Paleobiology

www.cambridge.org/pab

Different mammals, same structure: co-occurrence structure across the Plio-Pleistocene transition

Alex B. Shupinski[1,2], Matthew Craffey[2], Felisa A. Smith[3] and S. Kathleen Lyons[2]

[1]Department of Natural Resource Management, South Dakota State University, Rapid City, South Dakota 57703, U.S.A.
[2]School of Biological Sciences, University of Nebraska–Lincoln, Lincoln, Nebraska 68588, U.S.A.
[3]Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131, U.S.A.

Article

Cite this article: Shupinski, A. B., M. Craffey, F. A. Smith, and S. K. Lyons (2025). Different mammals, same structure: co-occurrence structure across the Plio-Pleistocene transition. *Paleobiology* **51**, 300–309. https://doi.org/10.1017/pab.2024.53

Received: 01 February 2024
Revised: 24 October 2024
Accepted: 01 November 2024

Handling Editor:
Graham Slater

Corresponding author:
Alex B. Shupinski;
Email: Alexandria.Shupinski@sdstate.edu

Abstract

A central goal in ecology is investigating the impact of major perturbations, such as invasion, on the structure of biological communities. One promising line of inquiry is using co-occurrence analyses to examine how species' traits mediate coexistence and how major ecological, climatic, and environmental disturbances can affect this relationship and underlying mechanisms. However, present communities are heavily influenced by anthropogenic behaviors and may exhibit greater or lesser resistance to invasion than communities that existed before human arrival. Therefore, to disentangle the impact of individual disturbances on mammalian communities, it is important to examine community dynamics before humans. Here, we use the North American fossil record to evaluate the co-occurrence structure of mammals across the Great American Biotic Interchange. We compiled 126 paleocommunities from the late Pliocene (4–2.5 Ma) and early Pleistocene (2.5–1 Ma). Genus-level co-occurrence was calculated to identify significantly aggregated (co-occur more than expected) and segregated (co-occur less than expected) genus pairs. A functional diversity analysis was used to calculate functional distance between genus pairs to evaluate the relationship between pair association strength and functional role. We found that the strength distribution of aggregating and segregating genus pairs does not significantly change from the late Pliocene to the early Pleistocene, even with different mammals forming the pairs, including immigrant mammals from South America. However, we did find that significant pairs, both aggregations and segregations, became more similar in their functional roles following the Plio-Pleistocene transition. Due to different mammals and ecological roles forming significant associations and the stability of co-occurrence structure across this interval, our study suggests that mammals have fundamental ways of assembling that may have been altered by humans in the present.

Non-technical Summary

Our study investigates the co-occurrence structure (types of taxonomic associations) of western North American mammal paleocommunities following the intensification of the great American biotic interchange. We address the impacts of invasion on community structure by calculating the strength of genus associations and differences in ecological roles of the associated pairs. Interestingly, despite a major climate shift and an influx of immigrant mammals from South America, co-occurrence structure remains consistent even though new mammals are forming significant associations. We suggest that this demonstrates a level of resiliency against biological invasions in mammalian communities before human impacts.

Introduction

Understanding the impacts of major ecological, environmental, and climatic transitions on biological communities is a primary focus for conservation paleobiology and modern ecologists (Hairston et al. 1960; Caswell 1976; Pearson 1977; Villéger et al. 2010; Bannar-Martin 2014; Lyons et al. 2016; Tóth et al. 2019; Fraser and Lyons 2020). The consistency of community structure is key in maintaining ecosystem functioning and resiliency against disturbances. However, the exploration and investigation of changes in community structure is exceptionally complex, because structure is driven by numerous components of biological systems and interactions (Caswell 1976). Species diversity, richness, and abundance are some of the most commonly examined components (Caswell 1976; Kempton 1979). Although ecologists are increasingly employing other metrics to examine the importance of biological relationships and functional roles on community structure (Villéger et al. 2008; Veech 2013, 2014), paleoecologists more recently have begun applying these methods to study critical intervals in the fossil record, including climate shifts and biological invasions. For example, periods of major climate transitions can lead to dramatic shifts in vegetation distributions, resulting in non-

© The Author(s), 2025. Published by Cambridge University Press on behalf of Paleontological Society. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (http://creativecommons.org/licenses/by/4.0), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

PALEOBIOLOGY
A PUBLICATION OF THE Paleontological SOCIETY

CAMBRIDGE UNIVERSITY PRESS

analogue habitats (Behling 1998; Blinnikov et al. 2002; Yang et al. 2011). Altering resource availability can cause extinctions, as well as shifts in geographic ranges (Lyons 2003, 2005; Pardi and Graham 2019). This results in the loss or gain of species interactions (Mitchell et al. 2006). Similarly, large-scale immigration likely impacts species associations, such as competition, mutualisms, and facilitations, altering the relative importance of underlying mechanisms that drive how communities of organisms assemble (Mitchell et al. 2006; Pardi and Graham 2019). Thus, evaluating changes in community structure across space and time during past disturbances is particularly informative in understanding mammalian community assembly.

The Plio-Pleistocene transition was a period of major environmental perturbation. The closing of the Isthmus of Panama intensified the intermingling of North and South American mammalian biota, while simultaneously there was the onset of Northern Hemisphere glaciation (Woodburne 2010; Bacon et al. 2016). These events led to the modification of North and South American mammal communities (Webb 1976, 1991; Marshall et al. 1982; Bacon et al. 2016; O'Dea et al. 2016). While the land bridge between North and South America was likely in place as early as 10 Ma, its low elevation meant it was continuously flooded until the late Pliocene (Whitmore and Stewart 1965; Coates et al. 2004; Woodburne 2010; Bacon et al. 2016). By 3 Ma, uplift caused by the meeting of the North and South American plates permanently divided the Gulf of Mexico and the Pacific Ocean and the ocean circulation between the Americas ceased (Coates et al. 2004; Schmidt 2007). The reorganization of ocean currents may have contributed to the onset of glaciation in the Northern Hemisphere (Huguet et al. 2022; Yi et al. 2023). The shift toward a cooling climate and the rapid expansion of glaciers in North America (Balco and Rovey 2010; Bacon et al. 2016) pushed mammals to lower latitudes (Morgan and Emslie 2010); steppe-tundra habitats were displaced southward (Morgan and Emslie 2010).

The movement of mammals between the Americas is known as the great American biotic interchange (GABI). Many studies have evaluated the taxonomic identification, functional roles, and timing of the movements (Webb 1976; Marshall et al. 1982; Carrillo et al. 2020). For example, although the Isthmus of Panama was in place by 10 Ma, the migration of mammals between continents remained minor until ~3–2.5 Ma (Webb 1976, 1991; Bacon et al. 2016) with only a few mammal taxa crossing before this time (Bacon et al. 2016). The earliest migrants into North America were giant ground sloths, which were large and more generalist in their lifestyle. By the middle to late Pliocene, armadillos, porcupines, and capybara-like rodents followed (Webb 1976; Woodburne 2010). Occurrences of South American taxa in North America were fairly rare before the Plio-Pleistocene transition, increasing by 50% afterward (Webb 1991; Bacon et al. 2016). The South American mammals that ultimately immigrated represented a diverse set of functional roles, including 36 families (Woodburne 2010). Although some of the South American mammals were successful and remain part of the North American fauna, others did not move northward beyond the subtropics or are no longer found in North America (Carrillo et al. 2020). In contrast, North American migrants into South America experienced far greater success, likely due to the higher extinction rates of native South American taxa (Carrillo et al. 2020). As a result of the rapidly changing climate and an influx of new mammals from South America, the North American fauna experienced major ecological disturbance. Although previous studies on the Plio-Pleistocene transition have evaluated migration, extinction, and origination rates across this interval (Webb 1976, 1991; Bacon et al. 2016; Carrillo et al. 2020), the impact on other aspects of community structure remains largely unexplored.

