Global acceleration in rates of vegetation

change over the past 18,000 years

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27 12. Lower Saxony Institute for Historical Coastal Research, Wilhelmshaven, Germany. 28 †Equal contribution. ‡ Deceased. 29 30 *Corresponding authors: Ondrej Mottl (ondrej.mottl@gmail.com), Suzette Flantua (s.g.a.flantua@gmail.com) 31 32 33 One sentence summary: A compilation of over 1000 fossil pollen sequences shows that global 34 vegetation change accelerated several thousand years ago. 35 **Abstract** 36 37 Global vegetation over the last 18,000 years was transformed first by the climate changes accompanying the last deglaciation and again by increasing human pressures, but the magnitude and 38 39 patterns of rates of vegetation change are poorly understood globally. Using a compilation of 1181 fossil pollen sequences and new statistical methods, we detect a worldwide acceleration in rates of 40 41 vegetation compositional change beginning between 4.6 and 2.9 ka that is globally unprecedented over 42 the last 18,000 years in magnitude and extent. Late Holocene rates of change equal or exceed deglacial rates for all continents, suggesting that the scale of human impacts on terrestrial ecosystems exceeds 43 44 even the climate-driven transformations of the last deglaciation. The acceleration of biodiversity 45 change demonstrated in last-century ecological datasets began millennia ago. 46 47 Main text One of the clearest forms of biodiversity change during the past century has been the increased rates of 48 49 species turnover across the marine and terrestrial biosphere (I-3). Today, over 75% of the Earth's ice-50 free land surface has been altered by human land use (4), with profound effects on the composition 51 and functioning of ecosystems. Globally, extinction rates are increasing (5), although trends in local 52 species richness are ambiguous (6). These increased rates of species turnover, as signified by local and regional changes in 53

community composition, are embedded within a longer-term context in which humanity's footprint

has steadily grown since humans first began to alter landscapes for food, energy, and other resources. Hominid use of fire began at least 700,000 years ago (7), low-intensity but extensive agricultural land use began ca. 8000 years ago, while intensive agricultural land use expanded after 6000 years ago (8) (Fig. 1B). Detectable human imprints on vegetation began thousands of years ago (e.g. 9, 10), and the composition and carbon sequestration of many contemporary ecosystems remain profoundly influenced by legacies of past centuries to millennia of anthropogenic land use (e.g. 11). Nonetheless, there remains a major knowledge and scale gap between contemporary studies of global biodiversity trends of the last century (2) and studies examining early anthropogenic effects on ecosystems. Observational syntheses of global biodiversity trends are limited to the past several centuries, while macroscale syntheses of vegetation changes from fossil pollen data have been limited to continental scales (e.g. 9) or are largely qualitative (e.g. 12). Consequently, global patterns and magnitudes of vegetation compositional change, which are important for understanding how biodiversity and ecosystem dynamics have been shaped by climate change and early human activity, are poorly understood.

In parallel, paleoecological studies have shown the high sensitivity of terrestrial ecosystems to the climate changes accompanying and following the last deglaciation (ca. 20,000 to 8200 cal yr BP; 20 to 8.2 ka, Figs. 1C,D) (12, 13). In temperate and boreal regions, forest expanded from glacial refugia as temperatures rose and precipitation patterns shifted, with widespread leading-edge range expansions and, for some taxa, trailing-edge range contractions (14). Novel ecosystems emerged in response to novel climates and the late Pleistocene extinction of megaherbivores (15). Tropical and subtropical ecosystems responded to rising temperatures linked to increasing greenhouse gases (Fig. 1D) and hydrological shifts driven by precessional controls on monsoons and the Intertropical Convergence Zone (16). Consequently, during the Pleistocene-Holocene transition, tropical ecosystems substantially changed in species composition and canopy structures across all elevations (17), while millennial- and centennial-scale hydroclimate variability caused abrupt changes in global vegetation during the Holocene (18).

