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INTO THE TROPICS: A QUANTITATIVE STUDY OF MAMMALS IN THE GREAT AMERICAN BIOTIC INTERCHANGE

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INTO THE TROPICS: A QUANTITATIVE STUDY OF MAMMALS IN THE GREAT AMERICAN BIOTIC INTERCHANGE

BY

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THESIS

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Into the Tropics: A quantitative study of mammals in the Great American Biotic Interchange

by

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Abstract

For almost 100 million years, North and South America were isolated from each other. This long period of geologic separation led to the evolution of strikingly different mammalian faunas: marsupials were prevalent in South America, while ecosystems in North America were composed of placental mammals. Roughly 3 Mya, a land bridge formed between the two continents leading to an accelerated exchange of mammalian fauna. The Great American Biotic Interchange (or GABI, as this has come to be called,) led to the successful colonization of many North American species, but few South American species. The highly asymmetrical nature of the faunal exchange has puzzled paleontologists for more than a century. We examined the GABI using an End-Pleistocene dataset of non-volant mammals and their associated ecological characteristics. We employed classification trees to quantify the relative importance of traits that led to successful colonization. Our analysis suggests the most important factor was body size. For species originating in North America, small body size was beneficial,

but the pattern was reversed for those moving north from South America. We believe this morphological asymmetry was due to the different climate regimes present in North and South America. We propose an "Into the Tropics" model of colonization for taxa that follow Bergmann's Rule. We find that dietary and environmental niche, or mode of birth (placental vs marsupial) were less important than suggested by previous studies. Our study strongly supports the role of climate in determining the composition of mammal communities.

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Introduction

The biogeographic and geological history of South America has led to a unique mammal community. Today, the Neotropics stretch from Tierra del Fuego to Mexico and Florida, where they transition to the Nearctic region with many shared flora and fauna. However, these ecoregion borders are recent phenomena. When Pangaea broke up in the Jurassic, what is now South America was part of Gondwanaland, a supercontinent that also included Africa, Australia, Antarctica, and the Indian subcontinent. Though mammals are a uncommon in the fossil record from this time, we know that, in the early Cenozoic, marsupials dominated the mammal fauna in Gondwanaland, while placental mammals had established in Laurasia (1). In South America, marsupial mammals, xenarthrans, and unusual placental ungulates continued to thrive into the Cenozoic alongside primates and caviomorph rodents that arrived sometime in the Eocene (2–4). Other than this incursion, the South American mammal fauna was remarkably isolated. Finally, some ~3 million years ago (Mya), the South American mammal fauna was greatly altered by connection with North America, in an event known as the Great American Biotic Interchange (GABI).

The biogeographic history of North America was quite different. Where South America was essentially an island for millions of years, North America was repeatedly interconnected with other land masses. Even after the breakup of Laurasia, North America was periodically connected with Asia via the Bering Land Bridge, allowing intermittent exchange between the mammal communities of the two continents (5–7). This lack of isolation meant the North American fauna was more cosmopolitan, and perhaps more competitive, than that of South America (5). The North American

mammals included proboscidians, true ungulates, carnivorans, insectivores, lagomorphs, and diverse rodent groups. Many mammals that are currently extinct in North America, such as camelids, were flourishing there in the Pliocene. Others, such as primates, became locally extinct in North America long before the GABI (5).

The GABI occurred after the Isthmus of Panama connected North America to South America. The Caribbean plate carried much of what is now known as Central America eastward between North America and South America, eventually causing collision of the three land masses. Simultaneously, volcanic activity in Central America caused islands and finally a land bridge to form in what is now Panama. The timing of these events is still debated. Recent geological studies (8–10) suggest a land connection between North and South America was in place as early as 15 Mya. Biostratigraphic work on terrestrial mammals (11, 12) as well as marine invertebrates (13, 14) indicates that the connection between the Atlantic and Pacific Oceans was at least intermittently present until roughly 3 Mya. I will use 3 Mya as the date the Isthmus of Panama permanently formed for the purposes of this paper, but this may need to be revised in future work. Once the continents of North and South America connected, plants and animals could move between the two continents. Once in the new region, a species could either die out, or thrive. Colonization is the process of dispersing to a new region, establishing there, and surviving. Some colonizer species may have speciated, while others maintained relatively low levels of diversity. For the purposes of this paper, we consider Central America as part of North America, because these two landmasses were in contact before the Isthmus of Panama formed. Therefore, South American mammals that colonized Central America were successful colonizers.

It has long been noted that mammal species from North America were apparently much more successful at colonizing South America than vice versa (5).These range expansions and dispersals began around 8 Mya with early dispersers such as ground sloths, and continued into the Pleistocene with animals such as canid carnivores (7, 12). North American groups that successfully colonized South America during this time include Proboscideans, Artiodactyls, Perrisodactyls, Carnivorans, and a truly stunning array of rodent groups. Conversely, only a few marsupials, primates, Xenarthrans, and rodents colonized North America from South America (7). The reasons behind this pattern have been sought after for nearly a century, but are still debated.

Table 1: Hypotheses that have been proposed to explain colonization patterns of mammals during the GABI. We used the variables listed to test these hypotheses. The relative importance of each variable in the trees will indicate which hypotheses are most relevant.

	Hypothesis	Citation	Predictor Variables
I	Phylogenetic Superiority	Simpson 1980, Webb 1985	Order, Origin (North America)
II	Placental Superiority	Lillegraven 1974, but see Hamilton et al. 2010	Birth (placental)
III	Lack of South American carnivores	Patterson and Pascual 1968, Marshall 1988, Vermeij 1991	Trophic group (meat and plant-Dominant Omnivores)
IV	Lack of South American small mammals	This study	Mass (small size advantage), Order (Rodentia)
V	Grassland vs. Forest corridors	Webb 1991	South America: Lifestyle (arboreal), Trophic (browser, frugivore). North America: Lifestyle (terrestrial), Trophic (grazer)
VI	Habitat Theory	Vrba 1993	South America: Diet Generality. North America: Lifestyle (terrestrial), Trophic (grazer)
VII	Climate Hypothesis	This study	South America: Mass (large size advantage). North America: (small size advantage)
VIII	Generalists	This study	Diet Generality
IX	Dispersal Ability, Range Size	This study	Mass (large size advantage)
X	Speciation Capacity	This study and Maurer, pers. comm.	Species per Genus
XI	Flexibility of Body Plan	This study and Maurer, pers. comm.	Genera per Family, Log Mass Range
XII	Fast Life History	This study	Mass (small size advantage)

There are a myriad of hypotheses that have been proposed to explain the asymmetry of the GABI (Table 1). Some have been based on the evolutionary history of New World mammals. G. G. Simpson proposed that North American mammals had a competitive advantage over those from South America, because the North American fauna had been enriched by immigration from and competition with mammals from Eurasia (Hypothesis I). When the North American fauna moved south, their greater fitness allowed them to competitively exclude South American mammals. This is now known as the "phylogenetic superiority" hypothesis (5, 7, 15). However, it appears some South American lineages, such as the Notoungulata, were already going extinct when the GABI occurred, possibly due to climate change caused by the gradual formation of the Andes (2, 11, 16). This may have made South American ecosystems even more vulnerable to colonization (17). A related but distinct hypothesis, Hypothesis II, is that placental mammals are more energetically efficient than marsupials (15, 18). This is based on the assumption that marsupials are more primitive and less adapted than placental mammals. Marsupials do have lower metabolic rates than placentals – they use 77% less energy than a placental mammal of the same body size (19), and have an average body temperature 2-3 °C lower than a similar placental mammal (20). Some have interpreted this to mean lower reproductive output in marsupials, but, in fact, marsupial reproduction has been shown to be as energy efficient as placental reproduction, and it may be advantageous under certain conditions (21, 22). It has also been suggested that there were few South American mammalian carnivores before the GABI, so the South American small mammals were naive to predators (Hypothesis III). When North American carnivores arrived in South America, the resident mammals were

easy prey, while the more savvy North American mammals evaded predation (2, 7). Since the fossil record in South America is less resolved than that of North America, especially in the smaller body size classes, this hypothesis has been difficult to evaluate. We hypothesize that South America may have had few small mammals filling small body size niches (Hypothesis IV). This could have been due to the isolation of the South American continent, which might result in unoccupied niche space. It could also be due to energetic constraints on small marsupials, which tend to have high field metabolic rates for their body size (23), but body size distributions of Australian marsupials show occupied small body size niches (24), which casts doubt on this suggestion.

