The global-scale ecological impacts of humans have accelerated over the last several thousand years[1–3]. Human-

taxonomic similarity. Our sensitivity analyses are designed to tease apart sampling effects from ecological signal. Graham, et al.[47] performed a broadly similar set of analyses, which we extend to create a comparison to modern mammal assemblages, while considering heterogeneity in spatiotemporal patterns of sampling and addressing differences between mammals from different body size classes.

Finally, we explore potential drivers of biotic homogenization by comparing to temporal changes in climate heterogeneity (i.e., differences in climate among sites measured within each time bin)[68], species geographic range sizes[53], human presence on the North American landscape (~20,000–14,000 ybp)[39], extinction of the mammalian megafauna (beginning ~15,000 ybp and culminating by ~11,700 ybp)[45], and the development of extensive agriculture (~2,000–1,000 ybp)[37]. We hypothesize that there were two periods of significant biotic homogenization, the first following the extinction of the mammalian megafauna (~12,000 ybp–10,000 ybp), and second the development of widespread agricultural activities (2,000–1,000 ybp). Support for our hypothesis would constitute strong evidence for an ancient origin of anthropogenic biotic homogenization and amplify calls for deep time perspectives in the study of human impacts on ecosystems.

## Results

**Mammal assemblages homogenized over time.** During the late Quaternary (30,000 ybp to modern), the average taxonomic similarity of mammalian assemblages was relatively stable and within null expectations (null model generated by shuffling sites among time bins; see Methods) until the Holocene (Fig. 1; Table 1). Mean assemblage similarity increased by 0.15 (Jaccard similarity) from the

10,000–5,000 ybp time bin through to the modern (Fig. 1; black line), occurring at the fastest rate between the final two time bins (5,000–500 ybp and 500 ybp–modern; Fig. 1). Assemblages composed of mammals larger than 1 kg and 5 kg showed the greatest degree of homogenization. They increased in similarity by 0.25 (Jaccard similarity) from the ~15,000–10,000 ybp time bin onward (Fig. 1; dashed lines), becoming more homogenous than null expectations from the 10,000 ybp–5,000 ybp time bin onward (Table 1). Large mammal (>1 kg) assemblages experienced two periods of rapid homogenization, from the 15,000–10,000 ybp bin to the 10,000–5,000 ybp bin and from the 5,000–0.5 ybp bin to the modern (Fig. 1; dashed lines). The same patterns are evident when aligning the time bins with the onset of deglaciation at the beginning of Heinrich Stadial 1 and the Pleistocene-Holocene



Figure 1

transition (Supplementary Fig. 3a), suggesting that the pattern is not an artefact of how we grouped sites into time bins.

**F** .. ₁ ₚ ₚ . **a** ₁ ᵥ . Re-sampling (i.e., randomly drawing the same number of sites for each time bin to homogenize sampling intensity) did not change the overall pattern of Holocene biotic homogenization (Supplementary Fig. 4, S5). Furthermore, mean taxonomic similarity as calculated using Jaccard similarity (1 − Jaccard dissimilarity) is uncorrelated with total within-time-bin species richness (i.e., size of the regional species pool; $p > 0.05$, $R^2 = 4.0 \times 10^{-4}$; Supplementary Fig. 6). Exclusion of sites from the Rocky Mountains westward (to reduce the effects of topographic heterogeneity; see Methods; Fig. 1; lighter brown line) and north of the Canadian border (to address trends in sampling area and density) does not alter our results (Fig. 1; gray dotted line). Thus, changes in spatial and taxonomic sampling are not likely to be responsible for the pattern of Holocene biotic homogenization.

**A** ₌ ₜ **a** . ₌ **a** ₌ . ₌ ₌ .. The pattern of Holocene biotic homogenization is apparent for most of the similarity metrics employed herein (Supplementary Fig. 7). The relative stability of nestedness through time suggests that much of the change in mean taxonomic similarity during the Holocene is a result of declining turnover (Supplementary Fig. 7A). The divergent patterns observed for distance decay of similarity and the corrected Forbes Index appear to reflect correlations with the number of sites (

assemblages, the magnitude of Pleistocene through Holocene biotic homogenization reported here (an increase of 0.15–0.25; >100%
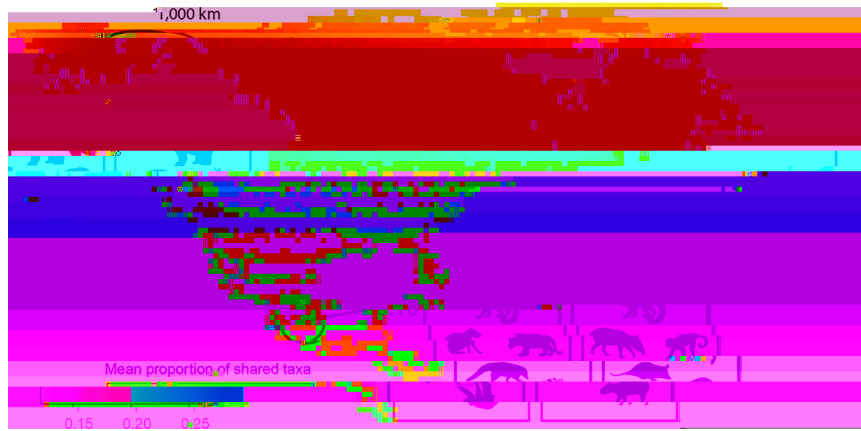
1,000 km
Mean proportion of shared taxa
0.15
0.20
0.25