Ecosystem responses to humans and climate change over long timescales can now be assessed globally, thanks to the century-long expansion of a global network of fossil pollen sequences anchored

by increasingly precise radiocarbon chronologies (e.g. 19), the building of open, community-curated data resources (20), and the development of new rate-of-change techniques (21). Here, we assess the global patterns and rates of vegetation change from the last deglaciation, through the Holocene and up to the current Anthropocene, based on 1181 fossil pollen sequences from the Neotoma Paleoecology Database (20) covering all continents except Antarctica (Fig. 1, Data S1). These analyses are based on continentally harmonized taxonomies and updated Bayesian chronologies with age-depth model uncertainties and an improved algorithm (R package R-Ratepol; 21, 22) for estimating Rates of Change (RoC) for paleoecological time series. RoCs are calculated as the compositional dissimilarity between consecutive time intervals (using the chi-squared coefficient) standardized by the length of time between samples, therefore providing an indicator of compositional change per unit time. R-Ratepol uses a moving-window approach (instead of the traditional calculation of dissimilarities between individual levels), which minimizes artifactual alterations in RoC due to variations in sample density and sedimentation rate (21). R-Ratepol also incorporates temporal uncertainty resulting from age-depth modelling calculations via randomization (21, 22). For each pollen sequence, we pooled data into 500-yr time bins (see also our 250-yr sensitivity experiment in SM (22)) and calculated RoC between bins to represent rate of compositional change through time. For each sequence, we also identified time intervals with a large increase in rate of change, called 'peak points' (for more detailed information see methods in SM (22)).

We analyze RoCs at the scale of continents and sub-continental clusters, defined by climatic and geographic variables (22). For each continent and sub-continental region, we binned the RoC scores per 500-yr time bins (with a 250-yr sensitivity experiment in SM (22)) and calculated the 95% RoC quantile to highlight intervals and places with large vegetation changes while filtering out outliers (see 22 for a comparison of the 95% quantile to median trends). Similarly, we calculated the proportion of sequences with a peak point in each time bin. The clustering of peak points among sequences indicates a synchronous period of abrupt vegetation change within a region. Generalized Additive Models (GAMs) were fitted to all RoC and peak point curves to summarize trends and test for significant accelerations (simultaneous confidence intervals of the first derivative differ from zero, 22).

We detect an unequivocal global acceleration of vegetation change during the late Holocene (4.2–0 ka; Fig. 2). The estimated start of acceleration differs among continents and ranges from 4.6 to 3.1 ka (**Table S1**). This estimated start is well supported by the dense availability of samples during the middle to late Holocene (Fig. 1E), but continental-scale estimates vary by ca. 500-1000 years (22). For most continents, late Holocene RoCs are close to or exceed RoCs over the last 18 ka, with a percent differential ranging from -6.3% to 22.2 % (Fig. 2, Table S1). Increases in RoC during the Lateglacial and early Holocene can be linked to temperature and atmospheric CO₂ variations (Figs. 1C,D) and to hydrological variations. Rapid vegetation changes concentrate near to the onset of the Holocene (11.7 ka) for most continents, expressed as a maximum in RoC or in peak points (Fig. 2). In North America and Europe, RoCs reached maxima during the abrupt millennial-scale climate oscillations characteristic of the North Atlantic and adjacent regions (ca. 15 to 11 ka), then substantially declined during the early Holocene (Fig. 2A, B). The heightened rates of deglacial vegetation change resembles the patterns of increased temperature variability in the North Atlantic and elsewhere in the Northern Hemisphere that were driven by a combination of orbital forcing, atmospheric greenhouse gas concentrations, meltwater pulses to the North Atlantic, and shifting patterns of heat transport (23). In Asia, rapid but asynchronous change characterizes the Lateglacial and deglaciation period, with a maximum in RoCs or a clustering of peak points between 10 and 8 ka (Fig. 2C). In Latin America and Africa, RoCs also reach maxima between 10 and 8 ka, which can be linked to altered monsoonal rainfall associated with declining Northern Hemisphere summer insolation (24).

