

## PALEOECOLOGY

# Human adaptation to diverse biomes over the past 3 million years

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To investigate the role of vegetation and ecosystem diversity on hominin adaptation and migration, we identify past human habitat preferences over time using a transient 3-million-year earth system-biome model simulation and an extensive hominin fossil and archaeological database. Our analysis shows that early African hominins predominantly lived in open environments such as grassland and dry shrubland. Migrating into Eurasia, hominins adapted to a broader range of biomes over time. By linking the location and age of hominin sites with corresponding simulated regional biomes, we also find that our ancestors actively selected for spatially diverse environments. The quantitative results lead to a new diversity hypothesis: *Homo* species, in particular *Homo sapiens*, were specially equipped to adapt to landscape mosaics.

**H**omo sapiens is the only surviving hominin species today, and it is largely unknown whether this is because our species was uniquely successful at adapting to the strongly fluctuating Pleistocene environmental conditions (1), because we outcompeted other species (1–3) through increased birth-rates or cognitive or social abilities, or because we outlived other *Homo* species by chance (4). To address *Homo* species' adaptation to environmental change (5–8) and extremes (9), we need to understand the connection between hominins and their ecological environment. This includes hominins' preferences for specific vegetation types, their tolerance to changes in biotic and climatic conditions, how such preferences and tolerances evolved, and their use of, adaptation to, and specialization toward different types of ecosystems.

Identifying the time-evolving habitat preferences of hominins using observational data alone is virtually impossible. With few exceptions, information on past vegetation and ecosystem changes near archaeological sites is sparse. Pollen data, leaf wax, and isotope reconstructions from terrestrial, lacustrine, or marine archives (10–14), which can provide valuable information on past vegetation and biome changes, are too limited in space and time to obtain a complete large-scale picture of how *Homo* species exploited environmental variation and responded to fluctuations in climate and available vegetation type. To overcome this limitation, various climate model simulations have been used to quantify the effect of orbital-scale changes in temperature, precipitation, and net primary productivity (NPP) on human migration and habitats (4, 15–17).

We examine the evolving linkage between hominins and different regional (mega-) biome types, from tropical forest to savanna to tundra and deserts, which depend on specific combinations of climatic factors, soil properties, and atmospheric CO<sub>2</sub> concentrations. We aim to determine the preferred environmental conditions of the different hominin species, ascertain whether their biome preferences changed in time and diversity over the Pleistocene, and identify potential regional environmental drivers of hominin adaptation. Studying biome preferences gives us a new perspective on how hominins have adapted to landscape changes, and how they exploited their habitats and food resources.

To this end, and to provide deeper insights into the adaptation patterns of the earliest members of our genus *Homo*, we extended our previously conducted quasi-transient 2-million years (Myr) Community Earth System Model (CESM version 1.2) simulation by another 1 Myr (17, 18). Monthly precipitation, temperature, and percent sunshine data from the 3-Myr simulation—which experiences changes in orbital insolation (19), greenhouse gases and, icesheet extent (20)—were subsequently used to force the offline equilibrium BIOME4 vegetation model (21) at 0.5° resolution (22). BIOME4 translates climate conditions and estimates of CO<sub>2</sub> forcing (20, 23) into 28 biomes, which are clustered into 11 megabiomes (table S2). The proxy-validated global 3 Myr climate and vegetation model simulations (figs. S1 to S4) (22) were then used to extract biome and NPP data for 3232 fossil and archaeological sites (17), compiled for 6 different *Homo* species (*H. habilis*, *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*) (Fig. 1). The hominin database used here attributes well-dated fossil remains and identifiable archaeological artifacts to different hominin species. This species attribution is naturally prone to uncertainties because (i) there is no universally accepted paleo-anthropological spe-

cies definition and (ii) different hominin species or even hybrids could have used similar tools (17, 24). These uncertainties have been discussed previously, and their effect on calculations of large-scale hominin habitat preferences has been shown to be relatively minor (17).