Fig. 4 [illegible] ( [illegible] ) ( [illegible] ). A [illegible] 0.15–0.25 [illegible] 15,000 [illegible] M [illegible] N [illegible] Am [illegible] mamma [illegible] A [illegible] 3 [illegible]

Nonetheless, North American mammal assemblages were significantly homogenized (i.e., outside the confidence intervals for the null model) by the 10,000 ybp–5,000 ybp (mammals larger than 1 kg) and 5,000–500 ybp time bins (all mammals) (Fig. 1; Table 1). We suggest a connection to the extinction of the majority of the megafauna that occurred between 12,000 and 10,000 ybp[45] (Fig. 1; star symbol). Although the loss of much of the North American megafauna did not directly drive Holocene biotic homogenization (Fig. 1; solid brown line), it may have done so via indirect ecological effects. Because most of the now extinct megafauna became extinct near the 10,000 ybp boundary[45], we suggest that biotic homogenization began late in the 15,000 ybp–10,000 ybp interval (mammals larger than 1 kg) and do not posit a long delay between the extinctions and their ecological effects.

Large mammals perform a variety of ecological functions, including facilitation of seed dispersal over long distances[89,90], maintenance of vegetation structure at the landscape-scale[91], moderation of small mammal populations through competition and predation, and, perhaps most importantly, lateral transfer of nutrients[92]. The causes for the global megafaunal extinctions are still debated and there is conflicting evidence regarding the direct or indirect role played by humans[42,44,93,94]. Regardless of causal mechanisms, removal of ecosystem engineering megafauna and the resulting dominance of smaller-bodied mammals with different functional roles[42,87] had continental-scale ecological consequences for North American terrestrial ecosystems[95–97], including geographic range expansions and shifts among surviving species[53,88].

Today, geographic range expansion, whether climate-mediated or via translocation, is one of the primary drivers of biotic homogenization[14,19,71] (Supplementary Fig. 1). After the 10,000–5,000 ybp time bin, we observe ~50% increases in average geographic range size among mammals larger than 1 kg (Fig. 3A) but not increases in range fill (Fig. 3B), consistent with previous studies of mammal range dynamics[86,88]. These range expansions exceeded the increase in newly available space and equitable climate resulting from glacial retreat alone[88], suggesting additional, possibly ecological, drivers. One possible ecological driver, landscape-scale ecosystem changes resulting from the loss of the megafauna, may have driven biotic homogenization for assemblages of mammals larger than 1 kg, given their close temporal association (Fig. 1). Assemblages including smaller mammals (<1 kg), however, showed much more moderate and delayed increases in geographic range size and biotic homogenization until after ~5,000 ybp (Figs. 1 and 3A), possibly reflecting differences in dispersal abilities[98].

Regardless of the taxonomic or spatial filters we applied to the data, the fastest rate of biotic homogenization occurred between the 5,000–500 ybp and modern time bins (Fig. 1), coincident with geographic range expansions of ~25% for assemblages including all mammals (Fig. 3A). This second phase of biotic homogenization began during enhanced fire regimes, considerable human population growth, and the development of extensive agriculture (i.e., noncontinuous but widespread cultivation) in North America[3,37]. Human populations may have increased by as much as 10-fold in North America during the penultimate time bin (5,000–500 ybp)[3]. Habitat alteration by human activities (e.g., clearing of forests, construction of villages) favors population growth among synanthropic species (i.e., those dependent on human-dominated habitats). Such species are favored due to their reliance on resources provided by human habitation (e.g., refuse) and the elimination of their natural predators (e.g., through hunting), among other factors. As human populations and habitation become more widespread, so do synanthropic species, leading to biotic homogenization[99]. Though it is likely such processes were operating during the mid to late Holocene (the 5,000–500 ybp time bin), they are very unlikely to have been as spatially extensive or intensive as is observed for modern urban environments. The incidence of fires also increased throughout the Holocene in North America, though, in most cases, this has been linked to climate change rather than anthropogenic activities[3]. Furthermore, fires may in fact produce less homogenous biotas[100].

Archeological evidence, however, suggests that, by ~2,000–1,000 ybp (within the penultimate time bin of this study), extensive agriculture was practiced throughout much of the central and eastern United States[3,37]. Modern agriculture results in spatially-extensive monocultures[101], favoring agricultural pests (e.g., voles)[102] and generalist species[103,104]. Today, agricultural intensification is one of the major drivers of biotic homogenization, largely due to reduced landscape heterogeneity and increased patch size[23]. Similarly, agriculture reduces the capacity of ecosystems to support large pools of species, resulting in spatially homogenous, depauperate floras and faunas[105]. Early farming practices did not produce the spatially extensive, single-species monocultures of today[106,107]. Our findings suggest,

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