

Cosmopolitan and provincialism dynamics of North American terrestrial mammals across the Cenozoic

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Abstract

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1 Introduction

Evolutionary paleoecology is the study of how ecological traits expressed at any level affect the macroevolutionary process, or long term patterns in speciation and extinction (Kitchell, 1985). Biotic interactions are a fundamental aspect and driver of evolution (Liow et al., 2011; Van Valen, 1973), however it is obvious that biotic interactions can only occur between organisms that at least share the same area (Roopnarine, 2006, 2010). Because of this, community structure plays a fundamental roll in determining which biotic interactions are possible at a given time.

How site similarity, and the underlying community structure, has changed over time has been the focus of both evolutionary and ecological research in both vertebrates and invertebrates (Clapham and James, 2012; Jernvall and Fortelius, 2002, 2004; Olszewski and Erwin, 2004, 2009; Raia et al., 2006). In vertebrate and mammalian communities community structure across the Cenozoic has been of particular interest, especially in relation to the relative importance of biotic and abiotic factors (Alroy, 1996, 1998; Badgley and Finarelli, 2013; Barnosky et al., 2003; Blois and Hadly, 2009; Figueirido et al., 2012; Jernvall and Fortelius, 2002, 2004), though this is a false dichotomy of importance (Liow et al., 2011). Of particular interest is the relationship between the three major mammalian trophic groups: carnivores, herbivores, and omnivores (Jernvall and Fortelius, 2004; Price et al., 2012).

While relative taxonomic abundance is considered extremely important for understanding community dynamics CITATIONS, the preservation of this informaiton in the terrestrial fossil record is poor at best (Damuth, 1982). The fossil record for a time span as long as the Cenozoic

is patchy and uneven in both sampling and outcrop availability (Alroy, 1996, 1998; Jernvall and Fortelius, 2004) meaning that fair and unbiased sampling of abundance information is virtually impossible (Damuth, 1982). Instead, presence-absence information must be used as proxy for community structure (Jernvall and Fortelius, 2004) OTHER CITATIONS. Site abundance and presence are linked in many taxa, with an increase in abundance correlated with an increase in site presence CITATIONS SEE (Jernvall and Fortelius, 2004). Because of this, taxa that are found at many sites can be considered common in abundance while taxa that are found at few sites can be considered rare in abundance.

Taxonomic occurrence information is frequently analyzed in a multivariate context (Legendre and Legendre, 2012), where sites are compared using the distances or dissimilarities in composition between each other.

In order to investigate how cosmopolitan–endemism dynamics vary across the Cenozoic, the terrestrial mammal records of North America, Europe and South America. The mammalian taxonomic dynamics of each of these three continents have been studied to different degrees (Alroy, 1996; Blois and Hadly, 2009; Eronen et al., 2009; Flynn and Wyss, 1998; Gunnell et al., 1995; Jernvall and Fortelius, 2002, 2004; Macfadden, 1997, 2006; Raia et al., 2006). While all of these continents transitioned from a principally closed and forested environment to a open and savanna like environment over Cenozoic, the timing of the start of this transition was different on each continent (Blois and Hadly, 2009; Eronen et al., 2009; Janis, 1993). Additionally, the mammal lineages present on each continent are divergent especially in the case on the isolated continent of South America (Flynn and Wyss, 1998; Macfadden, 1997, 2006). Because of this it can be expected that there will be a mix of similarities and striking differences between the continents in how taxonomic distributions change over the Cenozoic.

As the environment on each continent moved from a closed, forested environment to an open, savanna-like environment there are a few general predictions of shifts in cosmopolitan–endemism dynamics. It is expected that as the environment shifted, the ratio of arboreal to land dwelling mammals would shift to include an even greater proportion of land dwelling mammals. Additionally, it is expected there would be an increased similarity between localities, as reflected by decreased endemism in land dwelling taxa. Arboreal taxa, however, are expected to trend towards increasing endemism and decreased site similarity as driven by increasingly fragmented forests.

The shift to grassland environments is frequently connected with the shift from browser-dominated communities to grazer-dominated communities CITATIONS, however in this study the focus is instead on coarser trophic categories such as herbivore and carnivore. There is an expected correlation between herbivore dynamics and land dwelling mammal dynamics because of the expansion of terrestrial herbivores (e.g. horses) CITATIONS.