## Climate and vegetation changes over the past 3 Myr

To better understand how Pleistocene climate variability affected biomes and NPP, we first elucidate the response of the climate system and global vegetation to Milanković cycles and long-term shifts in atmospheric CO<sub>2</sub> concentrations (fig. S1, A and B). The simulated glacial/interglacial global temperature variations (fig. S1C)—primarily caused by the prescribed orbital-scale CO<sub>2</sub> variations in our model—have amplitudes of 7 to 8°C over the Late Pleistocene, are in good agreement with a transient simulation conducted previously with the CLIMBER intermediate complexity earth system model (20), and are slightly weaker than proxy-based paleotemperature reconstructions (fig. S1C) (25) for at least the past ~0.8 Myr (8 to 9°C). The global mean temperature variations are linked to global mean precipitation changes through the Clausius-Clapeyron relation, thus having a direct and indirect impact on global mean NPP in the offline forced BIOME4 model (fig. S1D).

Even though globally aggregated vegetation characteristics are controlled mainly by global mean temperature variations, the relationship between orbital-scale forcings (Milanković cycles, greenhouse gases, and icesheet effects) and vegetation is much more complex on regional scales (figs. S5 and S6). For instance, we find strong eccentricity-modulated precessional variability in northern Africa's expansion and contraction of grasslands and desert areas (fig. S5E). For low values of the precession index (northern summer perihelion; fig. S1A), the amplitude of the Northern hemisphere seasonal cycle of insolation increases, which leads to increased Northern Hemispheric summer rainfall, a northward expansion of grasslands, and a contraction of the Sahara desert, in qualitative agreement with paleo proxy data and other model simulations (26, 27). This process has been suggested to play a key role in creating green corridors, which may have supported multiple transcontinental migration events of archaic humans (15, 28). Migration from Africa into Eurasia exposed archaic humans such as *H. erectus*, *H. heidelbergensis*, and early *H. sapiens* to new environmental conditions and ecosystems.

According to our BIOME4 simulation, eastern African tropical forests gradually turned into grasslands during the early- to mid-Pleistocene (fig. S5E), which had clear implications for hominin migration and evolution. In contrast to the idea that this trend was caused

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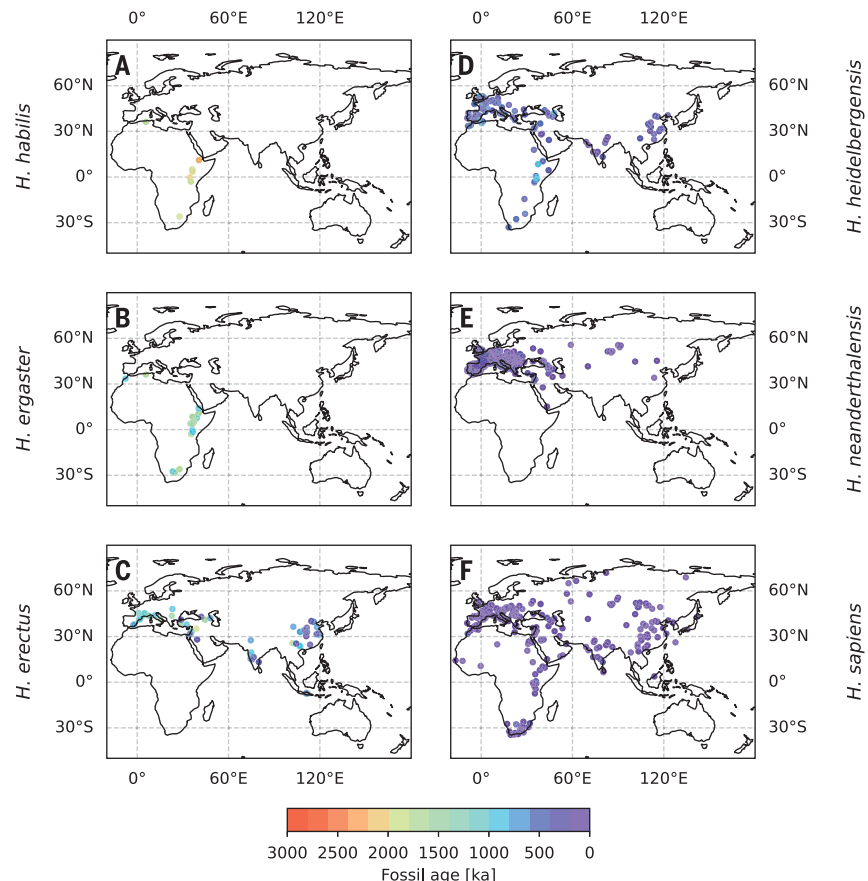
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by Pleistocene aridification (29, 30), we find only a weak negative rainfall trend over eastern Africa (fig. S2C), which indicates a more complex response of vegetation in this area to a variety of climate and biogeochemical drivers including CO<sub>2</sub> fertilization (fig. S7 and table S3). The CO<sub>2</sub> fertilization effect would affect C4 plants (e.g., savanna grasses) less than C3 plants because the latter exhibit a less efficient photosynthetic pathway (31–33). The simulated gradual vegetation changes, forced by orbital forcing and CO<sub>2</sub> changes, are important in understanding how archaic humans have adapted to their environment.