Another set of hypotheses draw on the ecological history of mammals involved in the GABI. In these explanations, the environmental niches of species determine advancement. Given that the environmental niche is crucial in determining a species' range (25), we might expect species to shift their ranges in accordance with changes in climate that were occurring during the Plio-Pleistocene. Webb (26) proposed that North American mammals moved south primarily during dry, glacial climates, when the Isthmus of Panama was a grassland ecosystem, while South American mammals moved north during wetter interglacial climates, across an Isthmus covered in tropical rainforest (Hypothesis V). Hence, grassland species moved from North to South America, and rainforest species moved from South to Central America. According to this hypothesis, more North American species moved south because the source area of North America is larger (27). However, there is not convincing evidence that the North American mammal fauna was more diverse than the South American fauna before the interchange (28), which this hypothesis assumes. In addition, pollen records from the Neotropics suggest

that areas that are currently tropical rain forest were probably forest or dry woodland rather than grassland during cool, dry climate phases (29, 30). Finally, there is no reason why species from both continents could not disperse across the Isthmus during both climate phases. Another hypothesis that focuses on ecological differences between taxa to explain the pattern observed in the GABI is Vrba's habitat theory (Hypothesis VI, 32). Vrba suggests that, because most of South America is tropical, only South American generalists could have established in northern reaches, while all but the most specialized North American species would have been able to find a niche in South America. Additionally, because of temperature fluctuations due to glaciations, tropical forest habitats would have become so sparse during glacial time periods that forest species would have had high rates of extinction. Therefore, we would expect South American generalists in both diet and habitat to be the most successful at advancing into North America (31). North American open habitat specialists should be particularly successful advancers, though generalists from North America should also do well. A variation of this is our climate hypothesis (VII). Rather than focusing on biotic niche, this focuses on how the abiotic niche must vary between North and South America. The temperate climate of North America required animals to be capable of coping with a wide range of temperatures, particularly during glacial ages. Mammals of larger body size tend to have an easier time coping with cold temperatures (32), so South American mammals of larger body mass may have been more likely to colonize North America. In contrast, animals moving into the tropics were exposed to a more constant, amiable temperatures, so smaller bodied mammals should have been able to colonize South America.

We have gathered a few basic hypotheses that haven't been widely considered in the context of the GABI, but are easily tested with this dataset. Based on the idea that dietary niches are relatively conserved within families (33), we assumed that families with the greatest number of different dietary niches were the most generalist. In Hypothesis VIII, we tested whether generalists were favored colonizers, as proposed for Xenarthra (34). In Hypothesis IX, we use body mass as a proxy for dispersal ability and range size, though these are only weakly correlated (35), and predict that larger genera will be more successful colonizers. Conversely, greater success colonizing success of smaller sized genera could indicate that a fast life history was needed to colonize a new continent, (Hypothesis XII.) Mammals of smaller size tend to have more offspring per year (22), and this could allow them to establish a new population more quickly and successfully than larger mammals. Finally, we use the number of species in a genus as an indicator of speciation capacity, (Hypothesis X,) and predict that, the more species a genus has, the more capable of colonizing it was. Colonizers may have been more successful because they possessed a body plan (36) which was inherently more adaptable to filling new niches, (Hypothesis XI.) We use the number of genera per family, as well as the range of log body mass, to approximate body plan flexibility.

There is a major challenge to most of these hypotheses. They predict that the same pattern of colonization in the GABI should be found in all taxa. Yet there appears to be no consistent pattern of dispersal across lineages, even within vertebrates. Plants show even colonization between continents (37). Amphibians advanced primarily north from South America, the exception being salamanders (38, 39). Reptiles primarily diversified in Central America and advanced both north and south from there (38). The colonization

patterns in freshwater fish (40, 41) and birds (42–44) are still ambiguous. Some differences might be explained by dispersal ability (e. g., higher in plants and volant animals,) or degree of cold tolerance (mammals are more cold tolerant than ectotherms,) but this is unexplored. We still lack a cohesive understanding of the GABI.

Here, we used a quantitative approach to distinguish between the many hypotheses that have been advanced. We used a machine learning method to examine the influences of a suite of evolutionary and ecological variables on colonization success. We employ a comprehensive database of Late Quaternary mammals (45), which includes information on body size, trophic group, birth mode, lifestyle, and taxonomy. We use a Late Quaternary dataset to avoid gaps in the fossil record of earlier periods, to exclude species that dispersed to new regions without establishing a population, and to be reasonably sure that the GABI was complete. Our analysis allows us to identify the evolutionary and ecological characteristics which contributed most to successful dispersal and colonization between the continents.