Two methods that have been used to quantify changes in mammalian community structure are pairwise co-occurrence analysis (Gotelli 2000; Lyons et al. 2016; Tóth et al. 2019) and functional trait analysis (Villéger et al. 2008, 2010; Cadotte et al. 2011). Co-occurrence analysis evaluates the extent to which pairs of species occupy the same communities (Gotelli 2000; Tóth et al. 2019). Species can be segregated (appearing together less often than expected), aggregated (appearing together more often than expected), or random (not significantly aggregating or segregating). Patterns of species associations over time and space give important insight into the mechanisms that determine how mammals filter into communities, including dispersal limitations, environment filtering, and competition (Cordero and Jackson 2019). Species functional traits (e.g., body mass, diet, life habit, locomotion) define a mammal's ecological role in an ecosystem (Villéger et al. 2008; González-Maya et al. 2016), and species associations are heavily influenced by the functional roles of the constituent species (Soliveres et al. 2014; Schamp et al. 2022). Moreover, functional traits provide a link to ecosystem functioning by interacting with assembly mechanisms in shaping communities and species associations (Villéger et al. 2008; Cadotte et al. 2011; Cadotte 2017; Stewart et al. 2023). Combining information on functional diversity with co-occurrence strengths allows us to characterize changes in communities more fully and potentially infer the underlying mechanisms driving mammalian community structure (Schamp et al. 2022). For the remainder of this paper, we will use "community structure" and "co-occurrence structure" interchangeably.

Our study aims to understand how the combined effects of climate change (e.g., glaciation) and species turnover (e.g., GABI) affected mammalian communities in western North American across the Plio-Pleistocene transition. Because other periods of glaciation (e.g., the late Pleistocene) have shown significant shifts in the structure of mammal (Lyons 2005; Pardi and Graham 2019; Tóth et al. 2019) and plant communities (Gill et al. 2009; Lyons et al. 2016), we predict similar changes in western North American mammals due to the combined influences of glaciation and immigration by South American species. Here we use the combined methodologies of functional diversity and co-occurrence to identify changes in western North American mammal community structure across the Plio-Pleistocene transition. Specifically, we compare the relative proportions of significant aggregations versus segregations before and after the transition. We also examine the relationships between functional role, association types, and the long-term survival of a genus. Finally, we investigate whether the continental origin of a genus influences the types of associations formed.

Methods and Data

Occurrence Data

Our study includes 126 North American localities spanning the Plio-Pleistocene transition (Fig. 1). Data on occurrences come from the Paleobiology Database (https://paleobiodb.org/#/) and include a total of 118 genera (Datafile1). References for the primary literature of the fossil localities can be found in Datafile4. Paleocommunities are divided into two equal time bins, pre-glaciation (4–2.5 Ma) and early Pleistocene (2.5–1 Ma). Each paleocommunity was a fossil locality or a combination of fossil localities. Paleocommunities were constrained using the following criteria: (1) because data were limited for the eastern region, we only used localities

https://doi.org/10.1017/pab.2024.53 Published online by Cambridge University Press

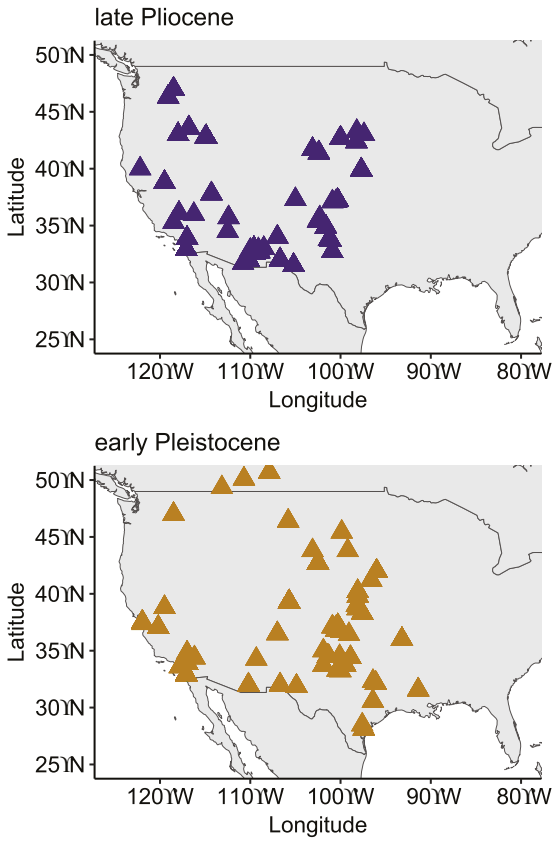


Figure 1. Map of the geographic locations of localities in the late Pliocene and early Pleistocene time intervals.

between 125°W and 90°W and less than 55°N. (2) Any paleocommunities with the same estimated date range and same longitude and latitude location were combined into a single site. (3) Due to preservation biases, only mammals above 1 kg were included. (4) Only terrestrial mammals were used, no volant or marine mammals were included in the data. Genera were defined as South American or North American based on the earliest occurrence of the family before 10 Ma. By using the family level to identify the continental origin of a genus, we ensured that the less robust fossil record of South America would not cause a potential bias in assigning continental origins. The continental species pool was also compiled using all terrestrial mammalian genera over 1 kg occurring in North America (minus Mexico) between 4 and 1 Ma.

Co-occurrence

We examined co-occurrence at the genus level. A minimum of five genera were required for a paleocommunity to be included in the co-occurrence analysis (Tóth et al. 2019). Co-occurrence analysis was run separately for the late Pliocene time bin (4–2.5 Ma) and the early Pleistocene time bin (2.5–1 Ma) using the cooccur R package (Griffith et al. 2016). The Veech (2013) pairwise method was used to determine whether significant genus pairs were either aggregated (occur together more often than expected), segregated (occur together less often than expected), or random (not significantly associated). This probabilistic method compares the observed number of times two genera occur together against the expected frequency (Veech 2006, 2013, 2014). The expected frequency is the result of multiplying the total number of sites with the probability that each genus occurs at a site: $E(N_{1,2}) = P(1) \times P(2) \times N$. Combinatorics were used to determine whether the expected frequency is significantly different from the observed frequency of two genera co-occurring. We ran 100 iterations of a random subsampling routine, pulling 30 random communities from each time bin, accounting for differences in sample size between time bins. This approach provided two *p*-values that determined whether the pair was significantly aggregating or segregating (Veech 2013). Subsequently, the Fisher's exact test mid-*P* variant provided a weight to score the strength of each significant pair. Co-occurrence strengths were calculated for each of the 100 iterations in our random sampling routine. These scores were averaged within each genus pair, providing mean co-occurrence strength for each pair accounting for variation between subsamples (Tóth et al. 2019). The raw scores were then z-transformed using the *qnorm* function in R to standardize them between positive and negative infinity (Tóth et al. 2019). This resulted in segregated pairs having negative scores and aggregated pairs having positive scores (Datafile2). The Kolmogorov-Smirnov test was conducted to determine whether there was a significant difference in the distribution of pair strengths between time bins. By identifying significant changes in pair strength distributions, we can detect shifts in community structure that may otherwise not be found when evaluating other components of community structure (species richness, diversity, etc.).