On a continental scale, our simulation reveals considerable changes in biome types (figs. S5 and S6). In Africa a gradual decrease of savanna and dry woodland in northern Africa and an expansion of grassland and dry shrublands in southern Africa occurred. Superimposed on the long-term trend are orbital variations on timescales of 20 thousand years (kyr) and ~100 kyr, which intensified after the Mid-Pleistocene Transition (MPT) ~1 million years ago (Ma) as a result of the increased amplitude of temperature and rainfall variability (fig. S1, C and H). In Asia the steady planetary cooling due to decreasing CO<sub>2</sub> concentrations and the expansion of the Northern Hemisphere ice sheets caused an expansion of tundra and grassland areas during glacial periods and a contraction of boreal and tropical forests. In Europe a massive increase in the latitudinal range of tundra, boreal forests, and grassland—at the expense of temperate forests—occurred following the MPT. Overall, the increasing frequency of cold climates throughout the Pleistocene led to an expansion of open biomes. This trend could have facilitated the migration of archaic humans, requiring adaptation to a broader range of environments.

### Preferred biome types of hominins

Although early hominin species during the late Pliocene and early Pleistocene (~3 to 2 Ma) might have benefited from open grasslands to exploit more accessible migration routes, the diversity of biomes experienced by later species might have given them the upper edge in terms of range expansion. To demonstrate this point, we extracted the biome types for the geographic coordinates and age estimates provided in the hominin database (17, 34). The resulting species-stratified biome histograms (Fig. 2) for the fossil and archaeological sites document that the habitats of both *H. habilis* and *H. ergaster* were predominately located in savanna and grassland areas (78 and 73%, respectively; table S1), in agreement with regional paleoclimate evidence (35). In contrast with the earlier African species, *H. erectus*—who left Africa no later than 1.8 Ma—selected for a much more diverse suite of habitats, with 58% of the sites associated with temperate or