Results

We find a similar proportion of colonizer taxa in each continent after the interchange (Fig. 1) as in previous studies (7, 30, 46). In North America, advancer taxa from South America make up 40% of the orders, but only ~6% of the species in the post-GABI mammal assemblage. In contrast, the North American advancers in South America make up 50% of the orders and 50% of the species.
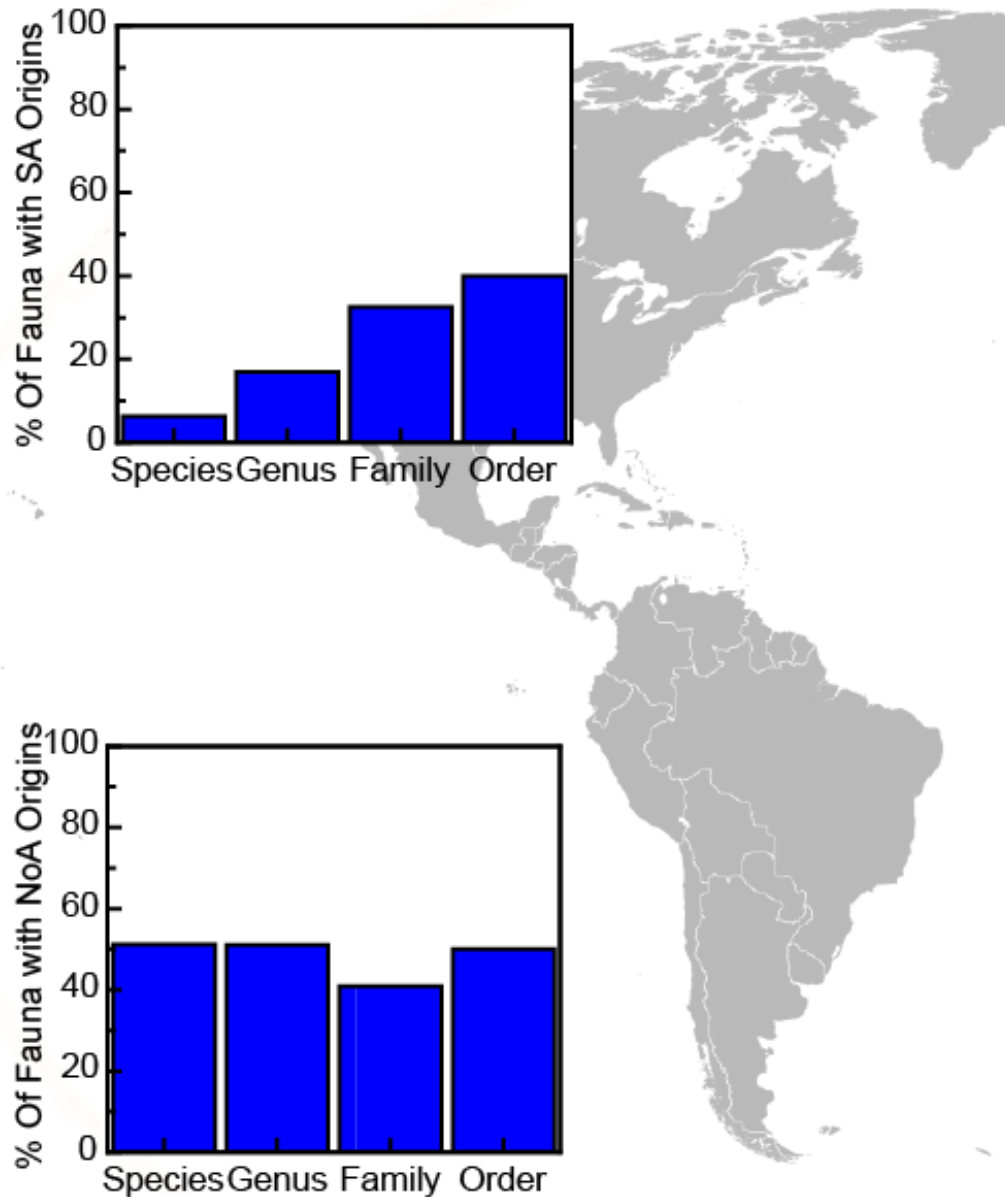
Figure 1. Percentage of mammal community composed of advancers across continent and taxonomic level. The North American mammal community (above) contains ~40% colonizer orders, but only ~6% colonizer species. In contrast, the South American mammal community (below) contains ~50% colonizer orders and ~50% colonizer species. This suggests that South American orders did not speciate as prolifically as their North American equivalents.

The body size distributions of mammals after the GABI on both continents are very revealing (Fig. 2). In North America, South American colonizers were mainly of medium to large body sizes; the smallest were around 50g. In contrast, the North American advancers in South America were spread across the entire body size distribution, but were concentrated in the smaller body sizes. Today, these lineages make up about half of the lower body size mode in the South American mammal assemblage. Based on this, we expect body size to be an important predictor of colonizing in our models, and the sizes favored in colonizing to vary between continents.

Post-GABI Continental Range
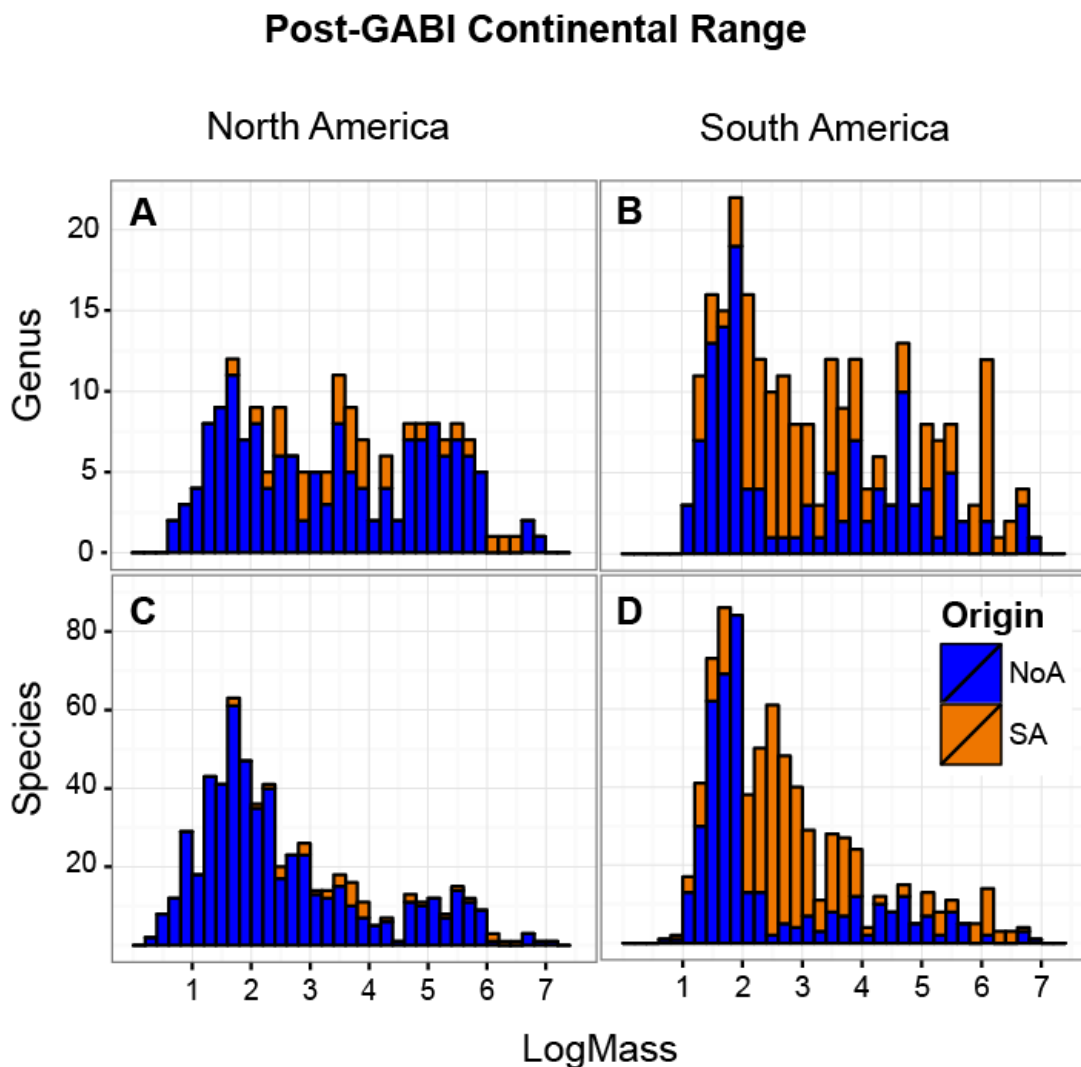
Figure 2. Body size distributions across continent and taxonomic level. North American mammals are shown in blue, South American mammals in orange. In North America, both at the genus (A) and species level (C), South American mammals only occupy medium to large size bins. In South America, at the genus (B) and more clearly at the species level (D), North American mammals are found throughout the body size distribution, but dominate in the very small size bins.

Many variables we tested showed an association with dispersal in a bivariate linear model; mass range, trophic group, diet generalization, continent of origin, and the number of genera per family were all significantly related to colonization ($p<0.05$, z and p values in Appendix). However, there are strong correlations between the predictor variables in this dataset. This complicates interpretations and violates the assumption of independence in linear regressions.