Functional Diversity and Functional Distance

To calculate functional diversity, we compiled four functional traits for each genus (body-mass category, diet, locomotion, and life habit). Traits were identified from the primary literature and online databases. The functional traits for each genus were determined based on species-level trait data found in Datafile3, where all trait references can be found. Body masses were averaged for a genus, and categorical traits were chosen based on the most prevalent category found in that genus. Body mass, diet, locomotion, and life habit were the traits chosen for this study because they are highly conserved at the genus level and interpretable from the fossil record. Locomotion and life habit are interpreted using morphological attributes of the postcranial skeleton and inferred based on phylogeny if postcranial data are not available. Body mass is estimated from teeth or postcranial measurements, depending on the specimen and mammal clade. Diet is inferred from tooth morphology or isotopic data. Furthermore, due to the young geologic age of many genera in this study, inferences about ecological roles can also be made from extant species. Numeric body-mass categories were based on Pineda-Munoz et al. (2016). They found that these body-mass categories were highly associated with the ecological role of a species (Table 1). Diet was a single category based on the most common dietary preference of the species within the genera. Locomotion was inferred from the morphological limb structure that determines a mammal's stance and was highly conserved across species within each genus. Life habitat reflected the commonly preferred habitat of the genera, and the most abundant category across species in a genus was chosen (Table 1).

Using these traits, we calculated functional diversity for all mammalian genera in our dataset to allow for direct comparisons of functional roles across both time bins. A genus by trait matrix was used to make a distance matrix with the Gower's dissimilarity method (Laliberté et al. 2014). In the distance matrix, categorical traits are not ranked or ordered, but they are identified as a 1 (match) or 0 (no match) between two genera. The distance matrix was analyzed with the *dbFD* function from the FD R package (Laliberté et al. 2014). A square-root correction was applied to

https://doi.org/10.1017/pab.2024.53 Published online by Cambridge University Press

Table 1. Functional trait categories are used to calculate functional diversity and ordinate each genus in functional trait space

Body-mass categories (g)	Locomotion	Life habit	Diet (exclusive)
Medium-sized (1000–29,512)	Plantigrade: animal walks with the sole of the foot completely on the ground.	Ground-dwelling	Mixed feeder
Large-sized (30,199–9,772,372)	Digitigrade: animal walks up on its toes.	Arboreal	Grazer
Extra-large-sized (>10,000,000)	Unguligrade: animal walks up on its nails/hooves.	Semi-fossorial	Browser
	Graviportal: animal is adapted to bearing massive weight.	Fossorial	Carnivore
	Saltatorial: animal is adapted to jumping/hopping.	Amphibious	Piscivore
			Frugivore
			Omnivore

the non-Euclidean dataset. The *dbFD* function uses a principal coordinates analysis (PCoA) to provide PCoA axes for each genus, allowing for the ordination of each genus in multidimensional space.

Subsequently, we used the four PCoA axes of each genus, provided by the functional diversity analysis, to calculate Euclidean distances between each pair of genera in multidimensional space using this Excel equation: *=SQRT(SUMXMY2(array_x,array_y))*. Array *x* is the first four axes of one genus, and array *y* is the first four axes of the second genus. Kolmogorov-Smirnov tests were used to assess differences in the distribution of functional distance between genera for significant associations between late Pliocene and early Pleistocene.

Extinction versus Survivorship of Genera

Survivorship of mammalian genera across the Plio-Pleistocene transition was determined by whether the first occurrence of each genus occurred before 1 Ma in North America. Information on first and last appearances can be found in Datafile5. We used the Paleobiology Database to collect information on the maximum and minimum date of the last appearance. We used the youngest estimated date (most recent) of their survival for all graphs in the main text, but included graphs using the oldest estimated date of extinction in the Supplementary Material.

Results

Co-occurrence Structure

The distribution of co-occurrence strengths for segregating and aggregating genus pairs does not significantly change even though the number of significant pairs declines from the late Pliocene to early Pleistocene (Kolmogorov-Smirnov: $p = 0.5731$; number of significant pairs: Pre = 291, Post = 255; Fig. 2). In addition, our results show that both time intervals have a greater proportion of aggregations than segregations. Moreover, the association strengths of segregations tend

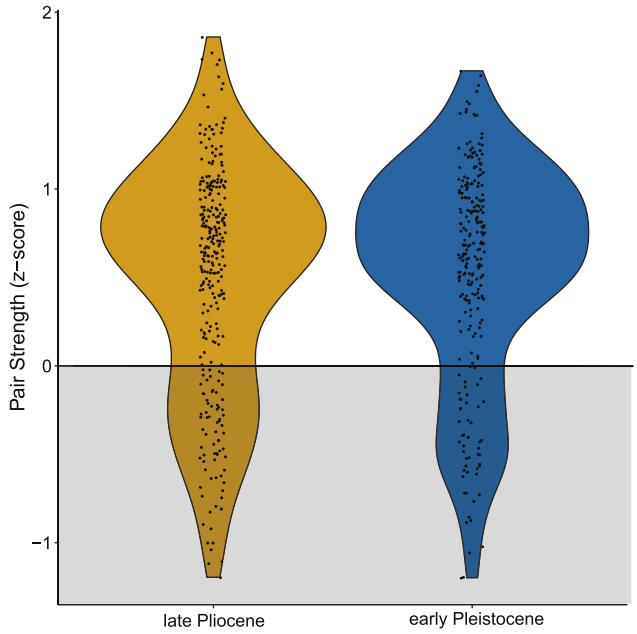


Figure 2. The distribution of z-scores for all significant pairs in pre- and post-transition time bins. Scores less than zero indicate segregations, and scores greater than zero indicate aggregations. The plot widens along the y-axis based on the number of genus pairs. The violin plot widens with a greater number of genus pairs and thins with fewer pairs.

to be weaker than those of aggregations on average. While the overall pattern of aggregations and segregations does not change, the identity of genera forming significant pairs does (DataFile1).

South American Migrants versus North American Native Mammal Co-occurrence Structure

There are 37 significant pairs that include a South American genus and a North American genus (NA-SA) in the late Pliocene time bin compared with 63 of these NA-SA pairs in the early Pleistocene (Fig. 3). Meanwhile, pairs containing only North American genera (NA-NA) decrease (Pre = 252, Post = 191). South American genera form few pairs with each other (SA-SA) in either time period (Pre = 2, Post = 1). Surprisingly, the proportion of South American genera in paleocommunities does not significantly change between the late Pliocene and early Pleistocene but does increase from 16 to 23 species and 8 to 11 genera in the early Pleistocene time bin (Kolmogorov-Smirnov: $p = 0.9651$; Fig. 4). In addition, the NA-SA pairs that occur in the early Pleistocene are not filling in ecological space vacated by the NA-NA pairs, and these areas are less densely occupied (Fig. 3). Instead, they are spread throughout the ecological space defined by co-occurrence strength and functional distance. We also find that the proportions of segregations to aggregations do not vary between genus pairs of different continental origins or the same continental origin (Fig. 5).