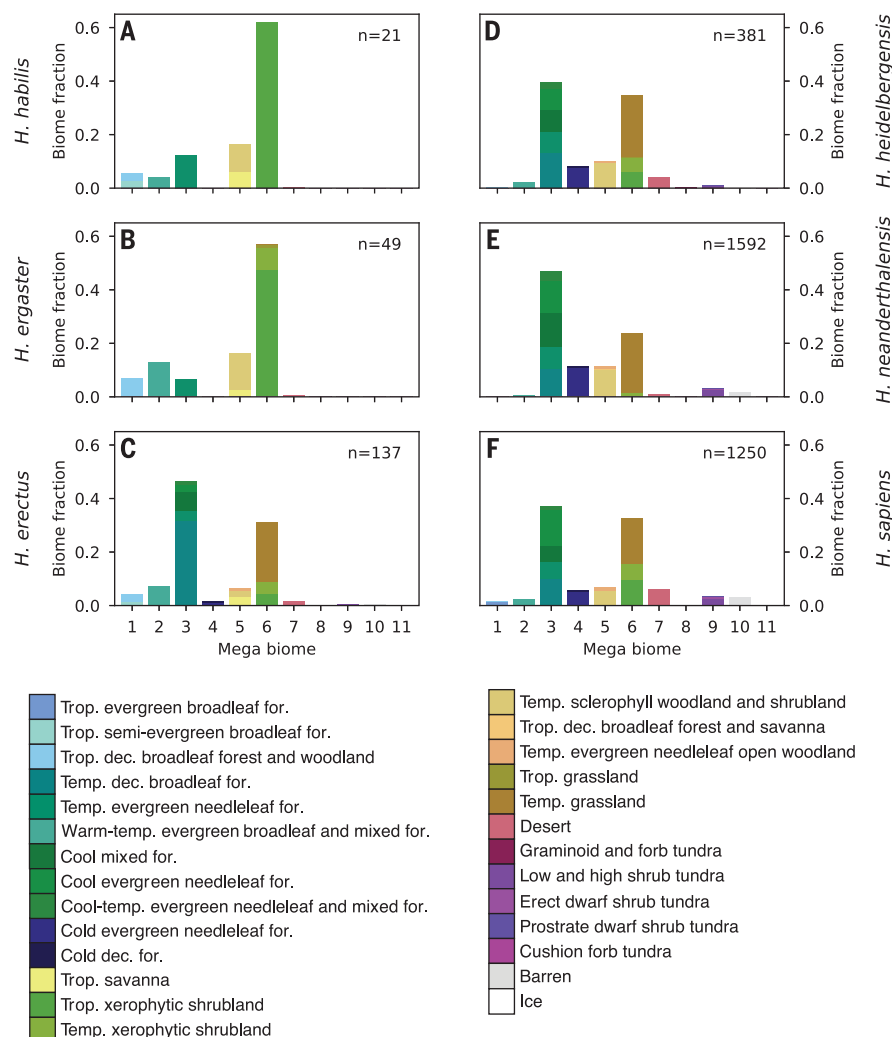


**Fig. 1. Locations of hominin species.** Anthropological and archaeological sites used in this study, corresponding to *H. habilis* (A), *H. ergaster* (B), *H. erectus* (C), *H. heidelbergensis* (D), *H. neanderthalensis* (E), and *H. sapiens* (F). Age estimates in ka (1000 years ago) are indicated in colored shading.

tropical forest and 38% with grassland and savanna regions. More recent species such as *H. heidelbergensis* and *H. neanderthalensis* were able to adapt to colder habitats, with 8 and 11.3% of their occurrences falling in the boreal forest biome, respectively. This post-MPT adaptation to cold environments is associated with the northward expansion of these species (36) (Fig. 1). *H. sapiens* managed to settle in extreme environments, including previously less occupied biome types such as tundra and desert (Fig. 2), revealing *H. sapiens* as a “generalist specialist” (9). This ability to occupy even extreme habitats suggests the acquisition of advanced, unparalleled cognitive abilities (36), which is consistent with reported changes in brain shape (8), more sophisticated technologies, and the transition from Middle to Upper Paleolithic toolmaking traditions around 0.05 to 0.03 Ma (3).

Overall, our hominin/biome occurrence analysis (Fig. 2) suggests a bimodal structure for habitat openness preferences. Early African hominins and Neanderthals appear to have preferred either open or closed habitats, where-

as other species favored mixed conditions. Our analysis suggests that *H. habilis* and *H. ergaster* mostly lived in savanna/dry-woodland and grassland/dry-shrubland. *H. neanderthalensis* became a temperate forest dweller, preferring closed environments (37, 38). According to our results, Neanderthals exhibited only limited capability to adapt to cold-climate open biomes such as tundra. This finding, along with the simulated Late Pleistocene biome variability (figs. S5 and S6), also suggests that Neanderthals went through a massive contraction of their habitat during glacial maxima, forcing them to settle in the warmer and more forested Mediterranean region, in agreement with recent studies (39, 40). This is also seen when comparing the spatial density of specimens found in deep glacial periods with those from interglacial periods (fig. S8, A and B). Our data suggest that in contrast to early African *Homo* and *H. neanderthalensis*, *H. erectus* and *H. heidelbergensis* were able to settle in both open and closed biomes. Diversifying their habitats translated into their much wider expansion across Eurasia. Subsampling of *H. sapiens* data (fig. S9, M to P) by matching



