation. At the same time, evaporation of these warmer waters increased near the poles, feeding the expansion of ice and inducing northern hemisphere glaciation (Bartoli et al. 2005; Webb 2006). Although there is a well-established correlation between the closure of the CAS and the reorganization of ocean circulation and the initiation of glaciations, some warn that this does not actually indicate causality (Molnar 2008).

The glaciations did, however, have a strong effect on the GABI. The increased reflectivity (albedo) resulting from the expansion of ice sheets acted to further cool the northern hemisphere. This changed the heat distribution in the oceans, which shifted the Intertropical Convergence Zone (ITCZ) southward. The ITCZ is a band of precipitation that wraps around the globe roughly along the equator. It shifts seasonally, as well as with long term climate changes, like glaciations (Chiang et al, 2003). The effects of a southern shift in the ITCZ are to reduce rainfall in the tropics above the equator allowing the formation of a more arid savanna habitat (Bacon et al. 2016).

In regard to the GABI this means that significant portions of habitat along the Isthmus of Panama became up to 6 °C cooler and more arid during glaciations and reverted back to warm, wet rainforest during interglacial time periods (Figure 1.) (Molnar 2008; Woodburne 2010; Woodburne et al. 2006; Bacon et al. 2016; Domingo et al. 2020; Marshall 1988). This process served to create a "corridor" of savanna habitat connecting pre-existing savanna in North and South America (Leigh et al. 2013). This means that during glacial time periods the dispersal of savanna adapted organisms between continents was favored. However, during interglacial time periods the formation of rainforest in Central America acted as a barrier to dispersal between North and South America (Woodburne et al. 2006; Bacon et al. 2015; Marshall 1988; Leigh et al. 2013).

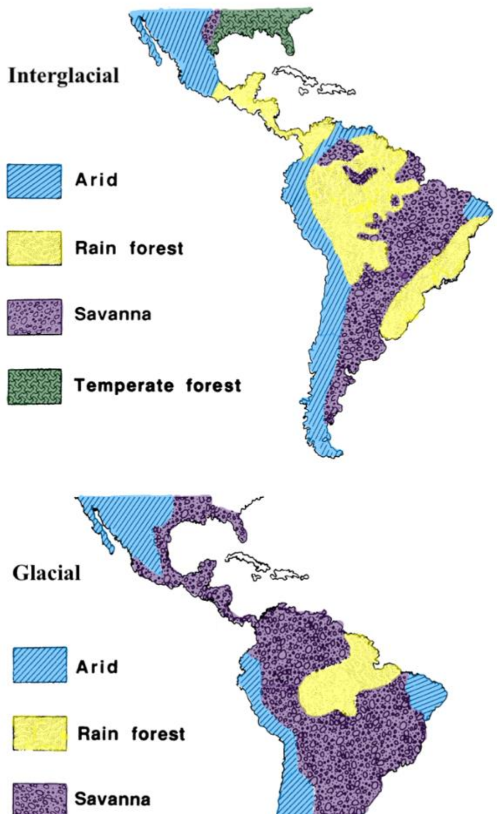


Figure 2. Coverage of arid, rain forest, savanna, and temperate forest habitat during both interglacial and glacial time periods. Rain forest habitat prevents organisms from dispersing during interglacials. Increased savanna habitat during glacial time periods serve to connect South and North America. Adapted from Webb 1991.

On top of this, lowered sea levels due to water being locked up in ice may have increased the width of the isthmus significantly. During these glaciations, sea levels may have dropped anywhere from 50-100 meters (Bacon et al. 2016; Marshall 1988; Molnar

2008). The increased width of the isthmus paired with the creation of savanna habitat has been claimed to be one of the main instigators of the GABI (Woodburne 2010; Bacon et al. 2015; Marshall 1988).

The GABI: An Overview

There were four main waves of the GABI, often labeled "pulses." The first was between 2.6 and 2.4 MYA, the second was 1.8 MYA, the third was between 1 and 0.8 MYA, and the fourth was 0.125 MYA (Woodburne 2010). During these time periods there was an increase in the number of organisms invading across the American continents. As mentioned above, these waves were not random, they were likely linked to climate changes and the expansion of savanna habitat. As a result of this, most of the mammals that participated in the GABI were savanna adapted (Woodburne et al. 2006; Bacon et al. 2016; Marshall 1988; Molnar 2008).