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RoC patterns at subcontinental scales are consistent with known histories of climate change and human land use. For example, in Eurasia, the western and northern European clusters show strong peaks in the rate of vegetation change between 15 and 10 ka (Figs. 3A,E), consistent with the response of vegetation to North Atlantic climate variations and the retreating Eurasian ice sheets (Fig. 1C). Late Holocene rates of vegetation change are high across western and central Europe and particularly in areas of high present and past agricultural activity (10). In Asia, high rates of vegetation change during the early Holocene can be linked to post-glacial forest expansion in northern Asia (25) and to

millennial-scale variability in temperature and monsoonal rainfall in eastern Asia (26) (**Figs. 3C,D,I**). Seven of ten Eurasian clusters show increased RoCs during the late Holocene.

In the Americas, vegetation RoCs vary by latitude and between Atlantic- and Pacific-adjacent regions (Fig. 4). Eastern North America resembles western Europe in its high vegetation RoCs between 15 and 10 ka, with a strong signal of synchronous vegetation change over the last millennium (Fig. 4G,H,I). All North American regions show increased RoCs during the late Holocene except for the high-latitude clusters. Driven by the topographic complexity of the Andes, vegetation responses in the Neotropical highlands were highly variable and asynchronous (Fig. 4D) likely a combined effect of changes in temperature, hydroclimate variability and atmospheric CO₂ (27, 28). In the lowlands, a peak in vegetation RoCs at 10 ka is likely due to hydrological variability linked to shifting monsoons (Fig. 4J) (27). These large vegetation changes challenge the common myth of the 'stable' tropics and suggest a strong sensitivity of the Neotropics to temperature, hydroclimate variability and orbital precession during the early Holocene (27, 28). In temperate South America, a period of synchronous vegetation change in the Holocene (Fig. 4E) is asynchronous with warm Neotropical regions (Fig. 4J), likely due to varying climate modes influencing different parts of the continent (29). The late Holocene acceleration of vegetation change is clearly manifested across most of the latitudinal gradient of the Americas, except for the high northern latitudes, with the highest RoCs in coastal western North America and eastern North America (Fig. 4).

The detection of globally accelerating rates of vegetation change during the late Holocene provides a longer-term perspective to the well-documented increase in species turnover during the 20th and 21st century (6). For terrestrial ecosystems at least, these recent increases in species turnover are the continuation of a longer acceleration that began millennia ago (**Fig. 2**). Moreover, this work suggests that contemporary communities and some current biodiversity trends may be partially due to legacies of past land use or environmental forcing (11) in combination with the strong anthropogenic imprint of the last decades. Hence, recent changes in biodiversity patterns represent only the most recent interval of our used planet (30) that has been altered by millennia of changing environments and human activities.

Our study has focused primarily on detecting patterns of rates of vegetation compositional changes over the last 18,000 years and secondarily on attributing causes. This approach follows the standard delineation in climate change research between detection studies that focus on establishing the significance and fingerprints of observed climate trends (31) and attribution studies that explore the potential causes of the observed events and patterns (32). Biodiversity research is now achieving the capability for global detection analyses (2, 6) across an increasingly broad range of timescales. The next major frontier is to disentangle and attribute the contributions of climatic variability and anthropogenic impacts to past vegetation changes. This attribution is challenged by the complex interplay among climatic, anthropogenic, and vegetation dynamics that varies within and among ecosystems, particularly at local to regional scales. For instance, in the Holocene in East Africa, land cover changes over the last 6000 years were driven by multiple cultural and technological innovations and by changes in rainfall amount and seasonality (33). In South America, Holocene climate variability contributed to regime shifts in human demography and displacement, which in turn affected ecosystems regionally (34). The worldwide spread of agricultural land-use over the last 3000 years suggests intensified resource management (8), but was accompanied in some regions by significant climate changes (16, 33). Deglacial vegetation dynamics, although strongly climate-driven, were also affected by global megaherbivore extinctions during the late Quaternary (15), that likely resulted from synergistic anthropogenic and climatic drivers (35). These interactions argue against single-cause attributions of rates of vegetation change.