**Fig. 2. Biome preferences by hominin species.** Biome preferences were calculated by taking an age-weighted average of the biome occurrences at the grid point closest to the hominin specimen: *H. habilis* (A), *H. ergaster* (B), *H. erectus* (C), *H. heidelbergensis* (D), *H. neanderthalensis* (E), and *H. sapiens* (F). Fossil occurrences with uncertain species attributions are included in their respective species groupings (22). The number in the biome preferences represent megabiomes: 1, Tropical forest; 2, Warm-temperate forest; 3, Temperate forest; 4, Boreal forest; 5, Savanna and dry woodland; 6, Grassland and dry scrubland; 7, Desert; 8, Dry tundra; 9, Tundra; 10, Barren; 11, Ice. Abbreviations in the color bar are as follows: trop, tropical; temp, temperate; dec, deciduous; for, forest.

the number of observations of older species continues to show the wide range of occupied biomes. Therefore, the variety in occupied biomes is not due to larger sample size but rather is a clear demonstration of *H. sapiens*' ecological plasticity.

The documented diversification of biomes occupied by each hominin species over time (Figs. 2 and 3) could be a byproduct of range expansion into different areas or the consequence of gradual acclimatization to changes in climate and available vegetation types, or a combination thereof. The former would represent an adaptation to different biomes driven by migration, whereas the variability selection hypothesis, which highlights the

role of regional adaptation to temporal environmental variability (6, 7, 41), could achieve the latter. To test for the influence of the temporal evolution of biomes on the presence or absence of hominins in different areas, we randomized the hominin presence data in time through bootstrap resampling (22), keeping the specimen locations the same, and repeated our biome preference analysis. If hominins adapted regionally to varying biomes without migrating, the original and time-shuffled analysis should yield the same results. For *H. neanderthalensis* and *H. sapiens* we find significant differences in specific biome preferences ( $P = 0.03$  and  $P = 10^{-5}$ , respectively, using Fisher's exact test) (22) (fig. S9, E, F, K, and L). Therefore, the exact

temporal biome trajectory might have played a role in determining where members of these species lived. The large age uncertainty around the fossil occurrences of older species, which often spans a full glacial cycle, and the corresponding reduced temporal localization could translate into insignificant differences relative to the time-shuffled biome trajectory. Repeating the time shuffling with *H. sapiens* data that was subsampled to match the other hominin group sample sizes, while maintaining the narrower age uncertainties, showed more significant results (fig. S9, M to T), indicating that the nonsignificant results for early species were likely due to the large age uncertainties.