The first mammals to make the crossing between North and South America likely did so before the land bridge was fully formed and have been referred to as "heralds" of the GABI (Woodburne 2010; Webb 2006). Most organisms probably did this by swimming between the islands of the forming volcanic arc in a process called island hopping. Others may have been swept offshore while clinging to debris, floating with the currents until they reached land (Coates and Stallard 2013). The first organisms to become invaders were mostly native to South America. These invaders include three genera of giant ground sloths who crossed around 9 MYA: *Megalonyx*, *Pliometanastes*, and *Thinobastides*. Some of the first North American families to move south were representatives of a family of small omnivores including raccoons who crossed around 7.5 MYA (*Procyonidae*), and Sigmodontine rodents who crossed around 6 MYA

(Woodburne 2010; Bacon et al. 2016; Webb 2006; Marshall 1988; Coates and Stallard 2013).

At first, the GABI was fairly symmetrical; roughly the same number of organisms that invaded North America also invaded South America. Over time though, more and more invaders originated from North America and moved south (Webb 2006; Vermeij 1991). Some examples of organisms that invaded South America include: *Smilodon fatalis* the saber-toothed cat, *Panthera atrox* the American lion, *Canis dirus* the dire wolf, and several other species of llamas, bears, horses, tapirs, gomphotheres, cats, and rodents (Baskin and Thomas 2007; Woodburne et al. 2006). Examples of mammals that invaded North America include porcupines, possums, armadillos, giant ground sloths, bats, and capybaras (Webb 2006; Woodburne et al. 2006). Of these, only possums, porcupines, and some giant ground sloths made it north of 50°N (Leigh et al. 2013). In total, representatives from 19 families moved north and 17 families moved south (Leigh et al. 2013; Bacon et al. 2016; Coates and Stallard 2013).

Today, about 50% of the mammalian genera living in South America are descendants of North American invaders from the GABI. In contrast, only about 10% of the living genera in North America, excluding Central America, are descended from South American invaders (Carrillo et al. 2020; Marshall 1988; Webb 2006). While some of the differences in these percentages can be assigned to the asymmetry of the interchange itself, there is another contributing factor. North American invaders in South America were more successful than South American invaders in North America. North American invaders underwent more radiations and were able to exploit more niches than their South American counterparts (Webb 2006; Vermeij 1991; Carrillo et al. 2020).

The explanation for different success rates between organisms from different continents has to do with South America's "splendid isolation". While South America was isolated, North America had been intermittently connected with Eurasia. These connections had allowed for frequent interchange between these two large land masses. As a consequence, the organisms present in North America at the time of the GABI had managed to withstand multiple invasions, and thus multiple attempts at being out competed. On the other hand, South American organisms had not been exposed to as many invasions and were highly vulnerable to competition. This led to a large number of extinctions in South America at the start of the interchange (Leigh et al. 2013; Webb 2006; Carrillo et al. 2020; Domingo et al. 2020). On top of that, some have suggested that the mammals present in South America at the start of the GABI had not managed to radiate and fill all the niches available. This implies that there were empty niches that North American invaders could fill right away, with little to no competition (Webb 2006).

In order for successful invasion an organism needs to accomplish three things, they need transport to the area they are invading, they need to find a niche that can support them, and they need to reproduce and increase their population numbers (Carrillo et al. 2020). Part of the success of the North American invaders has been linked to their diet. Of the invaders, most had broad dietary requirements, enabling them to find food wherever they went (Domingo et al. 2020). Another part of their success may be attributed to the enemy-release hypothesis, which suggests that invading organisms leave behind their predators, competitors, parasites, and diseases (Carrillo et al. 2020). This would help to increase the health and decrease mortality of a population.

Another factor potentially affecting the success and radiation of invading organisms includes what has been termed a “holding pen”. This refers to a scenario seen repeatedly in the fossil record; invading organisms seem to get stuck in Central America for up to 1.5 million years before making it to the other continent, if they ever arrive at all. Some have suggested that this time spent in Central America stimulated certain species to undergo radiation. Since researchers have not yet been able to find what caused these delayed dispersals, it is worth noting that it could just be the result of an incomplete fossil record (Woodburne 2010; Woodburne et al. 2006).

Most of what we know about the GABI comes from the fossil record. There is always a danger in relying on one source too heavily to make assumptions and draw conclusions. Therefore, it is necessary to note that the fossil record is incomplete. While many researchers have put in time establishing biostratigraphic records for locations throughout the Americas, there are still significant gaps in time, space, and species representation. This is important to keep in mind moving forward since the data used in this study is composed purely from the fossil record.

There are many things we still do not know about the GABI. What is the exact chronology of events leading up to and during the GABI? How much of an impact did the full formation of the Isthmus of Panama have on invading organisms? Why did some organisms invade and not others? What caused the asymmetry in the GABI? What caused North American invaders to be more successful and radiate when South American invaders did not? How did the invasion affect extinctions and how did extinctions affect the invasion? How did invading organisms affect native community structures? Scientists have been working for many years to answer these questions (Webb 1991; Vermeij 1991;

Woodburne 2010; Cody et al. 2010; Domingo et al. 2020; Bacon et al. 2015; Leigh et al. 2013).

