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Article:

Past and future global transformation of terrestrial ecosystems under climate change

Nolan, Connor[1], Jonathan T. Overpeck[2,1], Judy R.M. Allen[3], Patricia M. Anderson[4], Julio L. Betancourt[5], Heather A. Binney[6], Simon Brewer[7], Mark B. Bush[8], Brian M. Chase[9], Rachid Cheddadi[9], Morteza Djamali[10], John Dodson[11], Mary E. Edwards[6], William D. Gosling[12], Simon Haberle[13], Sara C. Hotchkiss[14], Brian Huntley[3], Sarah J. Ivory[15], A. Peter Kershaw[16], Soo-Hyun Kim[14], Claudio Latorre[17], Michelle Leydet[10], Anne-Marie Lézine[18], Kam-Biu Liu[19], Yao Liu[20], A.V. Lozhkin[21], Matt S. McGlone[22], Robert A. Marchant[23], Arata Momohara[24], Patricio I. Moreno[25], Stefanie Müller[26], Bette L. Otto-Bliesner[27], Caiming Shen[28], Janelle Stevenson[29], Hikaru Takahara[30], Pavel E. Tarasov[26], John Tipton[31], Annie Vincens[32], Chengyu Weng[33], Qinghai Xu[34], Zhuo Zheng[35], & Stephen T. Jackson[36*,1].

[1]University of Arizona, Department of Geosciences, Tucson, AZ 85721, USA

[2]University of Michigan, School for Environment and Sustainability, Ann Arbor, MI 48109, USA

[3]University of Durham, Department of Biosciences, Durham DH1 3LE, UK

[4]University of Washington, Department of Earth and Space Sciences, Seattle, WA 98195, USA

[5]United States Geological Survey, National Research Program, Reston, VA 20192, USA

[6]University of Southampton, Geography and Environment, Southampton SO17 1BJ, UK

[7]University of Utah, Department of Geography, Salt Lake City, UT 84112, USA

[8]Florida Institute of Technology, Department of Biological Sciences, Melbourne, FL 32901, USA

[9] Centre National de la Recherche Scientifique, UMR 5554, Institut des Sciences de l'Evolution de Montpellier, Université Montpellier, Bat.22, CC061, Place Eugène Bataillon, 34095 Montpellier, cedex5, France

[10]Institut Méditerranéen de Biodiversité et d'Ecologie, (IMBE UMR 7263 CNRS – Aix Marseille Université), 13545 Aix-en Provence Cedex 04, France

[11]University of New South Wales, Palaeontology, Geobiology and Earth Archives Research Centre (PANGEA), Sydney NSW 2052, Australia and State Key Laboratory of Loess and Quaternary Geology, Institute of Earth Environment, Chinese Academy of Sciences, Xi'an, 71002, Shaanxi, China

[12]University of Amsterdam, Institute for Biodiversity and Ecosystem Dynamics, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands and The Open University, Department of Environment, Earth & Ecosystems, Walton Hall, Milton Keynes, MK7 6AA, UK

[13]Australian National University, Department of Archaeology and Natural History, Canberra, Australia

[14]University of Wisconsin, Department of Botany, Madison, WI 53706, USA

[15]Pennsylvania State University, Department of Geosciences, State College, PA, 16802, USA

[16]Monash University, School of Earth, Atmosphere, and Environment, Melbourne VIC 3800, Australia

[17]Pontificia Universidad Católica de Chile, Departamento de Ecología, Institute of Ecology and Biodiversity (IEB), Santiago, Chile

[18]Sorbonne Université, CNRS-IRD-MNHN, LOCEAN/IPSL Laboratory, 4 Place Jussieu, 75005 Paris, France

[19]Louisiana State University, Department of Oceanography and Coastal Sciences, Baton Rouge, LA 70803, USA

[20]Northern Arizona University, School of Informatics, Computing, and Cyber Systems, Flagstaff, AZ 86011, USA

[21]North-East Interdisciplinary Scientific Research Institute, Far East Branch Russian Academy of Sciences, Magadan 685000, Russia