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A key next step is to integrate these paleovegetation sequences with other paleoclimatic and archaeological records in order to better understand the past feedbacks among climate, ecosystems, and humans (3, 10, 13, 36), and the legacy effects of these past interactions on the trajectory of contemporary ecosystems. Assembled networks of paleovegetation, paleoclimatic, and anthropogenic records need to be harmonized and quality checked in order to do this attribution correctly and handle the spatial variations in vegetation, climate, and human histories within and among continents (e.g. 36). Such an integration will also need carefully chosen numerical techniques to formally detect the onset of detectable human influence in paleoenvironmental time series and the variation in timing

within and among ecosystems (29). Additionally, a higher density of paleoecological records is still critically needed, especially in topographically rich regions such as the Himalayas and the Andes where climate heterogeneity is highest and human activities span millennia.

Despite these complexities, it is well known that the mean global temperature increases during the last deglaciation (ca. 6°C) were several times larger than those of the middle to late Holocene (ca. 1°C, 37). Hence, a reasonable working inference is that the globally enhanced rates of vegetation change over the last several thousand years were caused primarily by anthropogenic activities, while vegetation changes during the late Pleistocene to early Holocene were driven primarily by changing climates. If so, the magnitude and extent of late Holocene rates of vegetation change suggests that the global transformation of the terrestrial biosphere by humans now resembles or exceeds in rate and scope even the profound ecosystem transitions associated with the end of the last glacial period.

Moreover, the global ecosystem changes for this century may be greater yet, given current climate commitments and given that the climate changes expected for higher-end emission scenarios are similar in magnitude to those of the last deglaciation.

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- A.W.R.S., J.W.W. designed the study. S.G.A.F., K.P.B., V.A.F., A.W.R.S. and O.M. developed the
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272 T.G., S.H., H.H., S.I., S.G.A.F, and J.W.W. led Neotoma data mobilization efforts. S.G.A.F. and J.W.W. lead the writing. All authors contributed to the article and approved the submitted version. 273 274 Competing interests. The authors declare no competing interests. Data and materials availability: All the data and R codes are publicly available at Zenodo (40) and at https://github.com/HOPE-UIB- 275 BIO/Global RoC. Harmonization tables are available at Figshare (41). 276 277 SUPPLEMENTARY MATERIALS 278 279 Materials and Methods 280 Figs. S1-S7 Tables S1-S3 281 282 References (42-77) 283 Data S1 284

285 FIGURES AND TABLES

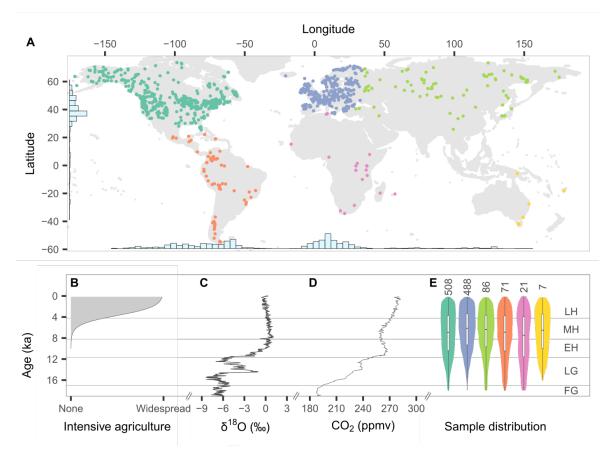


Figure 1 | Spatiotemporal distribution of the fossil pollen sequences analyzed here and climate and anthropogenic changes during the last 18.000 yr. A) Spatial distribution of used pollen sequences. Histograms indicate the frequency of sequences across longitude and latitude. B) Development of intensive agriculture based on archaeological expert elicitation (8). C) δ^{18} O, a temperature proxy, from the North Greenland Ice Core Project (NGRIP) (38). D) Atmospheric CO₂ concentration (ppmv; EPICA DOME C, 39). E). The number of pollen sequences per continent (colors match panel A) and sample density over the studied period. FG: Full Glacial; LG: Lateglacial; EH: Early Holocene, MH: Middle Holocene, LH: Late Holocene.