This study attempts to determine what body mass and diet can tell us about the organisms that invaded versus those that did not invade in the GABI. Past studies have mostly focused on family level relationships. Here we focus on genus level relationships to try and find more precise patterns between populations and observations from the fossil record. By examining life history traits, we aim to determine long term population dynamics that could be applicable to more scenarios than just the GABI (McGill et al. 2006). This is especially important in a modern context as attempts are being made to understand and predict future species movements. However, we need to keep in mind that past interchanges are not perfectly analogous to interchanges today. The presence of humans has altered the geographic extent, number of species involved, and speed of the invasion process (Ricciardi 2007).

METHODS

Data Collection

Data on the participants in the GABI was taken from the supplemental material in Carrillo et al. (2020) and converted into an Excel spreadsheet. Columns with irrelevant data were deleted. In order to incorporate all known mammals living in the Americas more species data was incorporated from the Paleobiology Database (PBDB Database). This data includes mammals from both South and North America between 0 and 10 MYA. Lastly, mass and diet data were downloaded from PHYLACINE_1.2 (Table 1.)(Faurby et al. 2018; Faurby et al. 2020).

Carrillo et al. (2020)	**Paleobiology Database**	**PHYLACINE_1.2**
Family Name Matched Name Matched Rank Early Interval Early and Late Age Genus Name Species Resolution Order Name Latitude and Longitude Country Code (cc) Continent Biome Label	*All North American Mammals between 0-10MYA*: Accepted Name Max and Min age *All South American Mammals between 0-10MYA*: Accepted Name Max and Min age	Mass Data Diet Data

Table 1. Shows data columns used from each source: Carrillo et al. (2020), The Paleobiology Database, and PHYLACINE_1.2.

From here, species in the data with no mass or diet data were removed. Also, duplicates with identical data for species name, continent specimen was found on, continent of origin, and early and late time estimates were removed. This was done because the mass of a given species, and the timing of when they were found on a continent, were the important pieces of data for this study. If the duplicates were kept, the mass and the time of fossil occurrences would not change. This was also an effort to simplify the data and to avoid double counting single events. Next, a random time of occurrence was selected for each species between their respective early and late ages. This was done in order to have an exact time for analyses rather than an age range for use in statistical methods. The data was then searched for any marine species, with 111 being identified. These were deleted in order to ensure results focused on terrestrial faunal exchange.

Before data analysis the data was grouped into species that invaded and those that did not invade. To avoid individuals being falsely categorized the data was sorted in a way that if any individual of a native species was documented on the opposing continent, then all individuals of that species were classified as invaders. This was done using R. The final datasheet had 2460 rows of fossil occurrence data that were analyzed.

Data Analysis

The analysis of the data was done using Excel. A regression analysis and ANOVA were run on the log of the invaders mass versus the time of their invasion. This was done to see if the trendline fit to this data was significant. A two-sample t test assuming unequal variance was run to test the significance in the difference of mass means between invaders and non-invaders. Multiple t-tests were run to test the significance between the means of categories of diet data (e.g., invader and non-invader percent plant diet, or North American invaders and South American non-invaders percent invertebrate diet; See Figure 5.).

RESULTS

Results show that the mass of invaders decreased through time (Figure 3) (regression test $R^2 = 0.0292$, $p < 7.19E-5$, with slope = -0.1645). The mean log mass of invaders was higher than the mean log mass of non-invaders (Figure 4.) (t-test $p < 1.73E-117$). The average log mass for invaders is around 5.1, while the average log mass for non-invaders is around 3.3. In t-tests, non-invaders were less likely to consume plants and vertebrates than invaders and were more likely to consume invertebrates ($p < 2.29e-05$ for percent plant diet, $p < 0.00035$ for percent vertebrate diet, and $p < 4.05e-56$ for percent invertebrate diet) (Figure 5.A) There was no significant difference between North American and South American invaders diet ($p < 0.0565$ for percent plant diet, $p < 0.0709$ for percent