[22]Landcare Research, Lincoln 7640, New Zealand

[23]University of York, York Institute for Tropical Ecosystems, Environment Department, York YO10 5NG, UK

[24]Chiba University, Graduate School of Horticulture, Matsudo-shi Chiba 271-8510 Japan

[25]Universidad de Chile, Departamento de Ciencias Ecológicas, IEB and (CR)2, Santiago, Chile

[26]Freie Universität Berlin, Institute of Geological Sciences, D-12249 Berlin, Germany

[27]National Center for Atmospheric Research, Climate and Global Dynamics Laboratory, Boulder, CO 80307, USA

[28]Yunnan Normal University, Key Laboratory of Plateau Lake Ecology and Global Change, Kunming, Yunnan 650092, China

[29]Australian National University, School of Culture, History, and Language, Canberra, Australia

[30]Kyoto Prefectural University, Graduate School of Life and Environmental Sciences, Kyoto, 606-8522, Japan

[31]University of Arkansas, Department of Mathematical Sciences, Fayetteville, AR 72701, USA

[32]Centre Européen de Recherche et d'Enseignement des Géosciences de l'Environnement (CEREGE), 13545 Aix-en-Provence cedex 4, France

[33]Tongji University, School of Ocean and Earth Science, Shanghai, China

[34]Hebei Normal University, Institute of Nihewan Archaeology and College of Resource and Environmental Sciences, Shijiazhuang 050024, China

[35]Sun Yat-Sen University, School of Earth Science and Engineering, Guangdong Provincial Key Lab of Geodynamics and Geohazards, Guangzhou 510275, China

[36]United States Geological Survey, Southwest Climate Science Center, Tucson, AZ 85721, USA

[*]Corresponding author at stjackson@usgs.gov

Abstract. Concern is growing that global climate change will have widespread impact on the world's terrestrial ecosystems, but future impacts are imperfectly constrained by ecosystem models and direct observations. All available data, including records of past ecological change, need to be utilized to assess the range of potential future outcomes. Here we show that pervasive ecosystem transformations occurred in response to warming and associated climatic changes during the last glacial-to-interglacial transition, which was of comparable magnitude to climatic change projected to occur in the next 100 to 150 years under high-emission scenarios. We used data from 596 published paleoecological records to examine compositional and structural changes in global terrestrial vegetation since the last glacial period, and to project the magnitude of ecosystem transformations under different emission scenarios in the future. Our results indicate that terrestrial ecosystems are highly sensitive to temperature change, and suggest that without major reductions in greenhouse-gas emissions to the atmosphere (i.e., in line with those targeted in the 2015 Paris Agreement), most terrestrial ecosystems worldwide are at risk of major transformation, with accompanying disruption of ecosystem services and impacts on biodiversity.

A crucial question facing policymakers in addressing climate change is how different levels of global greenhouse-gas (GHG) emissions to the atmosphere might translate into ecosystem transformations worldwide. Terrestrial-ecosystem function is governed largely by composition and physical structure of vegetation (*1-3*), and climate-change impacts on vegetation can potentially cause disruption of ecosystem services and loss of biodiversity (*4,5*). It is critical to assess the likely extent of ecosystem transformation as GHG emissions increase (*6*), and to understand the full potential magnitude of impacts should current GHG emission rates continue unabated.

Ecosystem transformation generally involves replacement of dominant plant species or functional types by others, whether recruited locally or migrating from afar. Observations from around the globe indicate that climate change may already be driving substantial changes in vegetation composition and structure (*3*). Ecosystem change is accelerated by mass mortality of incumbent dominants (*7,8*), and widespread dieback events and other large disturbances are already underway in many forests and woodlands (*9-11*), with further mortality events predicted

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under increasing temperatures and drought (*3,9,10,12*). Replacement of pre-disturbance dominants by other species and growth-forms has been documented in many places (*8,13,14*). In addition, evidence is accumulating for geographic range-shifts in individual species, and climate change is interacting with invasive species, fire regimes, land-use, and CO_2 increase to drive vegetation changes in many regions (*15,16*).