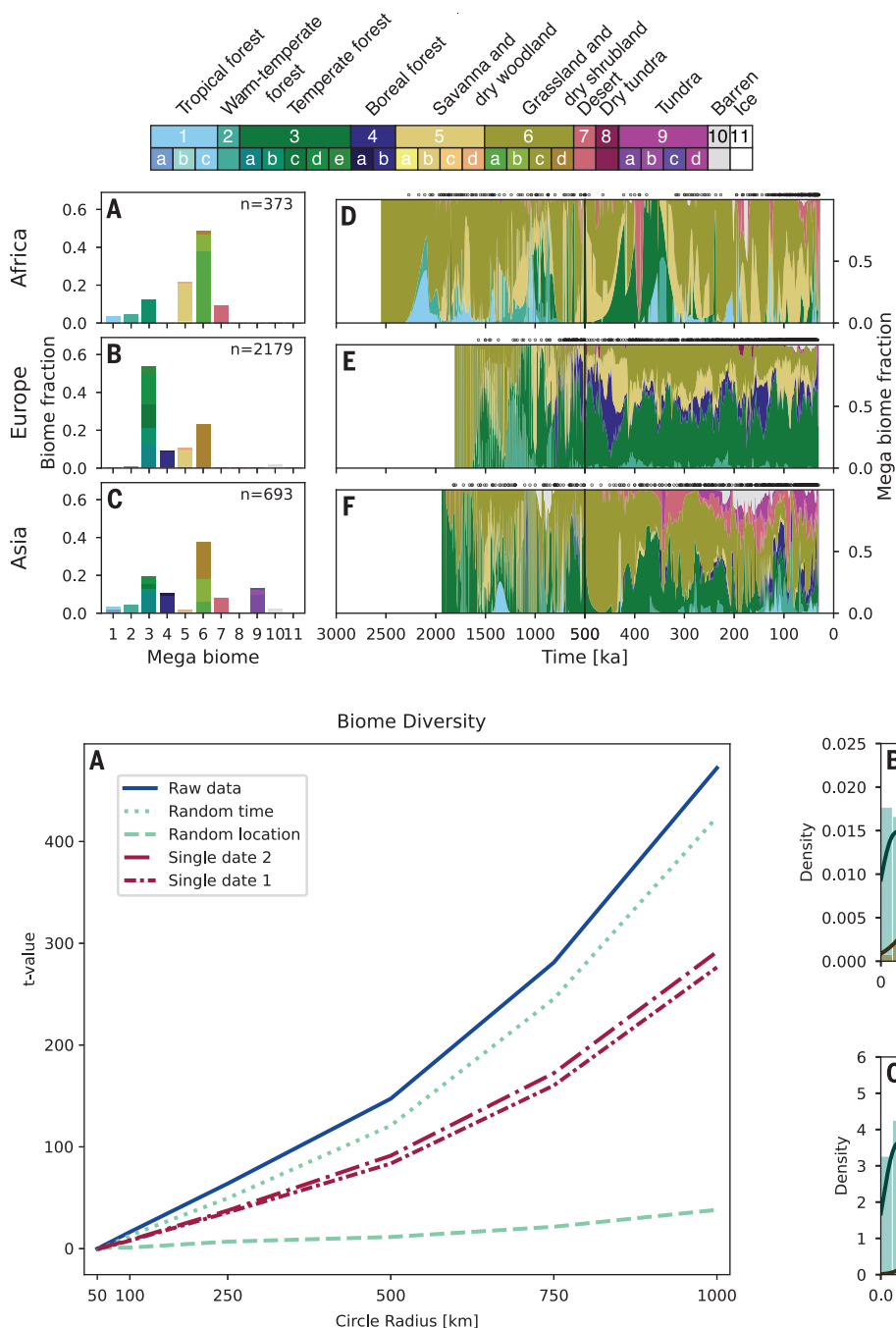
To determine the temporal evolution of hominin biome preferences on a continental scale, we further calculated the time-evolving ratios of the individual biomes in Africa, Europe, and Asia (Fig. 3) at the hominin sites. The main biome preference in Africa is the open environment (grassland and savanna). Nonetheless, we also find occasional episodes of tropical and temperate forest occurrences. Given that the mean biome types across Europe (59% temperate and 14% boreal forest) are quite distinct from those in Africa (49% of the land area is found occupied by savanna/dry woodland or grassland/dry shrubland), we also expect a different time evolution of regional habitat preferences. From 1.8 Ma onward, a gradual trend in biome preferences from open grassland to temperate forests occurred. In certain areas, biome preferences were further modulated by glacial cycle variability during the post-MPT period (fig. S10). More specifically, we find that after 600 ka, the fraction of European temperate and warm-temperate forest dwellers correlates with regional temperatures (fig. S10, C and D), suggesting that hominins migrated in response to the climate and vegetation changes they experienced. For other time periods and regions, the correlation is less robust, which could be explained by increasing age uncertainties, smaller sample size, and/or reduced climate-induced mobility of earlier hominins.

We further examined biome preferences for overlapping species along possible ancestor-to-descendant lines (22). Our analysis reveals significant biome differences only for the African *H. heidelbergensis* and *H. sapiens* pair (fig. S11), consistent with the notion of a major shift in the resource exploitation mode, potentially driven by speciation dynamics (42).