Functional Roles

We find that the average functional distance between significant associations decreases across the Plio-Pleistocene transition (Kolmogorov-Smirnov test: $p = 0.004$; Fig. 6). This pattern persists even when aggregated and segregated pairs are analyzed separately (Kolmogorov-Smirnov test: aggregating $p = 1.581 \times 10^{7}$ segregating $p = 0.001429$). The decrease in functional distance

https://doi.org/10.1017/pab.2024.53 Published online by Cambridge University Press

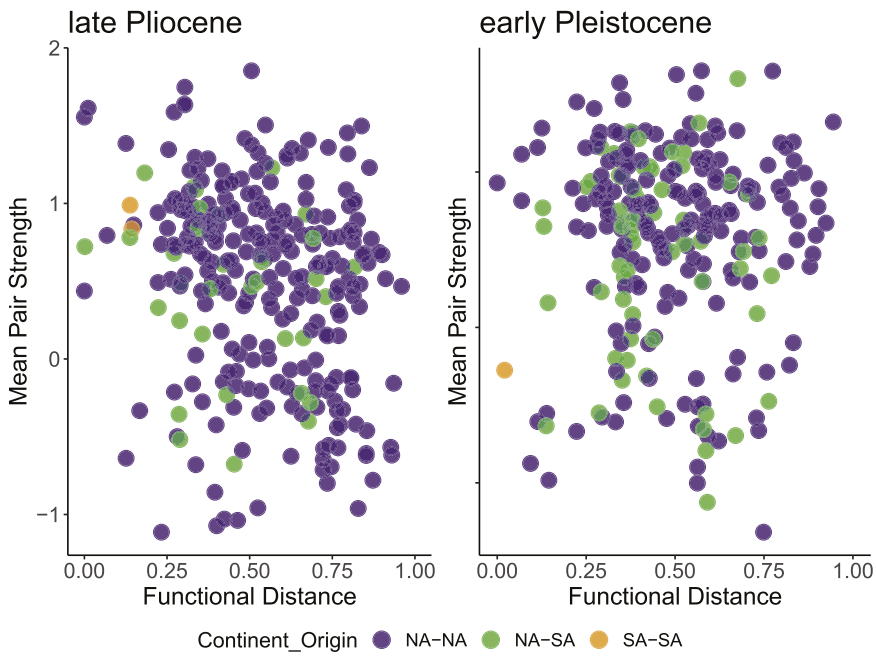


Figure 3. Graph showing the relationship between the mean strength of significant genera and the functional distance between them. The color of a point represents the origin of the genus. Functional distance is the Euclidean distance calculated between mammalian genera using the four principal coordinates analysis (PCoA) axes from the functional diversity analysis. NA, North America; SA, South America.

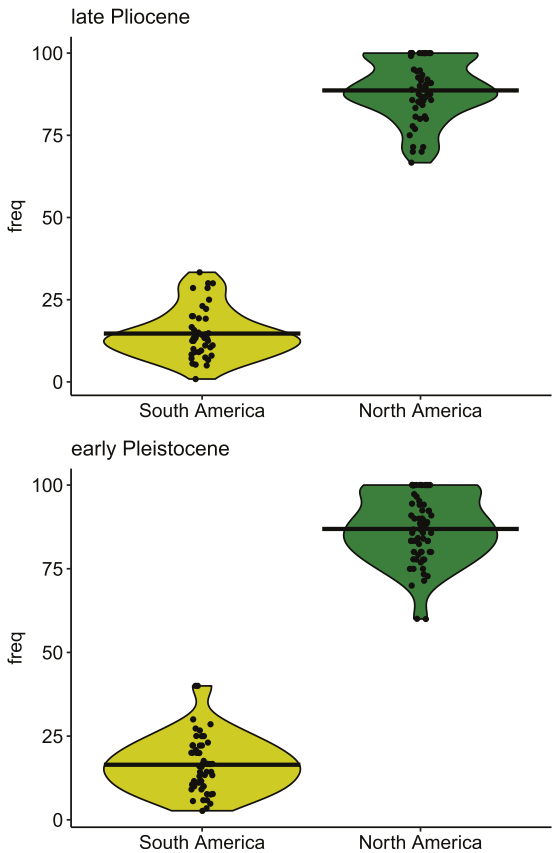


Figure 4. Proportion of South and North American genera within paleocommunities in the late Pliocene and early Pleistocene time bins. Each dot represents a paleocommunity. The proportion of North American genera within each community is represented in the dark green distribution. The proportion of South American genera within each community is represented in the yellow distribution.

of significant pairs is not caused by differences in the geographic distributions of the fossil localities between time bins (Kolmogorov-Smirnov test: $p = 0.1063$; Supplementary Figs. S1, S2). These results are also not determined by differences in community species richness distributions between each time bin (Kolmogorov-Smirnov test: $p = 0.2866$).

To further investigate the change in functional distance we found in significant pairs, we compared frequency distributions of traits within paleocommunities between the late Pliocene and early Pleistocene using all mammalian genera, not just the genera forming significant pairs. We identified changes in trait category frequency distributions within paleocommunities between the late Pliocene and early Pleistocene. We found that frequency distributions of locomotion, diet, life habit, and body-mass category change significantly (Kolmogorov-Smirnov test p-values: locomotion = 6.97×10^{8}, diet = 8.408×10^{9}, body mass = 0.0078, life habit = 1.425×10^{10}). Moreover, when all functional trait frequencies are combined for paleocommunities, there is also a significant change (Kolmogorov-Smirnov test: $p = 2.2 \times 10^{16}$.

South American versus North American Functional Roles

The diversity of South American functional types is much lower than that of North American functional types (Fig. 7), with South American mammals occupying the center of functional space, whereas North American genera have a greater abundance along the outside (Fig. 7). This pattern is more obvious when South American genera are only plotted with North American survivors (Fig. 8). However, the extinct North American genera occupy similar functional extent as the surviving genera (Fig. 8). There are no extinct South American genera that form significant associations. Most South American genera aggregate with carnivores, mixed feeders, or other browsers. The number of aggregations formed by browsers increases in the early Pleistocene (Supplementary Fig. S3). Moreover, body-size categories of significantly pairing genera change

https://doi.org/10.1017/pab.2024.53 Published online by Cambridge University Press

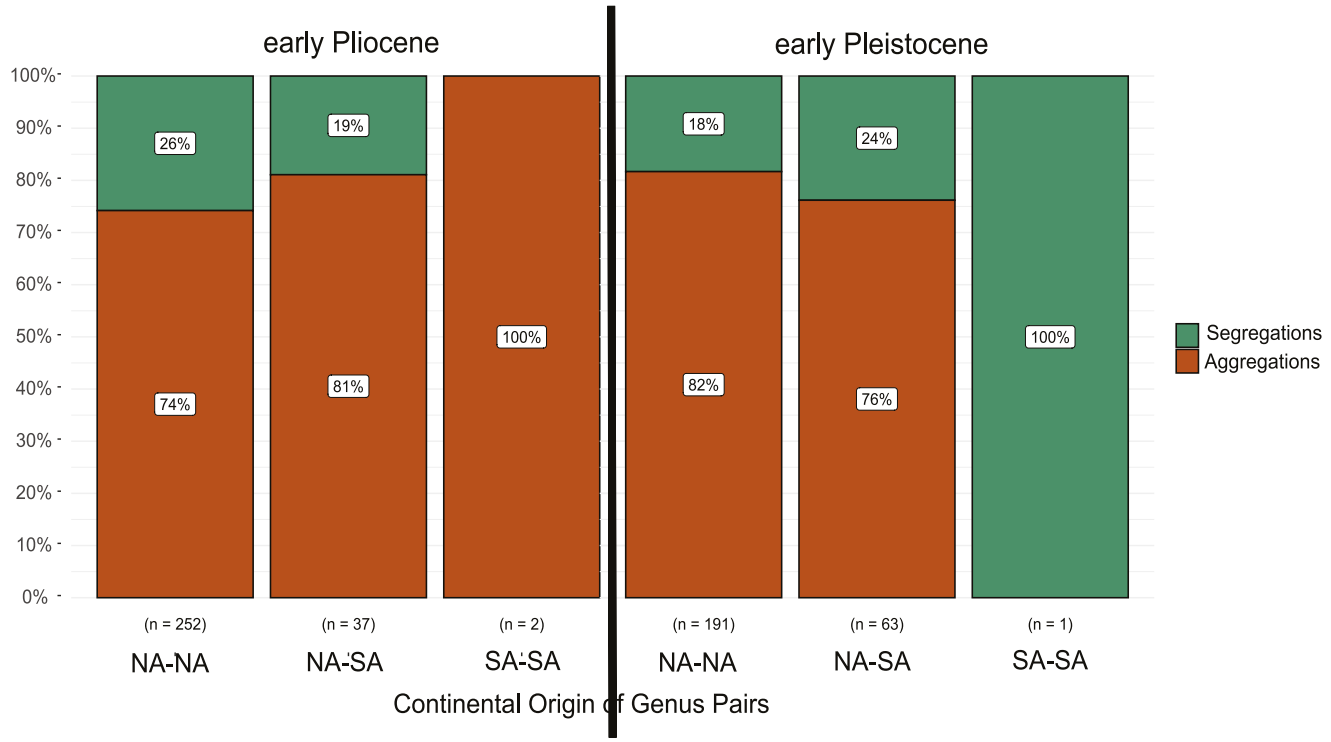


Figure 5. Within North America, proportions of genus pairs forming significant associations of the same and different continental origins. There is no significant difference in the proportion of aggregations and segregations based on the continental origins forming the pairs. NA, North America; SA, South America.