Beyond observations of recent and ongoing change, modeling studies indicate ecosystem transformation under climate projections for the 21st Century. These models include dynamic global vegetation models (*3,17*), species-distribution models (*18*), and comparison of the multivariate climate distance between biomes with that between modern and future climates (*19*). However, capacity for assessing the magnitude of ecosystem transformation under future climate scenarios is limited by the difficulty of evaluating model performance against empirical records, particularly when projected climate states are novel (*19,20*).

Paleoecological records of past ecological responses to climate change provide another means, independent of modern observations and model projections, for gauging the sensitivity of ecosystems to climate change. Several high-precision time-series studies have shown that local and regional ecosystems can shift rapidly, within years to decades, under abrupt climate change (*21-23*), but sites with such detailed chronologies are scarce. Here we pursue an approach based on a global network of radiocarbon-dated paleoecological records of terrestrial vegetation composition and structure since the Last Glacial Maximum (LGM), ca. 21,000 yr BP. Most postglacial warming happened between 16,000 and 10,000 yr BP, although it commenced earlier in parts of the Southern Hemisphere (*24,25*). Global warming between the LGM and the early Holocene (10,000 yr BP) was on the order of 4-7º C, with more warming over land than oceans (*25,26*). These estimates are roughly comparable to the magnitude of warming the Earth is projected to undergo in the next 100 to 150 years if GHG emissions are not reduced significantly (*27*). The magnitude of change in vegetation composition and structure since the last glacial period provides an index of the magnitude of ecosystem change that might be expected under warming of similar magnitude in the coming century (*28*). Although the rate of projected future global warming is at least an order of magnitude greater than that of the last glacial-to-interglacial transition (*25*), a glacial-to-modern comparison provides a conservative estimate of

the extent of ecological transformation to which the planet will be committed under future climate scenarios (See Supplementary text).

We compiled and evaluated paleoecological (pollen and macrofossil) records from 596 sites worldwide (fig. S1) to determine the magnitude of post-glacial vegetation change. We adopted an expert-judgment approach, in which paleoecologists with relevant regional experience compiled published records (table S1), and made informed judgments on the magnitude of the difference between glacial-age and Holocene ecosystems (see *Methods*). For the purposes of our analyses, we defined the last glacial period (LGP) as the interval between 21,000 and 14,000 yr BP. Although postglacial warming was underway in many regions by 16,000 yr BP (*24*), continental ice-sheets were still extensive 14,000 yr BP, and some climate regimes remained essentially 'glacial' in nature, particularly in the Northern Hemisphere (*29*). Extending the LGP window to 14,000 yr BP provides a larger array of records for the assessment, both in glaciated and unglaciated terrains, and renders our analysis more conservative (i.e., climatic and vegetation contrasts with the Holocene are likely to decrease between 21,000 and 14,000 yr BP).

For each record, experts were asked to judge the magnitude of compositional change and structural change since the LGP as large, moderate, or low, and to provide detailed justification for their judgment (see *Methods*) (table S2). For sites that experienced moderate to large ecological change, experts were also asked to assess the role of climate change (large, moderate, or none) in driving the observed vegetation change. For each of these four judgments, experts were asked to state their level of confidence as high, medium, or low. In assessing the role of climate change, experts were asked to focus specifically on whether climate change since the LGP was sufficient to drive the observed changes, acknowledging that other factors (e.g., human activity, post-glacial CO_2 increase, megafaunal dynamics) may have also played important roles. For sites with a long history of human land-use), experts used Holocene records predating widespread land clearance as a benchmark for comparison with the LGP records.

