PALEONTOLOGY

Reorganization of surviving mammal communities after the end-Pleistocene megafaunal extinction

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Large mammals are at high risk of extinction globally. To understand the consequences of their demise for community assembly, we tracked community structure through the end-Pleistocene megafaunal extinction in North America. We decomposed the effects of biotic and abiotic factors by analyzing co-occurrence within the mutual ranges of species pairs. Although shifting climate drove an increase in niche overlap, co-occurrence decreased, signaling shifts in biotic interactions. Furthermore, the effect of abiotic factors on co-occurrence remained constant over time while the effect of biotic factors decreased. Biotic factors apparently played a key role in continental-scale community assembly before the extinctions. Specifically, large mammals likely promoted co-occurrence in the Pleistocene, and their loss contributed to the modern assembly pattern in which co-occurrence frequently falls below random expectations.

Human activities have put extant large-bodied mammals at high risk of extinction (1), and their eventual loss may have severe ecological repercussions. For example, the loss of ecosystem engineers such as megaherbivores has the capacity to alter entire landscapes (2–4). Such human-mediated extinctions will have impacts lasting far beyond our lifetimes, making it important to examine long-term records of past extinctions to forecast the consequences of current biodiversity loss. A key example is the catastrophic and approximately synchronous (5) extinction of large mammals, including mammoths and saber-toothed cats, at the end of the Late Pleistocene in North America (6). The rich and highly resolved Pleistocene and Holocene fossil record provides a unique opportunity to explore how extinction alters communities.

The causes of Pleistocene extinctions have been debated for decades (7, 8). In light of the current biodiversity crisis, recent work has focused on understanding their ecological and evolutionary legacies instead (9). A compelling picture of ecological transformation across the continents has emerged, including the disappearance of the mammoth steppe (2), changes in vegetation and fire regimes (10, 11), loss of functional groups (12), rearrangement of interactions (13, 14), and shifts in global biogeochemistry (15) and biophysical feedback systems (16). However, empirical studies of changes in mammal community structure, including the extinction of most species over 40 kg (8), have often been centered on individual fossil deposits (17) or particular taxa [e.g., (18, 19), but see (20)].

Here, we used occupancy, niche size, and patterns of species co-occurrence to examine community assembly patterns of surviving large mammals across the Pleistocene-Holocene transition. We examined end-Pleistocene (21,000 to 11,000 years ago), Holocene (11,000 to 2000 years ago), and Recent (2000 years ago to the present) (21) mammal occurrence data (fig. S1) drawn from the FAUNMAP II database (22), comprising 93 species (>1 kg). Only survivor-survivor pairs were analyzed to ensure that community changes were not simply a result of reduced diversity or lost associations involving extinct species. Every possible species pair received an associ-

ation weight that quantifies how strongly the two co-occur. We refer to a species pair as aggregated when the species occur together more often than expected by chance, and segregated when they co-occur less often than expected. Segregations received negative weights. Broad shifts in community assembly may be influenced by both extinction and climate change. We estimated the contributions of these two factors by isolating the relative effects of abiotic and biotic changes on the association of each survivor-survivor pair across this interval.

Species associations are caused by a combination of abiotic and biotic drivers, which can be differentiated by first establishing species' geographic and environmental constraints. Geographic envelopes were constructed using Lambert azimuthal equal-area projected coordinates. The climatic envelope of each species was calculated from mean annual temperature, precipitation, temperature seasonality, and precipitation seasonality of sites falling within the species' geographic envelopes. Climate estimates were extracted from downscaled paleoclimate simulations (23, 24) and z-transformed. All envelopes were calculated with Blonder's hypervolumes (25). The set of sites falling within both geographic and climatic envelopes (fig. S2) was defined as the potential range of each species. The potential range represents sites where the occurrence of a species is not constrained by climate or dispersal ability. We also calculated background climatic and geographic hypervolumes for each species in each time interval to quantify how much of the available geographic and environmental space is being occupied by each species (21).