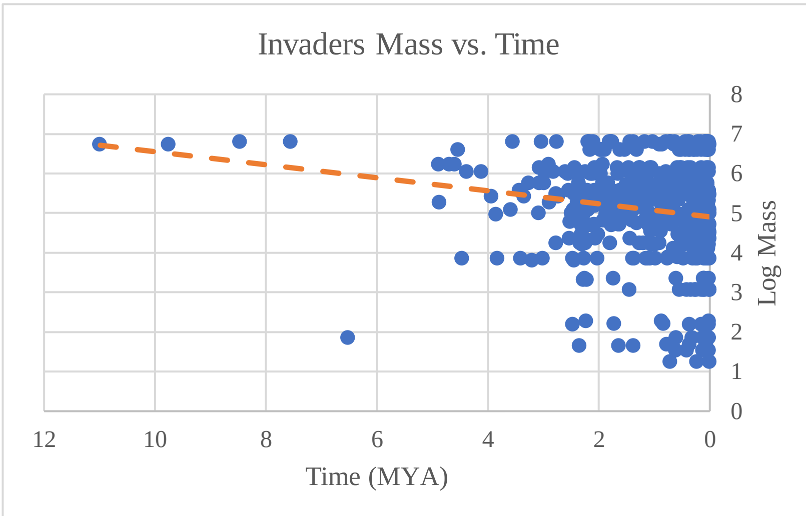


Figure 3. Log of invaders mass is plotted against time of invaders arrival on opposing continent. The equation for the trendline is y = -0.1645x + 4.9055.