Our results indicate that the magnitude of past glacial-to-interglacial warming was sufficient at most locations across the globe to drive changes in vegetation composition that were moderate (26% of sites) to large (72%), as well as moderate (28%) to large (67%) structural changes (Fig. 1, table S3). These changes were particularly evident at mid- to high latitudes in

the Northern Hemisphere, as well as in southern South America, tropical and temperate southern Africa, the Indo-Pacific region, Australia, Oceania, and New Zealand (Fig 1a). Compositional change at most sites in the Neotropics was moderate to large, but three sites showed little or no compositional change, all with medium to high confidence (fig. S2). Shifts in vegetation structure were also moderate to large at mid-to high-latitude sites, although a few sites showed low change (Fig. 1b). The Neotropics had nine sites with little or no structural change (Fig. 1b), all with high-confidence assessments (fig. S2). These sites have been occupied by tropical forest ecosystems since the LGM, although most have undergone moderate to large compositional change (*30,31*). For nearly all sites that experienced moderate or large ecological change, climate change since the LGP was judged as sufficient to explain the observed changes with high confidence (table S4). Atmospheric CO_2 concentrations also increased from 190 to 280 ppm during the deglaciation, interacting with and in some cases modulating ecological responses to climate change. However, CO_2 changes alone cannot account for postglacial vegetational changes (Supplementary Text).

Independent of the expert-judgment process, we used the estimated anomaly in mean annual temperature between the LGM and the present (pre-industrial) as a proxy for the overall magnitude of climate change since the LGP. LGM temperature estimates were derived using an assimilated proxy-data/model integration (*26*). Low-change sites were largely concentrated in regions where the estimated temperature anomaly was relatively small (Fig. 1). To explore this relationship further, we plotted the frequency distribution of the difference between estimated LGM and present-day mean-annual temperatures for individual sites in each of the three ecological-response categories. Nearly all sites with low compositional change between the LGP and today are associated with small projected temperature anomalies (median 2.4°C), whereas sites with moderate to high compositional change have larger temperature anomalies (Fig. 2a). Results for structural changes are similar, although a greater number of sites with low structural change include larger temperature anomalies (Fig. 2b). This difference is not surprising, because compositional change in vegetation can occur without an accompanying change in vegetation structure (Fig. 1). Europe and eastern North America experienced unusually large temperature changes since the LGM, owing to depressed temperatures near the large ice sheets, and these regions show significant compositional and structural changes since the LGP. However, results from other parts of the globe indicate that widespread ecosystem changes were driven by much

smaller temperature changes (fig. S3). We repeated our analysis using the TraCE-21ka model simulations (*32,33*), which yield lower magnitude of LGP-to-Holocene climate change (*34*); despite the potential conservative bias, results for compositional and structural change (fig. S4) were similar to those in Fig. 2. Temperature differences between LGP and the present were significantly greater for sites with large ecological change than those with low to moderate change, using both paleoclimate estimates (*26, 32*) (table S2).

We also used our database of ecological change since the LGM to assess the global distribution of the probability of large compositional and structural change given GHG emission scenarios (Representative Concentrations Pathways (RCP) 2.6, 4.5, 6.0 and 8.5, each as simulated by the CCSM4 coupled climate model) (*35*). The range of LGM-to-present temperature changes (Fig. 2) overlaps with the range of temperature changes projected for the coming century under these scenarios (Fig. 3a; fig. S5). We quantified the relationship between temperature and ecological change using a logistic spline regression with ordered categories (*36*). We fit models for compositional and structural change using the temperature change since the LGM as the independent predictor variable. In both models, LGM-to-modern temperature change is a significant predictor of ecosystem change ($p < 0.001$). We then used these models to predict the risk of large change for the future range of projected global temperature changes (Fig. 3b) and to map the probability of large change under RCP 2.6 and RCP 8.5 (Fig. 3c-3f) at the end of the 21st century (see fig. S6 for RCP 4.5 and RCP 6.0). Under RCP 2.6 the probability of large compositional change is less than 45% over most of the globe (Fig. 3c) and the probability of large structural change is generally less than 30% (Fig. 3e). In contrast, under the business-as-usual emissions scenario, RCP 8.5, the probability of large compositional change and large structural change are both greater than 60% (Fig. 3d, 3f). Analyses using the TraCE-21ka model yielded similar patterns (fig. S7).