We calculated the strength and direction of pairwise co-occurrence of species pairs with the mid-P variant of Fisher's exact test, which provides an association weight for each pair (26). We then individually calculated biotic and abiotic components of co-occurrence, such that the sum of the association weights of these two components equals the original association weight (fig. S3). We did this by calculating the association weight within the mutual potential range (i.e., the sites remaining after accounting for abiotic limits for both species), which represents the component of each association regulated by biotic factors. The abiotic component was defined as the difference between the full association and its biotic component (21). The abiotic component of a pair received a positive association weight if species had similar niches, and
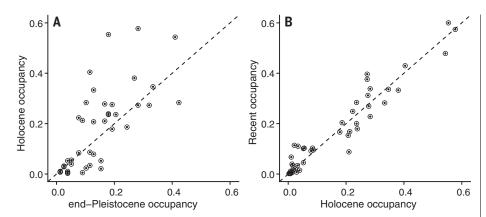
Fig. 1. Comparison of survivor occupancy across time intervals. (**A**) End-Pleistocene to Holocene (N = 44). (**B**) Holocene to Recent (N = 45). Points are species. The line of unity is shown.
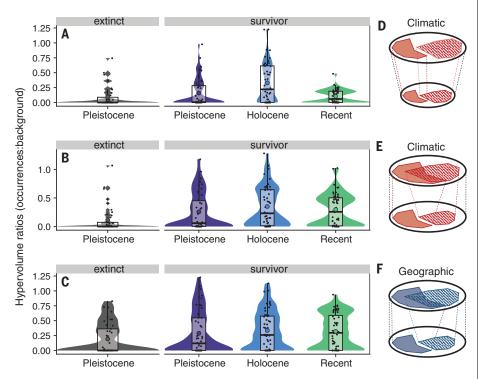

Fig. 2. Increases in niche overlap. (**A** to **F**) Climatic [(A) and (B)] and geographic (C) envelopes of species are compared to pooled climate envelopes (A) and background envelopes [(B) and (C)] in each time interval. In (A), larger ratios correspond with larger niches because niche space expands, as illustrated by oval sizes in (D); in (B) and (C), larger ratios result from proportionately higher fill that causes increased niche overlap [(E) and (F)]. In (A) to (C), each shaded distribution sums to an area of 1; circles are means. In (D) to (F), shared polygons represent hypothetical species niches.

negative if their niches were disparate (fig. S3). The biotic and abiotic components of a pair may have the same or opposite signs, and when the latter occurs, the full association weight may be close to 0 (fig. S3). Using this framework, we evaluated changes in co-occurrence patterns and their components across the Pleistocene-Holocene transition and into the Recent.

Across the Pleistocene-Holocene transition, common surviving species became even more common and rare species remained the same

or became rarer (Fig. 1A). There were no substantial changes in occupancy patterns between the Holocene and the Recent (Fig. 1B). Extinction victims had smaller climatic and geographic envelopes than survivors in the end-Pleistocene (Fig. 2). On average, climatic and geographic envelopes of surviving species expanded from the end-Pleistocene to the Holocene, even when compared to background variation (i.e., as a proportion of the total space each species could potentially occupy; Fig. 2).

Aggregations were dominant for survivor pairs in the end-Pleistocene, and segregations increased in the Holocene and Recent (Fig. 3, E and F). There was also a marked decrease in association weights for aggregations and an increase for segregations over the Pleistocene-Holocene transition (Fig. 3, K and L). We considered and ruled out several confounding factors such as sampling and dating biases (21). Observed occupancy changes between the time intervals predict stronger associations and an increased proportion of aggregations (21). Although this may partially explain why segregations became stronger, it cannot explain the increase in proportion of segregations or the decrease in aggregation strengths. When associations were split into their biotic and abiotic components, end-Pleistocene associations calculated within mutual potential ranges of pairs (i.e., biotic associations) were also dominated by aggregations, which diminished both in mean weight (Fig. 3I) and as a proportion of the pairs (Fig. 3C) across the Pleistocene-Holocene transition, whereas segregations increased in mean weight and proportionally (Fig. 3, D and J). Abiotic associations (i.e., the difference between the full association and the biotic association) exhibited the opposite pattern (Fig. 3, A, B, G, and H). Note that associations due to abiotic components were typically segregations, whereas those due to biotic components were typically aggregations, and this pattern was greatly weakened but not overturned by the trends described above.

The Pleistocene-Holocene transition was characterized by substantial changes in occupancy (Fig. 1), niche size (Fig. 2), and association patterns (Fig. 3). The fact that survivors of the extinction exhibited larger potential ranges than the victims (Fig. 2) is consistent with the concept that specialists with narrow ranges are at higher risk of extinction (1). The expansion of climatic niche fill in the Holocene may reflect the filling of empty niche space after competitive release.

The overall shift toward segregations starting in the Holocene resulted from changes in the relative effects of the biotic and abiotic components of species co-occurrence. Increasing climatic and geographic niche fill (Fig. 2E) drove increasing potential range overlap between pairs in the Holocene (fig. S4), and this caused the shift toward aggregations in abiotic associations. In contrast, co-occurrence decreased within mutual potential ranges (i.e., biotic associations; Fig. 3, C and D). All else being equal, these opposing forces might have nullified any trend in the full associations. We observe a trend, however, because of the change in the relative importance of biotic and abiotic factors, which can be quantified using the average magnitude (absolute value) of association weights within each component. Species responses to environmental factors contributed consistently to community assembly over time, despite the striking climatic changes driving species dispersal over this interval (27), whereas co-occurrence patterns due to biotic interactions diminished after the end-Pleistocene (Fig. 4). The loss of biotic associations increases segregations,

because biotic interactions tend to promote aggregations. Thus, the decrease in co-occurrence was driven by the combined effects of weakening biotic associations and a decrease in the tendency of biotic associations to be aggregated. Therefore, shifting biotic factors (i.e., the loss of the megafauna or the advent of humans), not climate change, were responsible for the ecological upheaval.