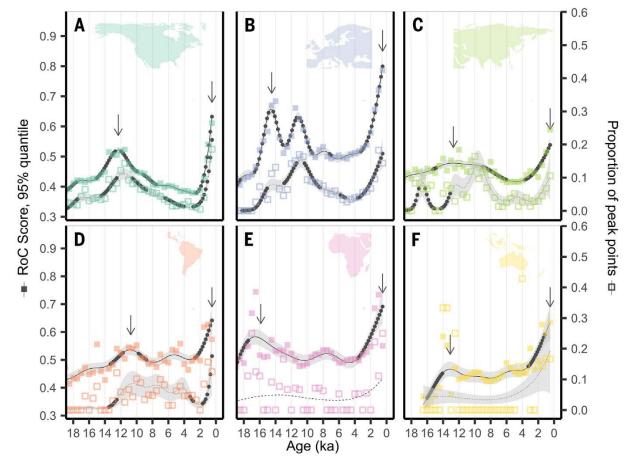


Figure 2 | Rate of Change (RoC) analyses by continent. The filled squares represent the upper 95% quantile RoC score (left y-axis) per 500 yr time bin with the solid curve representing the corresponding generalized additive model (GAM, 22). High values indicate high rates of vegetation change. Empty squares represent the proportion of peak points within each time bin (right y-axis) with the corresponding GAM curve (dotted line). High values indicate a high synchrony in RoC among sequences (22). When the relationship is not significant, the GAM line is shown as dashed and the error envelope is absent. Black asterisks on the GAM curves identify periods of significant acceleration in vegetation RoCs (i.e. where the derivative significantly differs from zero). Arrows indicate maximum RoC values for late Holocene and the Pleistocene-Holocene transition (Table S1).

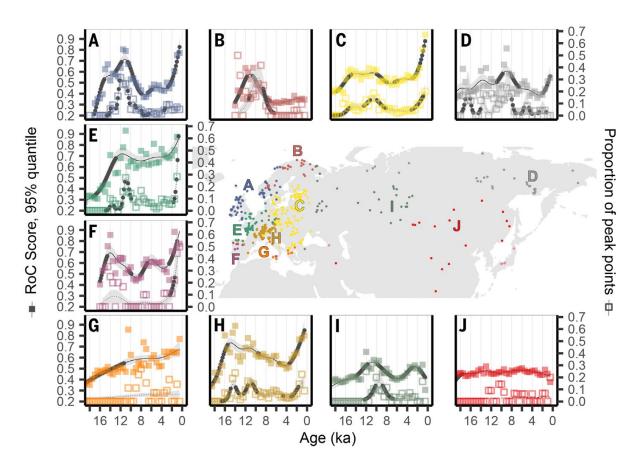


Figure 3 | Rates of Change (RoC) analyses by region across Eurasia. Figure design follows Figure 2.

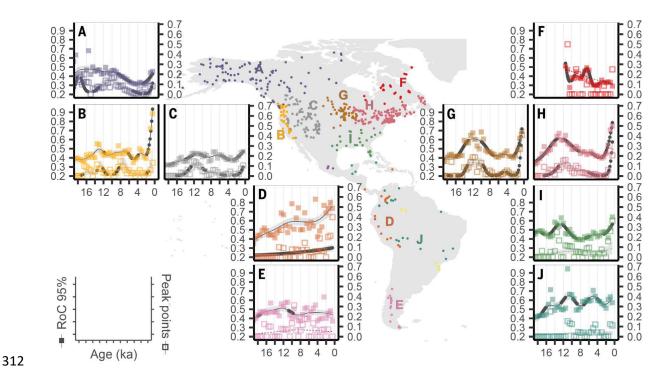


Figure 4 | Rates of Change (RoC) analyses by region across the Americas. Figure design follows Figure 2.