We carried out a classification tree analysis on the data from both continents. The resulting tree (Fig. 3,) shows several important trends. Variables that were of the most importance in our random forest model were mean mass, mass range, genera per family, species per genus, diet generalization, order, and fine trophic guild (Fig. 4A). Overall, those genera that produced more species were more likely to advance, as were families that produced more genera. Genera of smaller body size and larger size range were also more likely to advance, but there was considerable variation, with some lineages of larger-sized genera having a high likelihood of crossing. Greater generalization in diet was positively associated with crossing; though, again, there were exceptions, such as in genera with a large mass range but few species per genus. Trophic guilds with good chances of crossing included invertivores, omnivores, and frugivores in some cases. Orders with higher chances of advancing were Carnivora, Didelphimorphia, Perissodactyla, and Proboscidia, but chances of advancing varied with other characteristics. Despite their relationship with advancing in linear models, continent of origin, coarse trophic group, and birth mode were not significant contributors to the tree. This tree was 75.91% accurate and explained 94.6% of the deviance in the data. The random forest showed that our model has an out-of-bag error rate of 30.3%, which is

better than chance based on a 44% chance of advancing. This tree models the factors

contributing to advancement across continents, but we were also interested in

differences between continents.
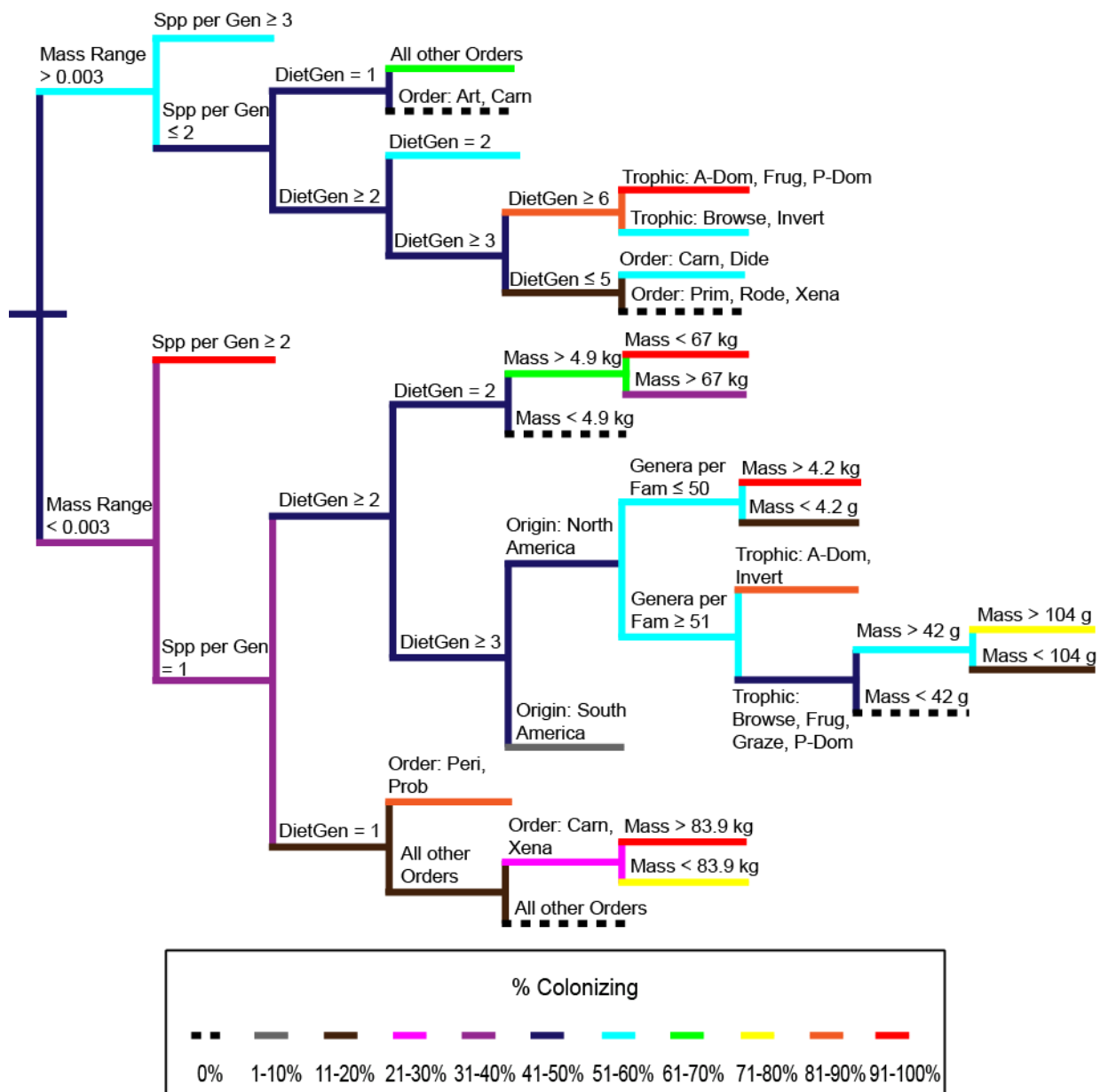
Figure 3. Classification tree for North and South America combined. The color of the branch indicates the likelihood of colonizing at that node. Variable abbreviations: Spp per Gen = Species per Genus, DietGen = diet generality, Genera per Fam = Genera per Family, Art = Artiodactyla, Carn = Carnivora, Dide = Didelphimorphia, Lago = Lagomorpha, Peri = Perissodactyla, Prim = Primates, Prob = Proboscidea, Rode = Rodentia, Xena = Xenarthrans, A-Dom = Animal-dominant Omnivore, Browse = Browser, Frug = Frugivore, Graze = Grazer, Invert = Invertivore, P-Dom = Plant-dominant omnivore.

Figure 4. Importance of variables in the random forests. The importance of variables in the combined tree (A) is similar to the importance values in the trees separated by origin (B). Body size is clearly the most important variable. Some variables, such as birth mode, have almost zero importance in the trees.