### Humans as diversity seekers

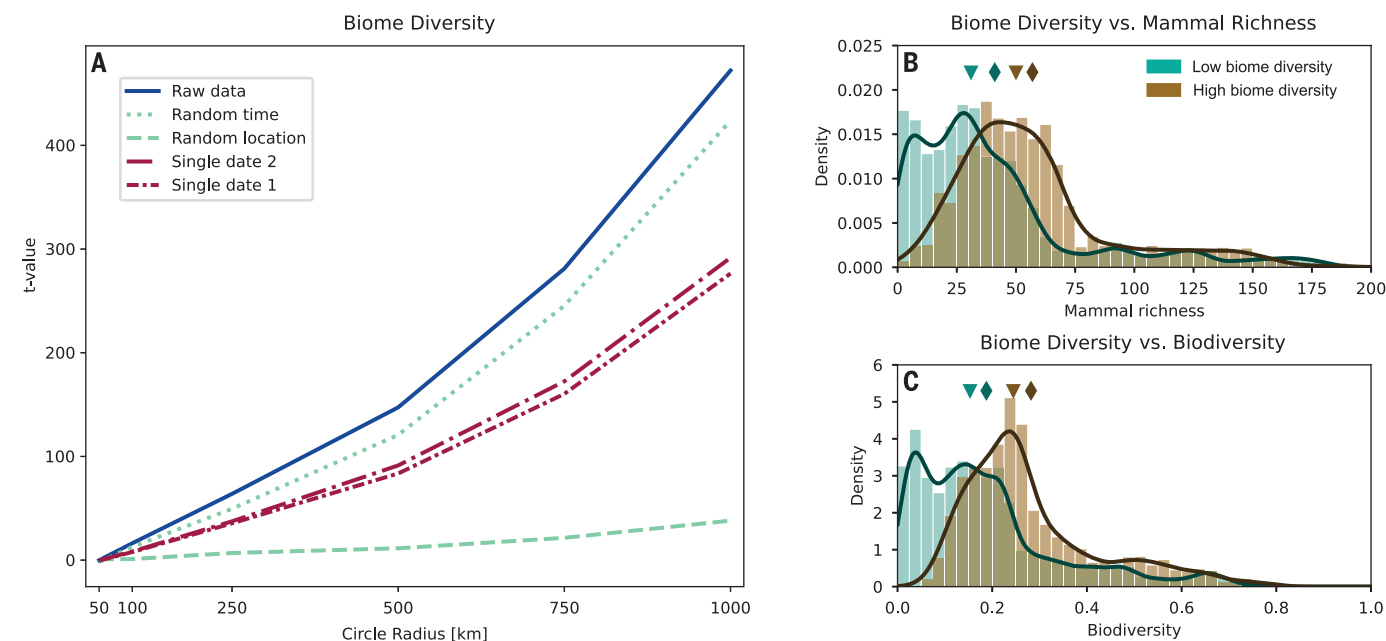
To further characterize the environmental preferences of hominins, we derive a biome diversity metric (22) that characterizes the number of different biome types nearest to a hominin site. If hominins preferentially lived in regions with a variety of biomes, then the biome





**Fig. 3. Hominin biome preferences by continent.**

Biome preferences for hominin specimens found in Africa (A), Europe (B), and Asia (C) and corresponding biome preferences over time (D to F). Continents are defined by geopolitical borders and biome preferences were calculated by taking an age-weighted average of the biome occurrence at the grid point closest to the specimen. The biome preferences over time were calculated by taking the age-weighted average, stacking this for all the fossils at each time point and normalizing the stacked values to 1 (22). Dots above the biome preferences over time represent the average ages of the findings.



**Fig. 4. Environmental preferences of early hominins.** (A) Student's  $t$ -value of differences in regional biome diversity at hominin sites and grid points in surrounding circles with increasing radii (fig. S14). Higher  $t$ -values indicate larger deviations from zero and stronger evidence for hominin selection for higher spatial biome diversity values. The  $t$ -values are calculated for the original data, spatially shuffled data (between 50°N, 142°E, 45°S, and 17°W), and temporally shuffled values to test for the effect of spatial and temporal preferences (random location, random time). We also tested datasets with different hominin age

uncertainties and species attributions (single date 1 and single date 2) (22) (fig. S13). Histograms of present-day mammal richness (B) (49) and biodiversity index computed from mammal, bird, and vascular plant richness (C) (43) for corresponding points with low biome diversity (blue) and high biome diversity (brown). For the low (1) and high (4) biome diversity cases the normalized histograms (bars and kernel density estimate in solid line) shift from low to high mammal richness and biodiversity in terms of mean value (diamond) and median value (triangle).