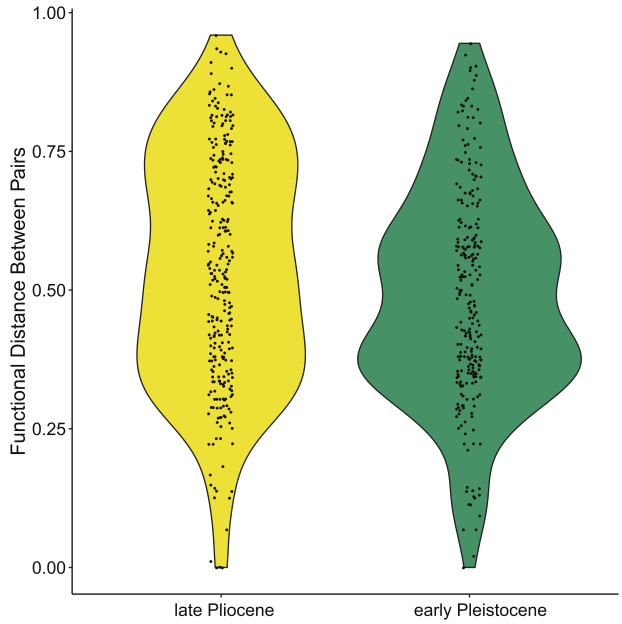


Figure 6. Distributions of functional distance between all significant pairs in the pre- and early Pleistocene times bins. Functional distance of the y-axis is found by calculating the Euclidean distance between significant genus pairs in multidimensional trait space. The violin plot widens with a greater number of genus pairs and thins with fewer pairs.

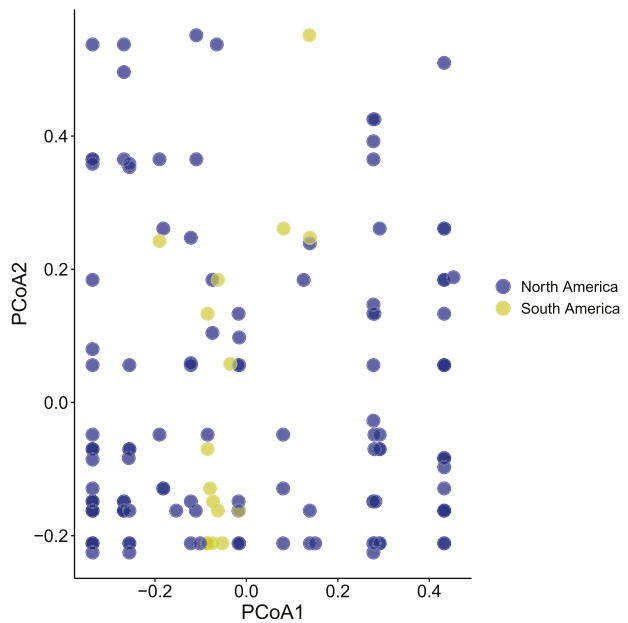


Figure 7. Distribution of North and South American genera in multidimensional space based on functional diversity principal coordinates analysis (PCoA) axes. South American migrants are primarily concentrated in the lower to mid-region of trait space with few overlapping North American genera.

over time (Supplementary Figs. S4–S10). NA-SA pairs show an increase in associations between large- and medium-sized genera, as well as associations between large-bodied genera across the transition. In contrast, NA-NA pairs between medium- and large-sized mammals and between large-bodied genera decline in abundance following the Plio-Pleistocene transition.

Discussion

Amid the onset of a major climate transition (Bartoli et al. 2005; Bacon et al. 2016; Yi et al. 2023) and the escalation of the GABI (Webb 1976; Woodburne 2010; Bacon et al. 2016), western North American mammal paleocommunities experience major ecological disturbance, yet community structure remains stable regarding genus associations. We find no difference in the proportion of

https://doi.org/10.1017/pab.2024.53 Published online by Cambridge University Press

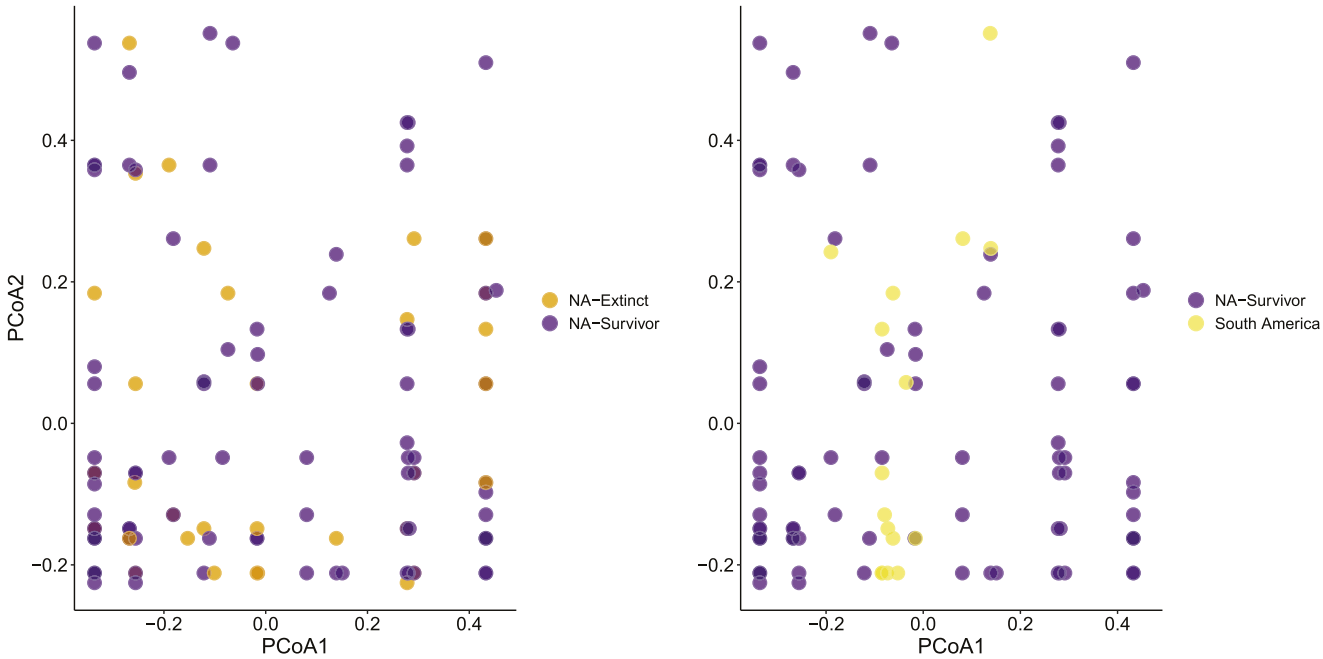


Figure 8. Left, Ordination of extinct and surviving North American genera in functional space using the first two principal coordinates analysis (PCoA) axes. **Right,** Ordination of surviving North American genera and South American immigrants in functional space using the first two PCoA axes. South American migrants are primarily concentrated in the lower- to mid-region of trait space with few overlapping North American genera.