We built separate decision tree models for genera from North America and genera from South America. Results for North America are similar to the cross-continent models (Fig. 5A). Mass range, diet generalization, animal-domina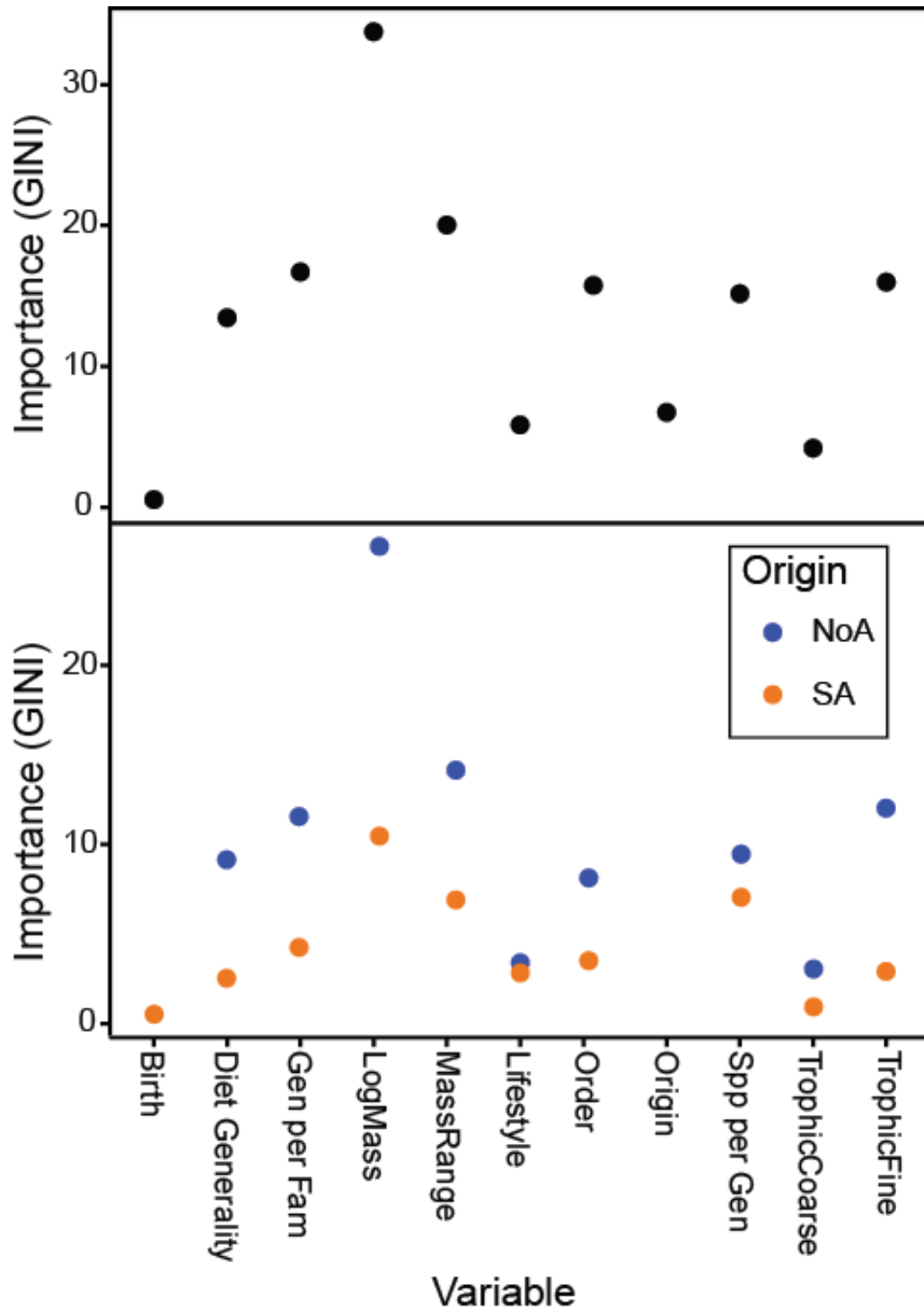nt omnivory, and the number of genera per family were all positively associated with colonization in linear regressions. Some trophic guilds were negatively associated with colonizing: frugivores, grazers, and plant-dominant omnivores were all less likely to cross. The decision tree model for North American genera shares the first few branches with the full tree, indicating the patterns in North America dominate that model. The importance of variables is also similar to the full tree (Fig. 4B), although fine scale trophic guild is of relatively greater importance. The tree for North America was 77.6% accurate and explained 97.7% of the variation in the data. Our random forest model of this data estimated the out-of-bag error rate at 35.3%, which is lower than the 54.7% chance of colonizing in the tree.

The tree for South America (Fig. 5B) is quite different from the North American tree, although several of the same variables are significant. Having a large range of body sizes, more species per genus, and a larger mass all increase the likelihood of colonizing. The most important variables in the tree are similar to those for North American genera (Fig. 4B), except trophic group is somewhat more important. Birth mode is not an important contributor to advancing. The South America tree explains 76.6% of the variation in crossing, with an accuracy of 84%. However, the out-of-bag error rate is 25.6%, and since this is higher than the 24% chance of advancing from South America, the results of this analysis must be interpreted with caution. This greater error rate is

likely a result of the small number of colonizers from South America: the smaller

sample size makes model verification difficult.
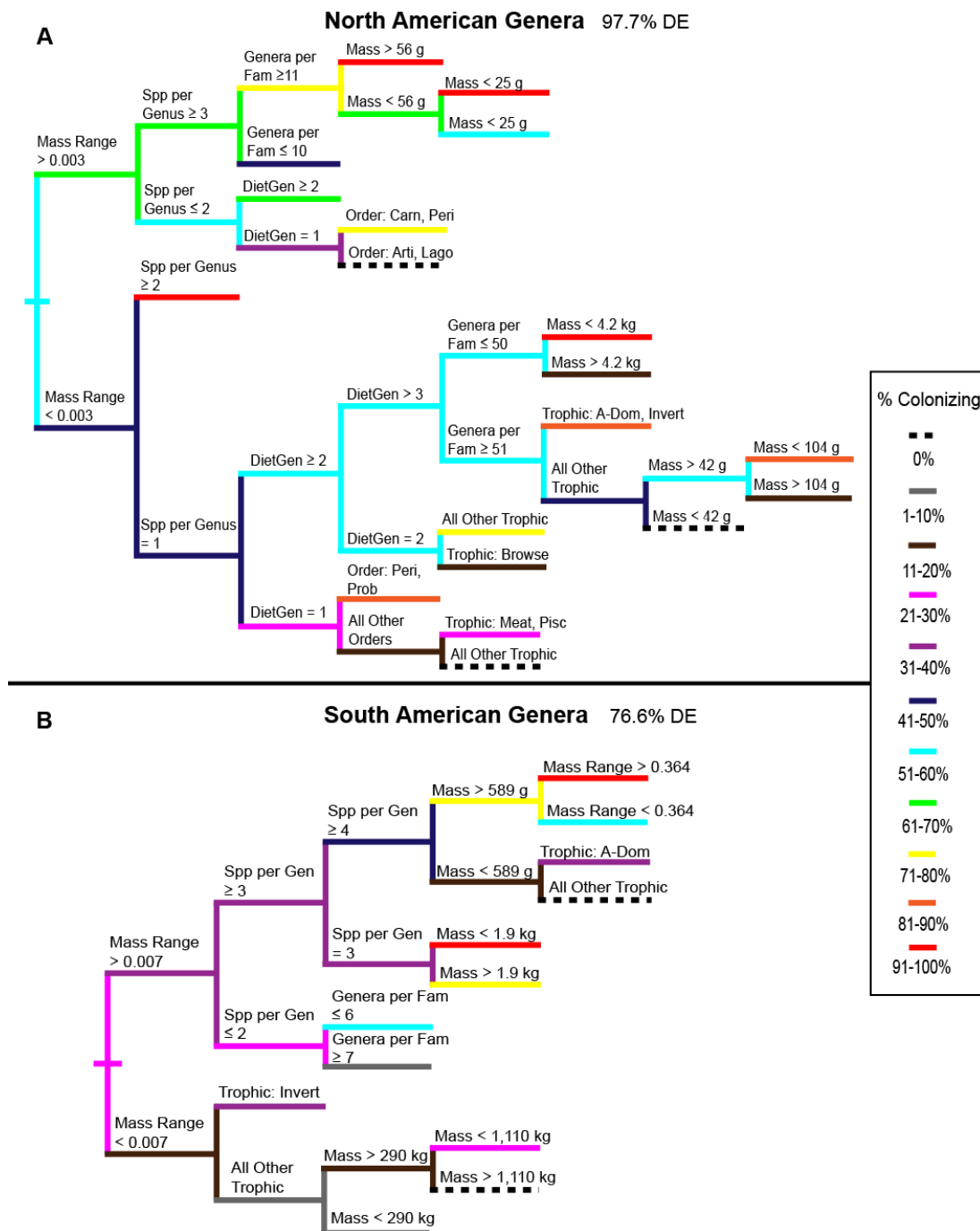
Figure 5. Classification trees showing the likelihood of advancing from each continent. The North American advancement tree (A) is similar to the full tree, though with a slightly higher chance of advancement at the first node, and notable variation in the outer and terminal nodes. The South American advancement tree (B) is much simpler, with a lower chance of advancing. The South American tree explains less of the deviance in the data, and has an error rate slightly higher than the likelihood of advancing, and so must be interpreted with caution. Abbreviations as in Fig. 3.