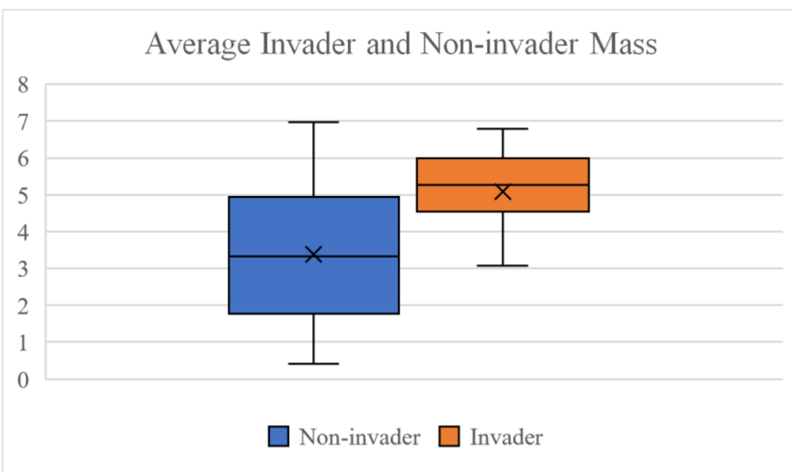
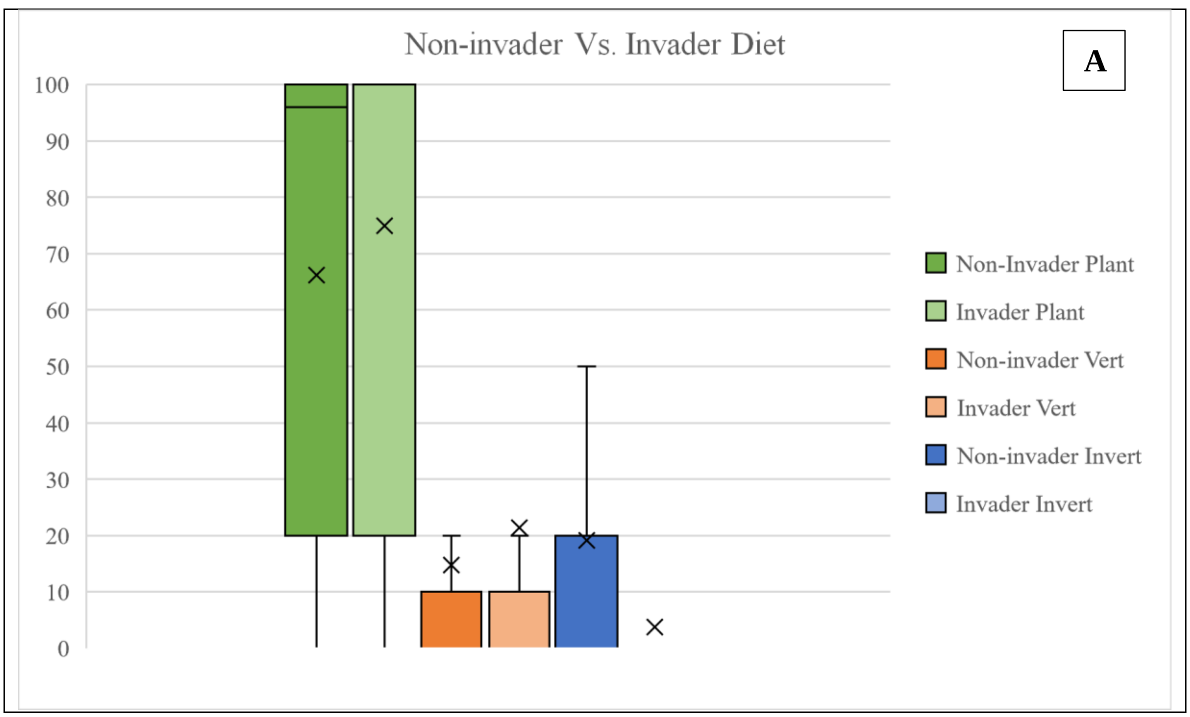
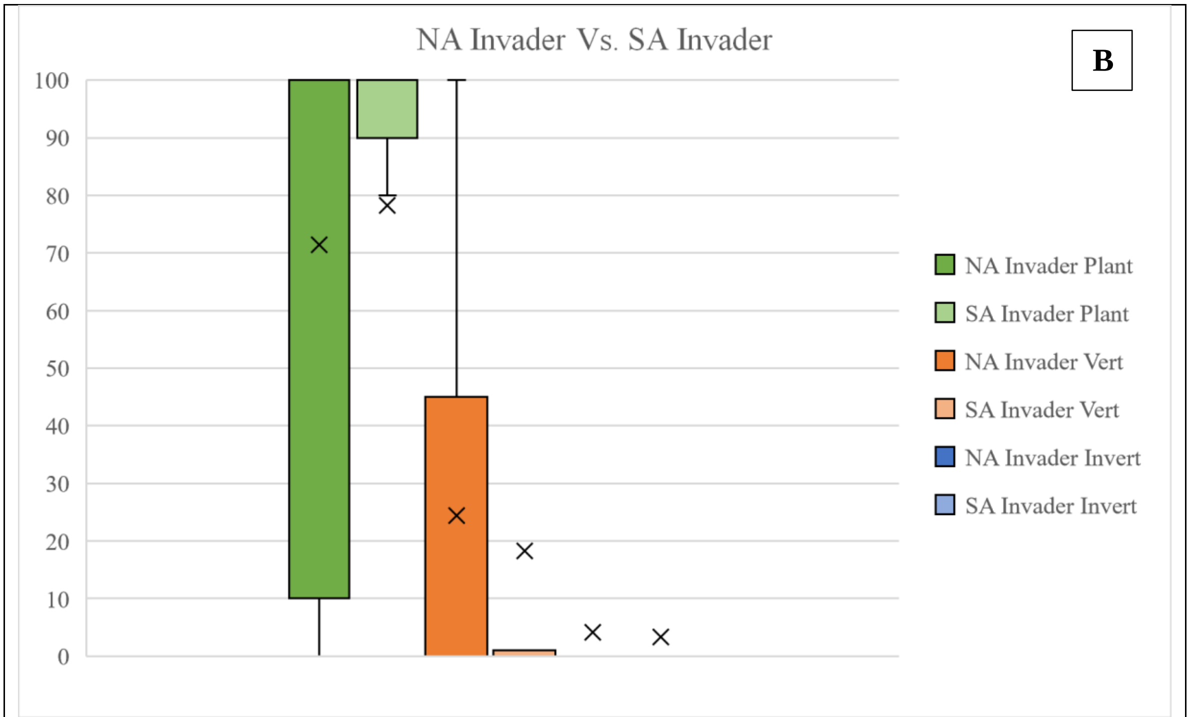
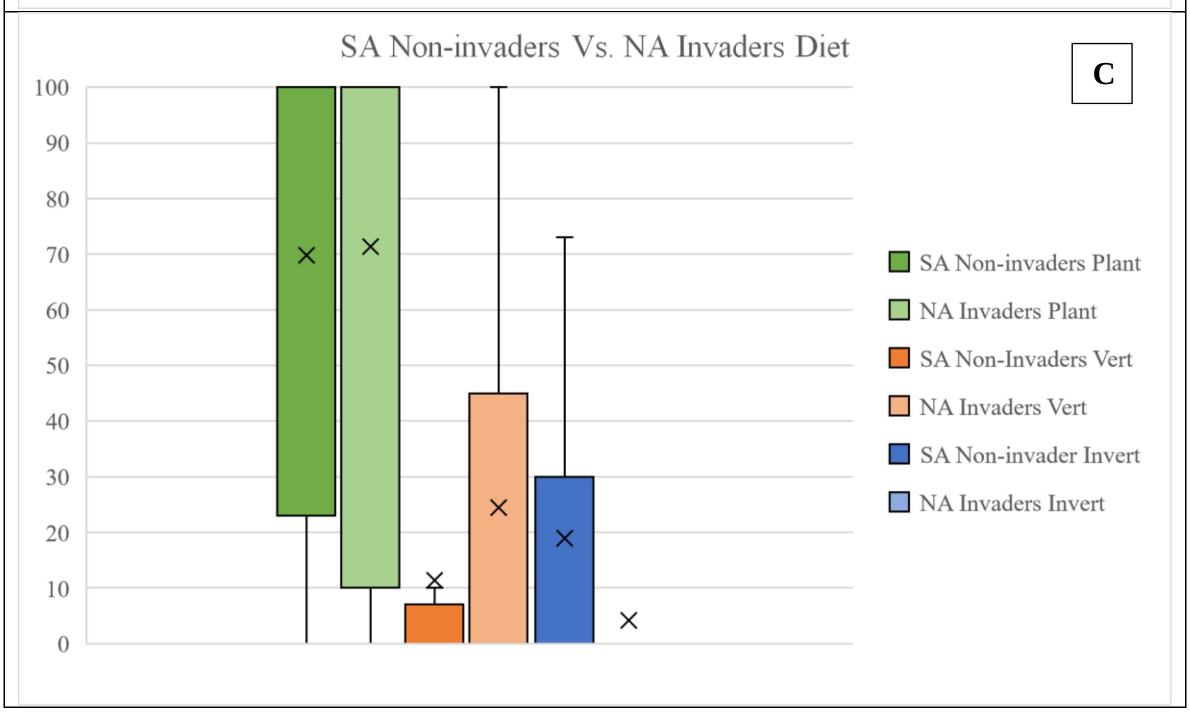