aggregated and segregated genus pairs across the Plio-Pleistocene transition, and no significant differences in the strengths of the associations (Figs. 2, 5). Our results are consistent with several recent studies that demonstrated community resiliency across major ecological and environmental change. Specifically, previous studies have shown that co-occurrence structure over evolutionary timescales is consistent across periods of climate change and mass extinctions unless humans are part of the ecosystem (Lyons et al. 2016; Tóth et al. 2019). Indeed, plant and mammalian communities primarily form aggregations rather than segregations for approximately 300 Ma until the Holocene (Lyons et al. 2016). In our study, western North American mammals shifted their distributions in response to climate change and the invasion of new species, forming new associations. Furthermore, they were able to maintain co-occurrence structure despite the formation of non-analogue habitats (Fig. 2). The individualistic responses to glaciation by vegetative species led to non-analogue habitats with the expansion and retraction of their geographic ranges (Jackson and Overpeck 2000; Williams and Jackson 2007). Thus, even with new members, different climatic gradients, and formation of non-analogue habitats due to glaciation (Jackson and Overpeck 2000; Williams and Jackson 2007), mammalian genera still formed the same types of associations in similar proportions (Figs. 2, 5). Our study, among others, may suggest that mammals may have a fundamental way of assembling that is maintained across intervals of climatic, ecological, and environmental shifts in the absence of human perturbations (Lyons et al. 2016; Tóth et al. 2019; Cooke et al. 2022).

Mammals of South American origin displayed the same co-occurrence structure found in North American mammals, further supporting the idea that mammals have a fundamental way of assembling (Fig. 5). Despite being from a continent that was isolated for millions of years, the mammals still form the same proportion of aggregations and segregations as their North American counterparts (Fig. 5). An increasing number of significant pairs including South American genera following the Plio-Pleistocene transition did not change the proportion of aggregated to segregated pairs. The increase in South American associations in the early Pleistocene is likely due to a heightened rate of migration between continents at ~3–2.5 Ma triggered by the closing of the Isthmus of Panama (Fig. 3; Schmidt 2007; O'Dea et al. 2016; Huguet et al. 2022). Before this period, few South American genera had reached western North America and were a smaller percentage of the North American communities (Woodburne 2010). However, it is unclear if South American genus co-occurrence structure shows a similar pattern because these genera are primarily paired with North American genera. Future studies are needed to determine whether paleocommunities of primarily South American genera would result in a similar community structure.

The success of some South American mammals infiltrating the North American fauna may be because they concentrate in an area of trait space underutilized by North American genera, who more densely occupy the outside of trait space (Fig. 7). The insinuation of South American genera into niche space is at least partially responsible for the shorter functional distances among associating genera following the glaciation event, as many of the South American genera were taxonomically and functionally unique (Marshall et al. 1982), for instance, the large, browsing, plantigrade clade of ground sloths. Ground sloths form more significant pairs with North American genera than any other South American clade. Multiple genera of ground sloths migrated into North America millions of years before the closing of the isthmus, providing time for them to form ecological relationships and even evolve species endemic to North America (Webb 1976; Woodburne 2010). Furthermore, *Glyptotherium* (glyptodonts) and *Erethizon* (porcupines) also form a large number of significant pairs with North American genera following the glaciation event. Both genera commonly form segregations with grazing mammals such as horses, camels, and mammoths and aggregations with mixed feeders and other browsing mammals. Ground sloths, glyptodonts, and porcupines have a strong presence in early Pleistocene paleocommunities, likely reflecting

https://doi.org/10.1017/pab.2024.53 Published online by Cambridge University Press

their ecological success (Datafile1). Glyptodonts and ground sloths survive until the megafaunal extinction, when many large-bodied mammals go extinct (McDonald 2021; Carlini et al. 2022). Porcupines survive this extinction and remain a common mammal in the North American fauna today (Ahlberg 1969). Due to the uniqueness of their functionality, there does not appear to be a similarity between the types of North American genera that stop forming pairs and the South American genera that begin building strong associations.

Extinct North American genera display a wide variety of functional roles. In fact, their distribution in functional space is similar to that of surviving genera (Fig. 8). Furthermore, the extinct genera, like surviving genera, do not overlap with South American functional roles, suggesting that any turnover in North American genera was not likely driven by competition with South American immigrants (Fig. 8). However, the landscape is thought to have opened up, with a spread of drier savanna-like habitats with the onset of glaciation (Morgan and Emslie 2010). For example, *Borophagus* and *Buisnictis* were two North American genera that had a strong presence pre-glaciation, but quickly diminished following the Plio-Pleistocene transition. *Borophagus* was a genus of canid with robust limbs thought to specialize at ambush hunting in closed habitats (Bōgner and Samuels 2022). *Buisnictis* is a medium-sized transitional genus of skunk that gave rise to modern skunks (Wang et al. 2014). Based on inferences about the habitat preferences of many of the extinct genera, it is possible that many closed-habitat mammals eventually went extinct due to the opening of the landscape. Nevertheless, more quantitative assessment is needed on this topic, and acquiring evidence of habitat preferences for individual genera is outside the scope of this paper.

Ecological theory predicts that factors such as invasion and climate change have large effects on community structure (Lomolino 1986; Robinson and Dickerson 1987; Schwindt et al. 2001; Spooner and Vaughn 2008; Smith et al. 2016; Tóth et al. 2019). For example, the composition of Swedish bird communities has changed rapidly in response to varying summer temperatures since the 1960s (Lindström et al. 2013). Similarly, the recent invasion of European house sparrows into west Mexico led to a significant decrease in richness but increased bird abundances, resulting in a dramatic difference between invaded and non-invaded bird communities (MacGregor-Fors et al. 2010). Interestingly, many studies examining changes in community structure using the fossil record before human impacts do not find significant changes in response to these factors (Rodríguez 2004; Lyons et al. 2016; Fraser and Lyons 2020). For instance, the immigration of three new orders of mammals from Asia around ~56 Ma and a rapid warming event did not result in community structure changes (Fraser and Lyons 2020). These major environmental and ecological events in the fossil record have been explored at various temporal grades. Although our study, like many paleoecological projects, works at a large temporal grade, those using shorter timescales (e.g., 1000 years or fewer) (Bercovici et al. 2012; Wing et al. 2012; Lyons et al. 2016) also find structural consistency across major events (Lyons et al. 2016). When looking at co-occurrence structure specifically, there is no relationship between the temporal grade of the data and the proportion of aggregated to segregated pairs (Lyons et al. 2016). Furthermore, taphonomic biases that vary over space and time favor the fossilization of different habitats, body types, and sizes. Regardless, paleoecological studies working in different time periods and geographic regions still find consistency in community structure across major transitional events except for the climate shifts and extinctions that occur at the terminal Pleistocene to early Holocene (Lyons et al. 2016; Tóth et al. 2019; Cooke et al. 2022). The onset of glaciation in the terminal Pleistocene led to non-analogue habitats due to range shifts in plants, drastically altering the landscape (Blinnikov et al. 2002; Williams and Jackson 2007; Yang et al. 2011). This suggests that the glaciation at the Plio-Pleistocene transition should have led to similar environmental changes and, ultimately, similar impacts on mammalian communities. Nevertheless, community structure is not significantly altered at the Plio-Pleistocene transition. This difference is likely not driven by taphonomic biases or different temporal grades, but rather is caused by the presence of humans during the terminal Pleistocene.