Table 2: Hypotheses that have been proposed to explain colonization patterns of mammals during the GABI, with our conclusions indicated in column 4.

	Hypothesis	Citation	Predictor Variables	Conclusion
I	Phylogenetic Superiority	Simpson 1980, Webb 1985	Order, Origin (North America)	Some Support
II	Placental Superiority	Lillegraven 1974, but see Hamilton et al. 2010	Birth (placental)	Not Supported
III	Lack of South American carnivores	Patterson and Pascual 1968, Marshall 1988, Vermeij 1991	Trophic group (meat and plant-Dominant Omnivores)	Some Support
IV	Lack of South American small mammals	This study	Mass (small size advantage), Order (Rodentia)	Some Support
V	Grassland vs. Forest corridors	Webb 1991	South America: Lifestyle (arboreal), Trophic (browser, frugivore). North America: Lifestyle (terrestrial), Trophic (grazer)	Not Supported
VI	Habitat Theory	Vrba 1993	South America: Diet Generality. North America: Lifestyle (terrestrial), Trophic (grazer)	Some Support
VII	Climate Hypothesis	This study	South America: Mass (large size advantage). North America: (small size advantage)	Strongest Support
VIII	Generalists	This study	Diet Generality	Some Support
IX	Dispersal Ability, Range Size	This study	Mass (large size advantage)	Some Support
X	Speciation Capacity	This study and Maurer, pers. comm.	Species per Genus	Some Support
XI	Flexibility of Body Plan	This study and Maurer, pers. comm.	Genera per Family, Log Mass Range	Some Support
XII	Fast Life History	This study	Mass (small size advantage)	Some Support

Discussion

Traditional Hypotheses

Our findings lend support to some of the traditional hypotheses surrounding the GABI

(Table 2.) The most famous, Simpson's phylogenetic superiority hypothesis (Hypothesis

I (5),) is tentatively supported. Regardless of taxonomic identity, North American

lineages were more likely to colonize South America (see the first nodes of Fig. 5A and

Fig. 5B.) Certain North American families and genera, particularly sigmodontine

rodents, were more diverse as a result of the GABI, which suggests that these groups

had advantages which made them more competitive and facilitated colonization. The

success of North American genera may indeed have resulted from competition with or

enrichment by Eurasian fauna in North America. An aspect of the greater colonization

success of North American genera may be that there were vacant niches in South

America, particularly among small mammals and carnivores, (Hypotheses III and IV

(2).) The great success of colonizing small mammals in South America would support

this (Fig. 2B.) Because we used Late Quaternary assemblages, our data cannot

differentiate between vacancies in these niches due to South American isolation,

vacancies due to recent extinctions related to the formation of the Andes, and

competitive displacement of South American small mammals and carnivores by North

American colonizers. We hope to compare between these scenarios using data with

greater time resolution in future work.

Our findings disprove several hypotheses that have been proposed in past literature.

Perhaps the oldest hypothesis about the GABI, the placental superiority hypothesis

(Hypothesis II (18),) is clearly incorrect once continent is accounted for. South

American marsupial and placental mammals were equally likely to colonize North America. Birth mode was the variable with the lowest importance in all our models (Fig. 4.) Despite their lower metabolic rate (19, 23) marsupials were as successful at colonizing as their placental counterparts. Nor do we find support for Hypothesis V, Webb's (26) grassland corridor hypothesis. There is apparently no significance in whether a genus was adapted to grasslands or forests in how they colonized new territory, as there was little effect of being a grazer vs. a browser or terrestrial vs. arboreal in either our full tree (Fig. 3,) or in trees separated by continent (Fig. 5.) Hypothesis VI, habitat theory (31), is based upon selective pressures that we think were important in determining the direction of the GABI; the changeable environment in North America made it more difficult to colonize than South America. However, habitat theory is focused on how these climatic factors affect the preferred environment and diet of species. According to our findings, lifestyle and trophic group were not very important factors in whether a genus was able to colonize a new region (Fig. 4.) Diet generality was a moderately important factor, as in Hypothesis VIII, but was actually less important for South American mammals than for North American mammals (Fig. 5.) Habitat theory is the right idea, with the wrong predictions.

New Hypotheses

This research shows that several important factors in the GABI were not emphasized by previous authors. Having a flexible body plan (Hypothesis XI,) was moderately important for mammal genera of both continents, as was having a high speciation capacity (Hypothesis X, Fig. 4.) A wide range in body size, which contributes to a

flexible body plan, was so important in our models that it split the first node in each of our trees (Fig. 3 and 5.) However, these hypotheses are supported with much caution, because of the potentially circular nature of the variables involved. It's not possible to be sure from our data that a flexible body plan or a high number of species per genus were a cause of, or a result of, the GABI. Also, were North American genera more likely to possess these characteristics, due to enrichment from Eurasia (Hypothesis I,) or was their greater success due to some other factor? Further investigation of Hypotheses X and XI is necessary.

Our analyses show that body size was the most important factor in determining colonization ability. Smaller was better when it came to colonizing South America. The North American genera in smaller size classes tended to be very successful colonizers. They made up the bulk of the genera in the smaller body size mode in South America after the interchange (Fig. 2.) Body mass was the most important variable in both our full tree and our North America tree (Fig. 4A and 4B.) We suspect the success of small North American genera is due to the correlation of fast life history with small body mass (Hypothesis XII (47).) Animals with fast life histories produce more offspring in a shorter amount of time than those with slow life histories (48). Species with fast life histories could have reproduced, established populations, monopolized resources, and even adapted to their new niches more quickly than species with slower life history (49). If more data were available, we could test this hypothesis by correlating the number of offspring per year with colonization. However, this is difficult because it is impossible to directly determine the number of offspring per year of extinct species, and adequate life history data are not available for many tropical extant species, particularly small

mammals living in South America. Conversely, for South American genera, larger bodied genera were more likely to colonize (Fig. 5B.) This supports Hypothesis IX; for South American genera, it was important to have a large range or greater dispersal ability.

Together, these findings support Hypothesis VII, the climate hypothesis. The differences in patterns between continents suggest that the environmental differences between North and South America contributed to the different colonization success of these two faunas. The South American genera evolved under tropical environmental conditions which favor narrow, specialized niches and small geographic range sizes (50). Tropical species have evolved in a diverse environment in which biotic interactions hamper dispersal, so species may evolve to be less likely to disperse. These characteristics, though beneficial in their tropical home ranges, would be detrimental to a genus's ability to disperse and establish in a new environment. Genera that reached North America met with a colder, unstable climate regime. (26, 31, 51). Only genera with the ability to cope with cold and shifting temperatures could adapt to this new environment (52, 53). Small bodied animals, with high surface areas relative to body volume, would be less likely to colonize this cold environment than larger bodied mammals. Larger genera could retain heat more effectively in cold conditions, giving them the opportunity to adapt to shifting conditions. This could contribute to the pattern of Bergmann's Rule that we observe today (32). Only the larger species within a genus, or in this case, genera within a family, could establish populations in a cooler, fluctuating environment. In addition to evolving larger body sizes in situ in colder climates, larger bodied species could be more successful at colonizing colder climates.