Figure 4. Box and whisker plot of the log of non-invader and invader masses. Averages are marked by the X.

vertebrate diet, and $p < 0.5327$ for percent invertebrate diet) (Figure 5. B). North American invaders were equally likely to consume plants, more likely to consume vertebrates, and less likely to consume invertebrates than South American non-invaders ($p < 0.6112$ for percent plant diet, $p < 2.79e-06$ for percent vertebrate diet, and $p < 4.02e-18$ for percent invertebrate diet) (Figure 5.C). South American invaders were more likely to consume plants, equally likely to consume vertebrates, and less likely to consume invertebrates than North American non-invaders. ($p < 7.11e-07$ for percent plant diet, $p < 0.2387$ for percent vertebrate diet, and $p < 1.57e-38$ for percent invertebrate diet) (Figure 5.D).




NA Invader Vs. SA Invader
B
100
90
80
70
60
50
40
30
20
10
0
NA Invader Plant
SA Invader Plant
NA Invader Vert
SA Invader Vert
NA Invader Invert
SA Invader Invert


SA Non-invaders Vs. NA Invaders Diet
C
100
90
80
70
60
50
40
30
20
10
0
SA Non-invaders Plant
NA Invaders Plant
SA Non-Invaders Vert
NA Invaders Vert
SA Non-invader Invert
NA Invaders Invert