It is difficult to determine from our results whether the change in survivor co-occurrence was a direct result of the loss of survivor-victim interactions, or was more indirectly influenced by the loss of megafauna (in their role as ecosystem engineers) or by other contemporaneous changes such as increasing human impacts. Pleistocene predators were often more specialized (28), and their loss may have allowed survivors to consume a wider range of prey species, reducing the need to co-occur strongly with primary prey species and weakening aggregations. In addition, the loss of large-bodied prey could have caused prey-shifting to more abundant smaller-bodied mammals and thus reduced fidelity to any particular prey species (18). Segregations also increased in abundance and magnitude within mutual potential ranges. One potential explanation is that the loss of predators and competitors increased the abundances of survivors in a rapid competitive release scenario (29) that eventually led to enhanced competition and increased exclusion.

Contemporary loss of keystone species causes direct and indirect effects on other species and communities (4, 30, 31) via the loss of biotic interactions. These include top-down biotic processes (4), higher-order interactions (i.e., a third species affecting the interaction of two others) (32), ecosystem engineering, pest control, and nutrient cycling (16). Such loss often results in reduced biodiversity and degradation of ecosystem health. The extinction of the megafauna may have caused substantial shifts in the biotic drivers of community assembly via similar pathways, particularly via the loss of top-down control and the liberation of resources. The trend away from aggregations is crucial because it has been suggested that coexistence enhances biodiversity through the emergence of higher-order interactions (32), and biodiversity is a central focus of modern conservation efforts.

The end-Pleistocene extinction caused measurable, lasting effects on the dynamics of mammal communities that went beyond simple biodiversity loss. Our analysis suggests that these losses disrupted a network of species interactions that supported high levels of aggregation, leading to a modern fauna in which continent-wide species associations are now regulated more strongly by climate and dispersal limitation and are characterized increasingly by segregation. We find that biotic mechanisms such as species interactions and range dynamics once played a measurable role in mammal community assembly by consistently affecting how species co-occurred on continental scales. Remaining species interactions among survivors likely take place opportunistically, on smaller scales, or within shorter time frames. Overall, we find that biotic mechanisms now play a reduced role in species co-occurrences on a continental spatial scale, and that this shift was most likely driven by the extinction of the Pleistocene megafauna.
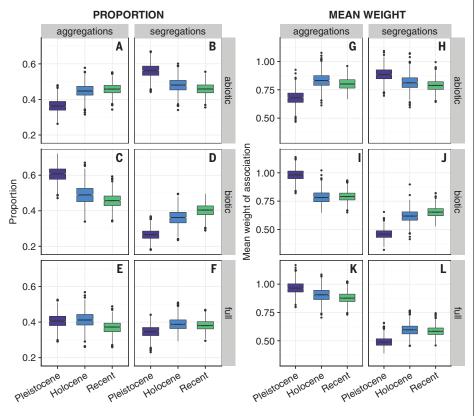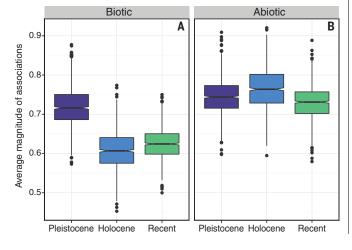

Fig. 3. Proportion and mean weight of aggregations and segregations. (A to L) Proportion [(A) to (F)] and mean weight [(G) to (L)] of aggregations and segregations for abiotic components [(A), (B), (G), and (H)], biotic components [(C), (D), (I), and (J)], and full associations [(E), (F), (K), and (L)] in each subsample (n = 1000). Associations with weight of 0 are excluded.

Fig. 4. Average magnitude of biotic and abiotic associations. Absolute values of association weights, broadly representing the relative importance of biotic (A) and abiotic (B) components for overall community assembly patterns, are shown. Box plots represent the variation among subsamples (n = 1000).

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Extinction leads to restructuring

By most accounts, human activities are resulting in Earth's sixth major extinction event, and large-bodied mammals are among those at greatest risk. Loss of such vital ecosystem components can have substantial impacts on the structure and function of ecological systems, yet fully understanding these effects is challenging. Tóth *et al.* looked at the loss of large-bodied mammals in the Pleistocene epoch to identify potential community assembly effects. They found that the demise of large mammals led to a restructuring and a shift from biotic to abiotic drivers of community structure. Understanding past changes may help predict the community-level effects of the extinctions we are currently driving.

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