Concurrently, conditions in the tropics, while not greatly conducive to dispersal, may favor establishing and speciating. North American genera invading South America found stable, productive environments favoring establishment of colonizers. They also found conditions that support high species diversity. The causes of high diversity in the tropics are debated and are probably manifold, but many of the hypotheses explaining this greater diversity could support colonization of new groups. If the tropics are a cradle of diversity (54), than colonizing genera could speciate more readily there. If they are a museum of diversity (55), colonizers would be less likely to go extinct. If evolutionary rates are faster there (50), than colonizers could rapidly adapt to their new environment. Conditions would particularly favor species with fast life histories, flexible body plans, and generalist niches, which could speciate and adapt to new niches readily. Conditions in temperate regions do not strongly favor specialization (56), giving the North American fauna an advantage in making it to a new region and adapting to a new environment. Genera with faster life histories, i.e. small body sizes, would be particularly favored colonizers, due to their ability to rapidly establish a population. Since high diversity in the tropics, fluctuating temperate climate regimes, and Bergmann's Rule are all more or less the same in different parts of the world, this pattern of colonization may be widespread (57). We suggest an "Into the Tropics" model to explain this pattern of colonization (as opposed to the "Out of the Tropics" model proposed by Jablonski et al. (58) using marine bivalves.)

"Into the Tropics"

We propose a general model for biotic interchange events based on this pattern. This model is geared toward taxa that demonstrate Bergmann's Rule, such as turtles and birds, which are under similar selection regimes to those experienced by mammals in the GABI. In an interchange event, initially, medium to large animals should disperse to temperate areas, and animals of all sizes to tropical areas. Conditions favoring diversification should then allow the animals moving into the tropics to establish populations and diversify, with small, fecund species favored. Meanwhile, larger animals in the temperate region will expand their ranges but experience little speciation, while smaller animals may go extinct. This is similar to the ideas behind habitat theory (Hypothesis VI (31),) but instead of dietary generalists from the tropics colonizing temperate areas successfully, it is the thermal generalists which are most successful. In the same respect, it is not temperate species with dietary niches adapted to a changing tropical environment that colonize – rather, it is those which can most readily adapt and speciate.

Further research must be done to confirm how dependent this pattern is on the isolation of the tropical area. It is possible we observe this pattern because of empty small mammal and carnivore niches in South America (Hypotheses III and IV,) and if this is the case, than the "Into the Tropics" model won't be supported in other biotic interchanges. If the model holds regardless of isolation of the tropical continent, then it is supported. If this pattern of colonization is only found when the tropical continent is isolated, than competition and empty niches in South America were likely the more important factors in the GABI. We hope to test this hypothesis in future work by

comparing the GABI with other biotic interchanges. For example, when the Tethyan

Seaway closed in the Early Miocene, tropical Africa/Arabia connected with temperate

Eurasia for the first time in roughly 150 million years (57). According to the "Into the

Tropics" model, small mammal genera from Eurasia should have successfully colonized

Africa, while only larger mammals from Africa should have colonized Eurasia.

The Trans-Indonesian interchange, over Wallace's line, could test the "Into the Tropics"

model as well. Oceania/Australia is the more isolated, but temperate area. Did species

move from tropical Asia toward isolated Australia? Or, did these species move from

more temperate Australia to more tropical Asia, as our hypothesis would predict? In

contrast, interchange across the Beringian land bridge, between Eurasia and more

isolated North America, should have been balanced. Though one continent was more

isolated, both were temperate, and so selection regimes should have been similar.

Based on the "Into the Tropics" model, we can also make predictions about how non-

mammalian taxa should have behaved during the GABI. Organisms which readily

disperse great distances, such as migratory birds and plants with wind-dispersed seeds,

shouldn't have been affected by the GABI. By the time the GABI occurred, they should

have dispersed throughout the Americas, and we expect them to already have greater

diversity in tropical areas. Taxa that do not show a clear body size trend with latitude,

such as marine bivalves (59), or that are larger toward the tropics, such as most

squamate reptiles (60) and freshwater fish (61), may show the opposite pattern. They

should be more diverse in South America and move into North America, regardless of

South America's isolation. This is in contrast to many previous hypotheses about the

GABI, which implied that all animal taxa should show the same colonization pattern as

mammals. Taxa that do follow Bergmann's Rule, such as turtles, salamanders, and dispersal-limited birds (32), should show the same pattern as mammals – an "Into the Tropics" colonization.

Conclusion

The patterns we observed in the GABI were the result of subtle interactions of environmental and intrinsic factors. Earlier hypotheses explaining these patterns emphasized environmental and particularly dietary niches of species, but our findings suggest these were not very important in determining the composition of mammal assemblages. Instead, we found that more general characteristics, such as body size, were the most important. Environmental characteristics of the destination continent were more important than the conditions on the continent where genera originated. The latitudinal diversity gradient and Bergmann's Rule played a much greater role in determining advancement of mammals than has ever been considered in previous research. Finally, we wish to emphasize the need to use quantitative approaches in answering paleoecological questions. Our decision tree approach revealed patterns that wouldn't have been elucidated otherwise. Our inclusion of small mammals in our analysis also added a dimension other researchers haven't looked at, and our results would not have been complete without this data.

Methods

Data

We used the MOM dataset, v. 3.6.1 (45) for all analyses. MOM contains taxonomic, trophic, body size, and distributional information about all known species of mammal worldwide extant at the End-Pleistocene. We limited our study to terrestrial, nonvolant North and South American mainland species. Species native to Central America are considered North American for the purpose of this dataset, based on the shared geological history between North and Central America. We excluded marine and volant mammals due to their unique metabolic requirements (35), though we included semi-aquatic mammals, which give birth on land. Analysis was conducted at the genus level, and genera in which any species was found on the continent opposite its origin were considered successful colonizers.

Variables employed in our analysis included: taxonomic order (62), continent of origin, mean log body mass, trophic group, diet generalization, mode of life, mode of birth, number of species per genus, and number of genera per family. Each variable related to one or more hypotheses discussed in Table 1. Order was used as a rough proxy for phylogeny in this study, (although some classifications used in this dataset, such as the group Insectivora, are now defunct.) The continent of origin was identified for each genus based on (5). Genera which originated in Eurasia and Central America were considered North American. We used two different scales of trophic group: coarse and fine. The coarse scale trophic variable examined whether genera consume plant material, animal material, or are omnivorous. The fine scale trophic variable contained more

specific detail, including distinctions such as grazer and browser. Diet generalization was the number of fine scale trophic groups found in the parent family of a given genus. The lifestyle variable was used to differentiate arboreal, aquatic, fossorial, and terrestrial genera. Birth mode differentiated between placental and marsupial mammals. We also looked at the number of species per genus and genera per family, to examine the contributions of speciation capacity and body plan flexibility, respectively (36).

The MOM dataset is constructed at the species level, which is inappropriate for our analyses. Species durations may be much shorter than the interval during which the GABI occurred, so species could have gone extinct between colonization and our Late Quaternary data. Thus, we aggregated data to a higher taxonomic level, which allowed us to reduce the effects of speciation in the millennia since the GABI. We averaged body mass of all within a genus to obtain a single mass estimate. We subtracted the smallest from the greatest log transformed body size within each genus to obtain the mass range. Doing this in log space controlled for bias toward large body size in size range. We used the most common trophic group and mode of life for each genus. In cases of ties, we used the trophic group or mode of life that was most common for the family and also found within the genus.

There are several variables we would have ideally included in our analysis if data were readily available. For instance, geographic range size and location could affect the opportunity a genus had to colonize, but these data are not available for both continents during the Pliocene. Similarly, life history data, such as number of offspring per year, are very limited for South American mammals, as well as many North American small

mammals, and are nearly impossible to determine for extinct species. We therefore assume that body size is a good proxy for life history (47).