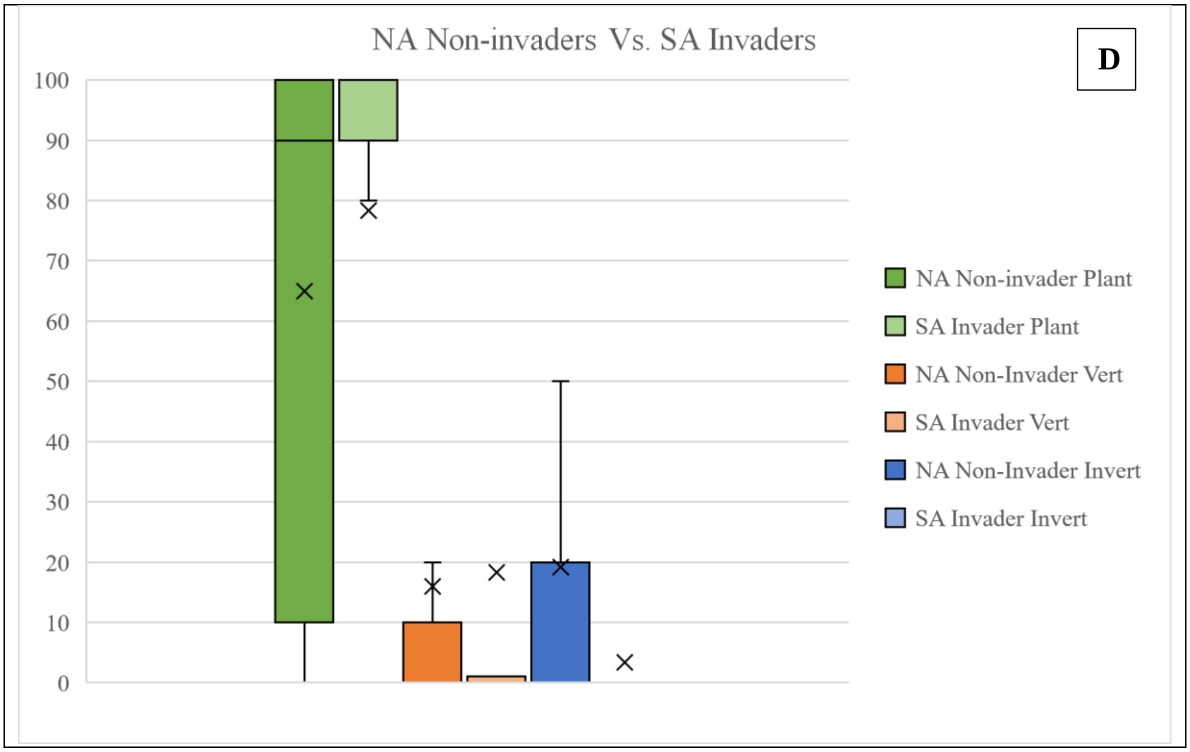


Figure 5. Four plots of different percent composition diet data of invaders and non-invaders from both contients. Averages are marked by the X. a) compares non-invader and invader percent diet compositions b) compares North American invader and South American invader percent diet compositions c) compares South American non-invaders and North American invaders percent diet composotion and d) compares North Amercian non-invaders and South American invaders percent diet composition.

DISCUSSION

Body mass was found to decrease significantly through time. However, the amount of variance explained was low and the results depended heavily on a few outlier points. The results overall suggest that the early invaders were large-bodied mammals, and as the GABI progressed more and more small mammals joined the invasion (Figure 3.). This is likely since larger mammals can disperse longer distances without food by storing energy and having a slower metabolism. This is supported by Debeffe et al. (2012) who concluded that larger organisms are able to disperse earlier and further. On the other hand, smaller mammals could more easily catch a ride on some floating debris. They require less food to sustain themselves for longer time periods. Even if the debris had limited resources, it might be enough for a small mammal to survive until land fall. One reason evidence for this is not seen in the data could be that there may have been strong currents sweeping debris away from land. Or there may have been a lack of large enough debris to support even small mammals, or a limited availability of freshwater. Lastly, in order for a species to successfully establish themselves on a new land, enough individuals need to disperse that the species as a whole can find mates, reproduce, and survive to increase the population numbers. So, even if debris and current conditions were ideal for an individual's dispersal, it would have to occur multiple times in the reproductive life span of many individuals in order for the species as a whole to disperse.

There are 5 different occurrences before 6 MYA. The two oldest occurrences at 10.9 MYA and 9.8 MYA both belong to the species *Notiomastodon platensis* with log masses at 6.74. The next two occurrences at 8.5 and 7.5 MYA are *Megatherium Americanum* and *Cuvieronius tropicus* respectively, both with log masses of 6.8. The last of these outliers is *Reithrodon auratus* at 6.52 MYA with a log mass of 1.85. Of these occurrences three are gomphotheres (*Notiomastodon* and *Cuvieronius*), one is a giant ground sloth (*Megatherium*), and the last is a rodent (*Reithrodon*). Of these, only *Cuvieronius* is endemic to North America, the others are endemic to South America. It is interesting that this data shows *Notiomastodon* arriving in North America before *Cuvieronius* arrived in South America. According to Lucas (2013) *Cuvieronius* dispersed to South America and then gave rise to *Notiomastodon*. The discrepancies seen here most likely reflect a combination of incomplete fossil record and gaps in data available in the databases this data was pulled from.

The average mass of all invaders was higher than the average mass of all non-invaders (Figure 4.). As in the regression, this shows that organisms with larger body mass sizes were more likely to participate in the GABI than organisms with smaller body mass sizes. While this may just show that organisms participating in the GABI were larger, Jenkins et al (2007) show that larger organisms worldwide tend to disperse further than smaller organisms. On the other hand, Forsyth et al (2004) show that successful human mediated invaders in Australia have all been smaller in size. This may indicate a shift in average body size of invaders due to human influence.

There was a higher proportion of invaders with plant-based diets than non-invaders. The average proportion of plants in invader diets is 75%, and the average for non-invaders is around 66%. There was also a higher proportion of invaders with vertebrate based diets than non-invaders. The average proportion of vertebrates in invader diets is around 22%, and the average for non-invaders is around 16%. Lastly, there is a lower proportion of invaders with invertebrate based diets than non-invaders. The average proportion of invertebrates in invader diets is less than 5%, and for non-invaders it is around 19%. From this we can conclude that invaders are slightly more likely to consume plants or vertebrates, and less likely to consume invertebrates than non-invaders (Figure 5.A).

There are no differences between the diets of invaders from South America and the diets of invaders from North America. The average proportion of plants in their diets was around 75%, the average proportion of vertebrates in their diet was around 20%, and the average proportion of invertebrates in their diets was less than 5% (Figure 5.B). This is interesting since South American mammals had been separated from other fauna for millions of years, yet the organisms that succeeded in invading had very similar diet ranges to the invaders from North America. So, although they had been in isolation for a long time, some South American organisms retained qualities useful for successful invasions. This is also interesting since the literature mentions that most invaders were savanna adapted due to that being the predominant habitat connecting the two continents. So, these results could be interpreted to support this hypothesis since supposedly savanna organisms on different continents still have similar diet compositions. However, the literature also mentions that most rainforest mammals that invaded North America were South American in origin. Overall, this data does not account for more fine scale diet analyses; for example, a savanna herbivore and rainforest herbivore are treated exactly the same in these analyses. If habitat was also considered, more definitive conclusions might be able to be made.