Conclusion

The closing of the Isthmus of Panama contributes to a number of ecological, environmental, and climatic events that alters the composition of western North American mammal communities. South American mammals increase their rate of migration across the land bridge with some genera successfully joining the North American fauna and filling an area of niche space with low occupancy and redundancy. Moreover, a shift in climate results in extensive glaciation in the Northern Hemisphere, altering the landscape and forcing range shifts. Fascinatingly, these events do not lead to a reorganization in community structure. While the continental origin and ecological roles of the genera forming strong associations are different, the types of associations remain the same (Figs. 2, 3). This suggests that mammalian communities can remain stable across periods of major environmental, ecological, and climatic changes without human disturbance. The deep, evolutionary timeline exhibiting these consistent mammalian community patterns across major transitions is evidence for the importance of preserving natural mechanisms.

Acknowledgments. Support for this research was provided by NSF-DEB 1257625 (SKL, AKB, NG) and 2051255 (SKL, SAFD, CVL, PJW). This is E6 (Ecological and Evolutionary Effects of Extinction and Ecosystem Engineers RCN) publication no. 12, Evolution of Terrestrial Ecosystems Program publication no. 414, and PBDB publication 505.

Competing Interests. The authors declare that they have no competing interests.

Data Availability Statement. All data are available in the main text or in the Supplementary Material, the code, and the data, which are also deposited on Dryad at: https://doi.org/10.5061/dryad.kprr4xhf7.

Literature Cited

Ahlberg, H. D. 1969. Geographical variation in the North American porcupine *Erethizon* (Linnaeus) Cuvier (Mammalia, Rodentia). Ph.D. dissertation. Boston University Graduate School, Boston, Mass. ProQuest Dissertations and Theses, https://www.proquest.com/docview/302480385/citation/F06C81401474461PQ/1.

Bacon, C. D., P. Molnar, A. Antonelli, A. J. Crawford, C. Montes, and M. Camila Vallejo-Pareja. 2016. Quaternary glaciation and the Great American Biotic Interchange. *Geology* **44**:375–378.

Balco, G., and C. W. Rovey II. 2010. Absolute chronology for major Pleistocene advances of the Laurentide Ice Sheet. *Geology* **38**:795–798.

Bannar-Martin, K. H. 2014. Primate and nonprimate mammal community assembly: the influence of biogeographic barriers and spatial scale. *International Journal of Primatology* **35**:1122–1142.

Bartoli, G., M. Sarnthein, M. Weinelt, H. Erlenkeuser, D. Garbe-Schönberg, and D. W. Lea. 2005. Final closure of Panama and the onset of Northern Hemisphere glaciation. *Earth and Planetary Science Letters* **237**:33–44.

https://doi.org/10.1017/pab.2024.53 Published online by Cambridge University Press

Behling, H. 1998. Late Quaternary vegetational and climatic changes in Brazil. *Review of Palaeobotany and Palynology* **99**:143–156.

Bercovici, A., V. Vajda, D. Pearson, U. Villanueva-Amadoz, and D. Kline. 2012. Palynostratigraphy of John's Nose, a new Cretaceous–Paleogene boundary section in southwestern North Dakota, USA. *Palynology* **36**(Suppl. 1):36–47.

Blinnikov, M., A. Busacca, and C. Whitlock. 2002. Reconstruction of the Late Pleistocene grassland of the Columbia Basin, Washington, USA, Based on phytolith records in loess. *Palaeogeography, Palaeoclimatology, Palaeoecology* **177**:77–101.

Bögner, E., and J. X. Samuels. 2022. The first canid from the Gray Fossil Site in Tennessee: new perspective on the distribution and ecology of *Borophagus*. *Journal of Paleontology* **96**:1379–1389.

Cadotte, M. W. 2017. Functional traits explain ecosystem function through opposing mechanisms. *Ecology Letters* **20**:989–996.

Cadotte, M. W., K. Carscadden, and N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* **48**:1079–1087.

Carlini, A. A., J. D. Carrillo-Briceño, A. Jaimes, O. Aguilera, A. E. Zurita, J. Iriarte, and M. R. Sánchez-Villagra. 2022. Damaged glyptodontid skulls from late Pleistocene sites of northwestern Venezuela: evidence of hunting by humans? *Swiss Journal of Palaeontology* **141**:11.

Carrillo, J. D., S. Faurby, D. Silvestro, A. Zizka, C. Jaramillo, C. D. Bacon, and A. Antonelli. 2020. Disproportionate extinction of South American mammals drove the asymmetry of the Great American Biotic Interchange. *Proceedings of the National Academy of Sciences USA* **117**:26281–2687.

Caswell, H. 1976. Community structure: a neutral model analysis. *Ecological Monographs* **46**:327–354.

Coates, A. G., L. S. Collins, M.-P. Aubry, and W. A. Berggren. 2004. The geology of the Darien, Panama, and the Late Miocene–Pliocene collision of the Panama Arc with northwestern South America. *GSA Bulletin* **116**: 1327–1344.

Cooke, R., W. Gearty, A. S. A. Chapman, J. Dunic, G. J. Edgar, J. S. Lefcheck, G. Rilov, et al. 2022. Anthropogenic disruptions to longstanding patterns of trophic-size structure in vertebrates. *Nature Ecology and Evolution* **6**: 684–692.

Cordero, R. D., and D. A. Jackson. 2019. Species-pair associations, null models, and tests of mechanisms structuring ecological communities. *Ecosphere* **10**: e02797.

Fraser, D., and S. K. Lyons. 2020. Mammal community structure through the Paleocene–Eocene thermal maximum. *American Naturalist* **196**:271–290.

Gill, J. L., J. W. Williams, S. T. Jackson, K. B. Lininger, and G. S. Robinson. 2009. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* **326**:1100–1103.

González-Maya, J. F., L. R. Víquez-R, A. Arias-Alzate, J. L. Belant, and G. Ceballos. 2016. Spatial patterns of species richness and functional diversity in Costa Rican terrestrial mammals: implications for conservation. *Diversity and Distributions* **22**:43–56.

Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* **81**:2606–2621.

Griffith, D. M., J. A. Veech, and C. J. Marsh. 2016. Cooccur: probabilistic species co-occurrence analysis in R. *Journal of Statistical Software* **69**(Code Snippet 2), https://doi.org/10.18637/jss.v069.c02.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* **94**:421–425.

Huguet, C., A. Jaeschke, and J. Rethemeyer. 2022. Paleoclimatic and palaeoceanographic changes coupled to the Panama Isthmus closing (13–4 Ma) using organic proxies. *Palaeogeography, Palaeoclimatology, Palaeoecology* **601**:111139.

Jackson, S. T., and J. T. Overpeck. 2000. Responses of plant populations and communities to environmental changes of the Late Quaternary. *Paleobiology* **26**:194–220.

Kempton, R. A. 1979. The structure of species abundance and measurement of diversity. *Biometrics* **35**:307–321.

Laliberté, E., P. Legendre, and B. Shipley. 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology, R package version 1.0-12.3. https://CRAN.R-project.org/package=FD, accessed 12 March 2019.

Lindström, Å., M. Green, G. Paulson, H. G. Smith, and V. Devictor. 2013. Rapid changes in bird community composition at multiple temporal and spatial scales in response to recent climate change. *Ecography* **36**:313–322.

Lomolino, M. V. 1986. Mammalian community structure on islands: the importance of immigration, extinction and interactive effects. *Biological Journal of the Linnean Society* **28**(1–2):1–21.