South America is expected to have experienced rather different cosmopolitan–endemism dynamics than both North America and Europe because of both its long-term isolation and extremely biome provincialism (Flynn and Wyss, 1998; Macfadden, 2006) OTHER CITATIONS. The Amazonian lowland and Andean highlands are radically different biomes

that diverged in similarity approximately during the Miocene (Ortiz-Jaureguizar and Cladera, 2006; Pascual and Ortiz-Jaureguizar, 1990) and are now a rainforest and an arid desert, respectively. Because of this, it is expected that there may be increasing and extreme endemism over the Cenozoic. However, the relative paucity of the South American record in comparison to North America and Europe may be a potential confounding factor for interpreting these results.

Of all three regions, there are a few expected or potential differences in cosmopolitan–endemism dynamics relating to timing to community shifts and degree of endemism.

2 Materials and Methods

Mammalian occurrence information was obtained from the Paleobiology Database (PBDB; <http://www.paleodb.org>). Occurrence information was restricted to terrestrial mammals from the North American fossil record of the Cenozoic. For each occurrence, the locality information was also recorded, most importantly formation name and estimated age. Hierarchical taxonomic information was recorded for each taxon. All partially, ambiguously, or incompletely identified genera or species (e.g. aff., cf., ?) were excluded from analysis.

For each taxon, dietary and life habit information recorded in the PBDB was gathered. Dietary information was then simplified into three categories: herbivore, omnivore, and carnivore. Herbivorous taxa were the amalgam of the PBDB classifications herbivore, grazer, browser, folivore, and granivore. Omnivorous taxa were the amalgam of frugivores and omnivores. Finally, carnivores were the amalgam of all carnivores and insectivores. These three categories were chosen because they represent coarse groups which are identifiable from most mammalian teeth which are the primarily mammalian fossil material. Additionally, these groupings have been used in prior analysis of the effect of ecology on site similarity (Jernvall and Fortelius, 2004).

Temperature information was estimated using the δO^{18} isotope information from the benthic foram record for the entire Cenozoic (Zachos et al., 2008). An increase in δO^{18} levels are associated with a decrease in atmospheric temperature (Zachos et al., 2008, 2001). Benthic foram δO^{18} information has been used previously as climatic information in studies of mammalian macroevolutionary patterns (Alroy et al., 2000; Figueirido et al., 2012; Rose et al., 2011).

Taxonomic presence-absence was recorded for each formation. Abundance information was not included in this analysis, though it is possible (Sidor et al., 2013), because the highly variable preservation conditions not just between formations but across the Cenozoic may not accurately record abundance information (Damuth, 1982).

Bipartite biogeographic networks were constructed, following Sidor et al. (2013) and Vilhena et al. (2013), with species as the taxonomic occurrence and formation as the locality of

interest. As explained in Sidor et al. (2013), biogeographic networks have many advantages over ordination based methods that are frequently used in numerical ecology (Legendre and Legendre, 2012). Principally, both taxonomic and locality information are preserved in analysis which allows for a more complete understanding of community structure. For each temporal bin biogeographic networks were constructed for all taxonomic information, individually for each dietary category and each locomotor category.

Four measures of biogeographic network structure were used to assess community change: code length as measured via the map equation (Rosvall et al., 2010; Rosvall and Bergstrom, 2007, 2008), biogeographic connectedness, average number of locality occurrences per taxon, and average number of endemics per site. Biogeographic connectedness is defined

$$BC = \frac{O - N}{LN - N} \quad (1)$$

where O is the number of edges or number of occurrences in the biogeographic network, N is the number of taxa, and L is the number of localities (Sidor et al., 2013). All four of these measures have previously been used to assess cosmopolitan and endemism dynamics (Sidor et al., 2013). The four measures of biogeographic network were then calculated for each temporal bin for the total network, each of the dietary networks, and each of the locomotor category networks.

Network analysis, including calculation of network code length, was done using the `igraph` package (Csardi and Nepusz, 2006) for the R language (R Core Team, 2013).

3 Results

4 Discussion

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