The average number of South American non-invader and North American invader plant consumers are the same, while the average numbers of vertebrate and invertebrate consumers are different. The average proportion of plants in the diet of these mammals was around 70%. There was a higher proportion of North American invaders that were vertebrate consumers than South American non-invaders. The proportion of vertebrates in invaders diet is around 25%, while the proportion of vertebrates in non-invaders diet is a little over 10%. There was a lower proportion of North American invaders that were invertebrate consumers than South American non-invaders. The proportion of invertebrates in invaders diet is less than 5%, while the proportion of invertebrates in non-invaders diet is almost 20% (Figure 5. C). From these interpretations we can conclude that North American invaders were more likely to depend on plants or vertebrates for their diet, with a higher proportion of invaders depending on plants. It also supports what is found in the literature that there was a higher proportion of successful North American carnivores in South America than there were successful native South American carnivores.

The average number of South American invader and North American non-invader vertebrate consumers are the same, while the average number of plant and invertebrate consumers are different. The average proportion of vertebrates in the diets of both groups is around 18%. There was a higher proportion of South American invaders that were plant consumers than North American non-invaders. The average proportion of plants in South American invaders diet is around 79%, while the average proportion of plants in North American non-invaders diet is 65%. There was a lower proportion of South American invaders that were invertebrate consumers than North American non-invaders. The average proportion of invertebrates in South American invaders diet is less than 5%, and the average proportion of invertebrates in North American non-invaders diet is 20%

(Figure 5.D). Overall, South American mammals who invaded North America were most likely to depend on herbivory for a major portion of their diet.

These observations of the GABI can be compared to observations of modern invasions to advance our knowledge of how biological invasions work. Comparisons can also help to determine the impact of human presence on interchange and allow for more accurate predictions of the future. This study found that on average during the GABI organisms with larger body masses invaded, and of these the largest ones invaded first. However, Clout and Russell (2008) show that in modern invasions smaller organisms tend to invade. These authors also found that modern invaders tend to be carnivores or omnivores. In contrast, results from the GABI indicate that invaders were more likely to consume vertebrates and plants, implying that herbivory was also important in past invaders diets. Lastly, one of the most obvious differences is the lack of a human presence during the GABI. Many sources state that invader success today is strongly influenced by organisms having an association with humans (Jeschke and Strayer 2006; Novillo and Ojeda 2008).

CONCLUSIONS

The purpose of this research was to find any patterns defining invaders and non-invaders in the GABI. Body mass analyses indicated that the average mass of invaders decreased through time. Also, organisms with larger body mass sizes were more likely to participate in the GABI than organisms with smaller body mass sizes. These results support data in the literature that suggests larger organisms are more likely to disperse earlier and further than smaller organisms.

Analyses of diet data showed more scattered results. Invaders were slightly more likely to consume either plants or vertebrates, and less likely to consume invertebrates than non-invaders. There were no differences between the diets of invaders from South America and the diets of invaders from North America. There was a higher proportion of North American invaders that consumed vertebrates than South American non-invaders. Lastly, South American invaders were most likely to depend on plants for a major portion of their diet than North American non-invaders. Overall, these results suggest that successful invaders tend to eat plants and vertebrates over invertebrates. More North American invaders ate vertebrates, which likely reflects the success of North American carnivores in South America.

The results of this study support what is found in the literature and help to build on what is known about large scale species invasion events. As more is learned about the past, we can begin to more accurately predict how and why species may move in the future. Keeping in mind the key differences between present day invasions and ones seen in the fossil record will be important when making these predictions.

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Emily M. Jackson was born in Portland, Maine on January 15th, 1999. She was raised in Otisfield, Maine by her parents Richard and Shirley Jackson. While growing up on the family's small rural farm Emily enjoyed raising chickens for both eggs and meat, turkeys, pigs, bees, and working in the vegetable and herb gardens. She currently has two cats named Mister and Pussywillow, a bunny named Rascal, and a goldfish named Font. For fun, Emily enjoys getting outside, ice skating, reading, and painting.

After graduating from Oxford Hills Comprehensive High School, Emily went to the University of Maine to major in biology, minor in earth science, and be a member of the Honors College. After graduation she plans on taking a gap year, then attending graduate school abroad. From there she is possibly planning on going into research, but is still unsure about where the future may take her.