Lyons, S. K. 2003. A quantitative assessment of the range shifts of Pleistocene mammals. *Journal of Mammalogy* **84**:385–402.

Lyons, S. K. 2005. A quantitative model for assessing community dynamics of Pleistocene mammals. *American Naturalist* **165**:E168–E185.

Lyons, S. K., K. L. Amatangelo, A. K. Behrensmeyer, A. Bercovici, J. L. Blois, M. Davis, W. A. DiMichele, et al. 2016. Holocene shifts in the assembly of plant and animal communities implicate human impacts. *Nature* **529**:80–83.

MacGregor-Fors, I., L. Morales-Pérez, J. Quesada, and J. E. Schondube. 2010. Relationship between the presence of House Sparrows (*Passer domesticus*) and Neotropical bird community structure and diversity. *Biological Invasions* **12**:87–96.

Marshall, L. G., S. D. Webb, J. J. Sepkoski, and D. M. Raup. 1982. Mammalian evolution and the Great American Interchange. *Science* **215**:1351–1357.

McDonald, H. 2021. Yukon to the Yucatan: habitat partitioning in North American Late Pleistocene ground sloths (Xenarthra, Pilosa). *Journal of Palaeosciences* **70**:237–251.

Mitchell, C. E., A. A. Agrawal, J. D. Bever, G. S. Gilbert, R.A. Hufbauer, J. N. Klironomos, J. L. Maron, et al. 2006. Biotic interactions and plant invasions. *Ecology Letters* **9**:726–740.

Morgan, G. S., and S. D. Emslie. 2010. Tropical and Western influences in vertebrate faunas from the Pliocene and Pleistocene of Florida. *Quaternary International* **217**:143–158.

O'Dea, A., H. A. Lessios, A. G. Coates, R. I. Eytan, S. A. Restrepo-Moreno, A. L. Cione, L. S. Collins, et al. 2016. Formation of the Isthmus of Panama. *Science Advances* **2**:e1600883.

Pardi, M. I., and R. W. Graham. 2019. Changes in small mammal communities throughout the Late Quaternary across eastern environmental gradients of the United States. *Quaternary International* **530**–531:80–87.

Pearson, D. L. 1977. A pantropical comparison of bird community structure on six lowland forest sites. *The Condor* **79**:232–244.

Pineda-Munoz, S., A. R. Evans, and J. Alroy. 2016. The relationship between diet and body mass in terrestrial mammals. *Paleobiology* **42**:659–669.

Robinson, J. F., and J. E. Dickerson. 1987. Does invasion sequence affect community structure? *Ecology* **68**:587–595.

Rodríguez, J. 2004. Stability in Pleistocene Mediterranean mammalian communities. *Palaeogeography, Palaeoclimatology, Palaeoecology* **207**:1–22.

Schamp, B. S., R. Gridzak, D. A. Greco, T. M. Lavender, A. Kunasingam, J. A. Murtha, A. M. Jensen, A. Pollari, and L. Santos. 2022. Examining the relative influence of dispersal and competition on co-occurrence and functional trait patterns in response to disturbance. *PLoS ONE* **17**: e0275443.

Schmidt, D. 2007. The closure history of the Panama Isthmus: evidence from isotopes and fossils to models and molecules. Pp. 429–444 *in* M. Williams, A. M. Haywood, F. J. Gregory, and D. N. Schmidt, eds. *The Micropalaeontological Society, Special Publications: Deep-time perspectives on climate change: marrying the signal from computer models and biological proxies*. Geological Society of London, London.

Schwindt, E., A. Bortolus, and O. Osvaldo Iribarne. 2001. Invasion of a reef-builder polychaete: direct and indirect impacts on the native benthic community structure. *Biological Invasions* **3**:137–149.

Smith, F. A., C. P. Tomé, E.A. E. Smith, S. K. Lyons, S. D. Newsome, and T. W. Stafford. 2016. Unraveling the consequences of the terminal Pleistocene megafauna extinction on mammal community assembly. *Ecography* **39**: 223–239.

Soliveres, S., F. T. Maestre, M. A. Bowker, R. Torices, J. L. Quero, M. García-Gómez, O. Cabrera, et al. 2014. Functional traits determine plant co-occurrence more than environment or evolutionary relatedness in global drylands. *Perspectives in Plant Ecology, Evolution and Systematics* **16**:164–173.

Spooner, D. E., and C. C. Vaughn. 2008. A trait-based approach to species' roles in stream ecosystems: climate change, community structure, and material cycling. *Oecologia* **158**:307–317.

https://doi.org/10.1017/pab.2024.53 Published online by Cambridge University Press

Stewart, K., **C. P. Carmona**, **C. Clements**, **C. Venditti**, **J. A. Tobias, and M. González-Suárez**. 2023. Functional diversity metrics can perform well with highly incomplete data sets. *Methods in Ecology and Evolution* **14**:2856–2872.

Tóth, A. B., **S. K. Lyons**, **W. A. Barr**, **A. K. Behrensmeyer**, **J. L. Blois**, **R. Bobe**, **M. Davis**, et al. 2019. Reorganization of surviving mammal communities after the end-Pleistocene megafaunal extinction. *Science* **365**:1305–1308.

Veech, J. A. 2006. A probability-based analysis of temporal and spatial co-occurrence in grassland birds. *Journal of Biogeography* **33**:2145–2153.

Veech, J. A. 2013. A probabilistic model for analysing species co-occurrence. *Global Ecology and Biogeography* **22**:252–260.

Veech, J. A. 2014. The pairwise approach to analysing species co-occurrence. *Journal of Biogeography* **41**:1029–1035.

Villéger, S., **N. W. H. Mason, and D. Mouillot**. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**:2290–2301.

Villéger, S., **J. Ramos Miranda**, **D. Flores Hernández, and D. Mouillot**. 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications* **20**:1512–1522.

Wang, X., **Ó. Carranza-Castañeda, and J. Jorge Aranda-Gómez**. 2014. A transitional skunk, *Buisnictis metabatos* sp. nov. (Mephitidae, Carnivora), from Baja California Sur and the role of southern refugia in skunk evolution. *Journal of Systematic Palaeontology* **12**:291–302.

Webb, S. D. 1976. Mammalian faunal dynamics of the Great American Interchange. *Paleobiology* **2**:220–34.

Webb, S. D. 1991. Ecogeography and the Great American Interchange. *Paleobiology* **17**:266–280.

Whitmore, Frank C., Jr., and Robert H. Stewart. 1965. Miocene mammals and Central American seaways. *Science* **148**:180–185.

Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* **5**:475–482.

Wing, S. L., **C. A. E. Strömberg**, **L. J. Hickey**, **F. Tiver**, **B. Willis**, **R. J. Burnham, and A. K. Behrensmeyer**. 2012. Floral and environmental gradients on a Late Cretaceous landscape. *Ecological Monographs* **82**:23–47.

Woodburne, M. O. 2010. The Great American Biotic Interchange: dispersals, tectonics, climate, sea level and holding pens. *Journal of Mammalian Evolution* **17**:245–264.

Yang, H., **M. Wu**, **W. Liu**, **Z. Zhang**, **N. Zhang, and S. Wan**. 2011. Community structure and composition in response to climate change in a temperate steppe. *Global Change Biology* **17**:452–465.

Yi, L., **M. Medina-Elizalde**, **L. Tan**, **D. B. Kemp**, **Y. Li**, **G. Kletetschka**, **Q. Xie**, et al. 2023. Plio-Pleistocene deep-sea ventilation in the Eastern Pacific and potential linkages with Northern Hemisphere glaciation. *Science Advances* **9**: eadd1467.

https://doi.org/10.1017/pab.2024.53 Published online by Cambridge University Press