Ideally, our analysis would employ a dataset constructed for the End-Pliocene. Such a dataset does not currently exist. This is largely due to the low resolution of the South American fossil record; much of the continent is tropical and therefore has poor fossilization conditions, and screen washing to uncover small fossils has only recently become routine. However, there are several reasons we believe our approach of employing an End-Pleistocene record is valid. First, the GABI was not an event that occurred in a single time period. Some species crossed the Central American Seaway via island chains at least 8 Mya, while others crossed closer to when the Isthmus formed around 3 Mya. Other species may not have crossed until the Pleistocene. There is no single time slice in the fossil record that includes all of the GABI. Using the End-Pleistocene, we can be reasonably sure that the GABI has completed. We can avoid bias towards large body sized species in the fossil record. We can also remove any effect from species that crossed the land bridge but did not establish. Therefore, we believe this the best possible way to study the GABI given the data available.

Analysis

We carried out bivariate linear regressions between colonization and each predictor variable to examine general trends, both with the full dataset and within individual continents. All analyses were performed in the R statistical environment (63).

We used classification trees to relate likelihood of colonization to the predictor variables in our dataset (64). Classification trees are an excellent method for this type of study.

They make no assumptions about the normality or independence of variables. Moreover, classification trees can incorporate quantitative and categorical variables, and they can identify nonlinear interactions and context dependency within data. We built trees using the *rpart* package (65) for the entire dataset and for genera native to each continent, to examine different influences on advancement success in different regions. We quantified model fit using percent deviance explained (%DE).

To compare the relative importance of different predictor variables within our models, and to control for the effects small changes in the data can sometimes have on classification trees, we also carried out three random forest models, using the R package *randomForest* (66). Random forest models build a series of bootstrapped trees (in this case, 500), using a random subsample of the data. These trees are then combined, and the importance of different variables is determined based on those that appear across all trees. We used the GINI index to measure the relative importance of each variable in the models. Random forests also give an out-of-bag (OOB) error rate for the trees, which we used to determine significance of the model. If the error rate was lower than that of a null model, it was considered significant. In this case, the null model was the overall chance of colonizing without incorporating any predictor variables.

Appendix

Table A. The results of analyses for the full dataset and with continents separated are shown in this table. Regressions shown are between each variable and colonization. For categorical variables, a different z and p value is returned for each category (* ~ p < 0.05; ** ~ p < 0.01; *** ~ p < 0.001.) Importance is the GINI index from the random forests of each tree. This value is relative within each tree, and isn't directly comparable across trees.

		Both Continents		North America		South America	
Variable	Category	Regression	Importance	Regression	Importance	Regression	Importance
Order	Artiodactyla	z = -0.631, p = 0.527	15.75	z = -0.631, p = 0.528	8.13	-	3.51
	Carnivora	z = 1.231, p = 0.281		z = 1.231, p = 0.218		-	
	Didelphimorphia	z = -0.333, p = 0.739		-		z = -0.769, p = 0.442	
	Insectivora	z = -1.813, p = 0.070		z = -1.813, p = 0.070		-	
	Lagomorpha	z = -1.235, p = 0.217		z = -1.235, p = 0.217		-	
	Litopterna	z = -0.010, p = 0.992		-		z = -0.006, p = 0.995	
	Microbiotheria	z = -0.007, p = 0.995		-		z = -0.004, p = 0.997	
	Notoungulata	z = -0.010, p = 0.992		-		z = -0.006, p = 0.995	
	Paucituberculata	z = -0.012, p = 0.991		-		z = -0.008, p = 0.994	
	Perissodactyla	z = 0.014, p = 0.989		z = 0.022, p = 0.983		-	
	Primates	z = -0.939, p = 0.348		-		z = -0.508, p = 0.612	
	Proboscidea	z = 0.969, p = 0.333		z = 0.969, p = 0.333		-	
	Rodentia	z = 0.097, p = 0.922		z = 1.457, p = 0.145		z = -2.099, p = 0.036*	
	Xenarthra	z = -1.305, p = 0.192		-		z = -0.636, p = 0.525	
Origin	North America	z = 1.166, p = 0.244	6.74	-	-	-	-
	South America	z = -5.291, p < 0.001***		-	-	-	-
Birth	marsupial	z = -1.567, p = 0.117	0.55	-	-	z = -1.567, p = 0.117	0.52
	placental	z = 1.068, p = 0.286		-	-	z = -0.835, p = 0.404	
Trophic (coarse)	animal	z = -0.311, p = 0.756	4.2	z = 0.471, p = 0.638	3.05	z = -1.497, p = 0.134	0.93
	omnivore	z = 1.602, p = 0.109		z = 2.107, p = 0.035*		z = -0.134, p = 0.893	
	plant	z = -1.992, p = 0.046*		z = -0.704, p = 0.481		z = -1.248, p = 0.212	
Trophic (fine)	animal dom. omni.	z = 1.689, p = 0.091	15.98	z = 2.832, p = 0.005**	12.03	z = -1.449, p = 0.147	2.91
	browser	z = -3.172, p = 0.002**		z = -2.579, p = 0.010**		z = -0.595, p = 0.552	
	frugivore	z = -1.757, p = 0.079		z = -1.735, p = 0.083		z = -0.073, p = 0.446	

Table A continued

Variable	Category	Both Continents		North America		South America	
		Regression	Importance	Regression	Importance	Regression	Importance
	grazer	z = -2.498, p = 0.012*		z = -3.005, p = 0.003**		z = -0.763, p = 0.446	
	invertivore	z = 1.951, p = 0.051		z = -2.451, p = 0.014*		z = 0.342, p = 0.732	
	meat	z = -0.186, p = 0.852		z = -1.358, p = 0.174		z = 0.206, p = 0.837	
	plant dom. omni.	z = -0.676, p = 0.498		z = -1.613, p = 0.107		z = 0.506, p = 0.613	
	piscivore	z = -1.598, p = 0.110		z = -2.560, p = 0.010*		-	
Lifestyle	aquatic	z = -0.444, p = 0.657	5.85	z = -0.566, p = 0.571	3.39	z = 0, p = 1	2.83
	arboreal	z = -0.144, p = 0.886		z = 0.980, p = 0.327		z = -0.582, p = 0.561	
	marine BOL	z = -0.709, p = 0.478		z = -0.367, p = 0.713		-	
	terrestrial	z = 0.280, p = 0.779		z = 0.775, p = 0.438		z = -0.994, p = 0.320	
	terr/aquatic	z = 0.719, p = 0.472		-		z = 0.371, p = 0.711	
	terr/fossorial	z = -1.096, p = 0.273		z = -0.558, p = 0.577		z = -0.015, p = 0.988	
Diet Generalization	-	z = 4.636, p < 0.001***	13.45	z = 3.869, p < 0.001***	9.15	z = -0.079, p = 0.937	2.53
Mass	-	z = -1.156, p = 0.248	33.74	z = -0.965, p = 0.335	26.65	z = 0.742, p = 0.458	10.47
Mass Range	-	z = 2.484, p = 0.012*	20.03	z = 2.009, p = 0.045*	14.15	z = 1.624, p = 0.104	6.91
Species per Genus	-	z = 0.999, p = 0.318	15.16	z = 0.558, p = 0.577	9.46	z = 0.540, p = 0.589	7.05
Genera per Family	-	z = 5.370, p < 0.001***	16.7	z = 3.686, p < 0.001***	11.56	z = -0.348, p = 0.728	4.25

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