diversity metric should be higher closer to hominin sites than within the larger surrounding areas (fig. S12 for illustration). To test whether this hypothesis holds, the value of biome diversity at hominin sites was sub-

tracted from the surrounding grid points within circles of increasing radii (fig. S13) and those differences were weighted by the age uncertainty (fig. S14) (22). Subsequently, the differences for all sites were aggregated

and the Student's  $t$ -value was used to measure the deviation of the mean of the subsequent distribution from zero. Comparison of the hominin site values to those in an increasing circle (Fig. 4A) reveals increasing  $t$ -values,

which implies that hominins on average preferred regions with higher spatial biome diversity. Repeating our *t*-value analysis with randomly selected hominin locations in Africa and Eurasia, between 50°N, 142°E, 45°S, and 17°W, we find major differences with respect to the original data, thereby confirming that hominins did not choose their whereabouts at random. Shuffling the data in time, we see smaller differences with respect to the original data, which suggests that the exact temporal evolution played less of a role in selection compared with spatial biome diversity. Our analyses (movies S1 to S3, Fig. 4, and figs. S13 and S15) clearly illustrate that hominins lived in areas with multiple biome types in close proximity, suggesting that hominins preferred landscape mosaics rather than uniform environments. We repeated the *t*-value analysis for NPP (figs. S15, C and D, and S13, G to L) and found similar behavior: hominins preferred regions with locally high NPP.

Furthermore, using modern biodiversity estimates previously derived by combining mammal, bird, and vascular plant richness data (43), we find a connection between biome diversity and this particular measure of biodiversity (Fig. 4, B and C, and fig. S16). Taken together, our findings suggest that human species were actively seeking out more abundant (figs. S15, C and D, and S13, G to L) and diverse food resources (Fig. 4A) in regions with higher ecosystem diversity (Fig. 4C). Using a relationship between densities of historical hunter-gatherer populations (44) and our calculated preindustrial biome diversity (fig. S16, I to L) as a proxy for the past, we propose that diverse landscapes may have also sustained larger hominin populations, serving as hotspots for cultural innovation and playing an important role in genetic diversification (44).

The derived inclination of humans toward landscape mosaics and their ability to adapt to regionally diverse vegetation conditions has not been shown before at continental scales, leading us to propose the diversity selection hypothesis: *Homo* species, and *H. sapiens* in particular, were specially equipped to exploit heterogeneous habitat conditions. Such heterogeneity, which correlates to high plant and vertebrate richness in current ecosystems (Fig. 4, B and C), may have conferred hominin resilience to environmental perturbations by providing a wider and more stable resource base (44). Here we suggest that behavioral and cultural plasticity may have allowed humans to exploit habitat diversity and diverse food resources.

Several single-site studies have alluded to the fact that hominins may have favored heterogeneous habitats (45–47), leading to the formulation of the microhabitat variability hypothesis (48). Combined with our large-scale results, we conclude that Pleistocene hominins selected for

increasing regional biome heterogeneity. We acknowledge that temporal variability selection (6) may have been present in specific regions and time periods. However, our analysis does not reveal any statistically robust continental-scale linkage between where hominins lived and temporal changes in orbitally driven vegetation variance.

Our data-based diversity selection hypothesis may also add context to our more recent human history. According to our analysis, our genus *Homo* has adapted over the Pleistocene and migrated to areas with higher landscape diversity. Utilizing resources from various biomes provided a resilient and successful strategy over hundreds of millennia. However, during the Anthropocene, our species has caused a massive decline in global ecosystem diversity due to land use practices, gradually shifting away from integrated agricultural practices and toward monocultures. Modern humans have clearly taken an unprecedented path away from our ancestors' resilience and diversity-based strategies.

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## SUPPLEMENTARY MATERIALS

[science.org/doi/10.1126/science.abq1288](https://science.org/doi/10.1126/science.abq1288)  
Materials and Methods  
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