Our study uses a single variable, mean annual temperature, as a metric for the broader array of climatic changes that can drive vegetation change, and it compares vegetation and climate states separated by 10,000-20,000 years. Future climate change, like that in the past, will be multivariate, involving shifts in seasonal temperatures, seasonal precipitation, climate extremes, and variability regimes. As mean annual temperature increases, other ecologically important variables will change, often in complex or counterintuitive ways (*20,37,38*), and

ecological responses will often be episodic or non-linear (*8, 13-15*). Although the temperature increases since the LGP provide crude analogs for ongoing and future climate changes – for example, boundary conditions and forcings are different now (*25,39,40*) – our results nevertheless provide concrete evidence that vegetation composition and structure are sensitive to changes in mean annual temperature of the magnitudes forecast for the coming century, and that vegetation transformations will become increasingly extensive as temperatures increase. Under the RCP8.5 scenario, the rate of warming will be on the order of 65 times greater than the average warming during the last deglaciation (*25*). Although many ecological processes (e.g., species migration, colonization, succession) will likely lag climate changes, ecosystem transformations will probably be accelerated by disturbance and mortality events, land use, and invasive species (*7-15*).

We therefore conclude that terrestrial vegetation over the entire planet is at substantial risk of major compositional and structural change in the absence of dramatically reduced GHG emissions. Much of this change could occur during the 21st century, especially where vegetation disturbance is accelerated or amplified by human impacts (*7*). Many emerging ecosystems will be novel in composition, structure, and function (*41*), and many will be ephemeral under sustained climate change; equilibrium states may not be attained until the 22nd Century or beyond. Compositional transformation will affect biodiversity, via disintegration and reorganization of communities, replacement of dominant or keystone species, pass-through effects on higher trophic levels, and ripple effects on species interactions (*16,42*). Structural transformation will have particularly large consequences for ecosystem services (*4*), including achievement of nature-based development solutions under the United Nations' Sustainable Development Goals (https://sustainabledevelopment.un.org/sdgs). Structural changes will also influence biodiversity, driving alterations in habitats and resources for species at higher trophic levels. Compositional and structural changes may also induce potentially large changes to carbon sources and sinks, as well as to atmospheric moisture recycling and other climate feedbacks. Our results suggest that impacts on planetary-scale biodiversity, ecological functioning, and ecosystem services increase substantially with increasing GHG emissions, particularly if warming exceeds that projected by the RCP2.6 emission scenario (i.e., 1.5°C).

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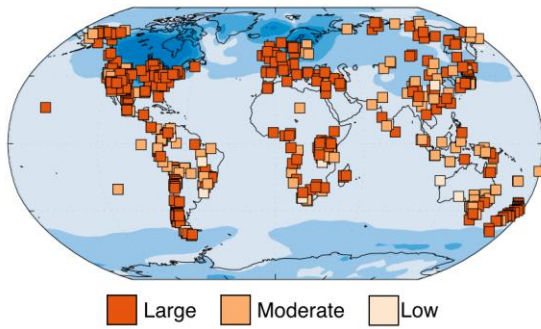
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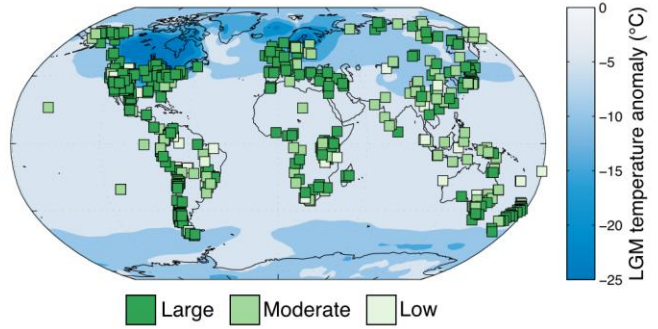
Fig. 1. The degree of estimated compositional (*a*) and structural change (*b*) between the last glacial period and the present. Each square represents an individual paleoecological site, and the color density indicates the extent of vegetation change since the last glacial period (21,000-14,000 yr BP). Background shading denotes the estimated temperature anomaly between the last glacial maximum (LGM) 21,000 years ago and today, based on assimilated proxy-data and model estimates (*26*).
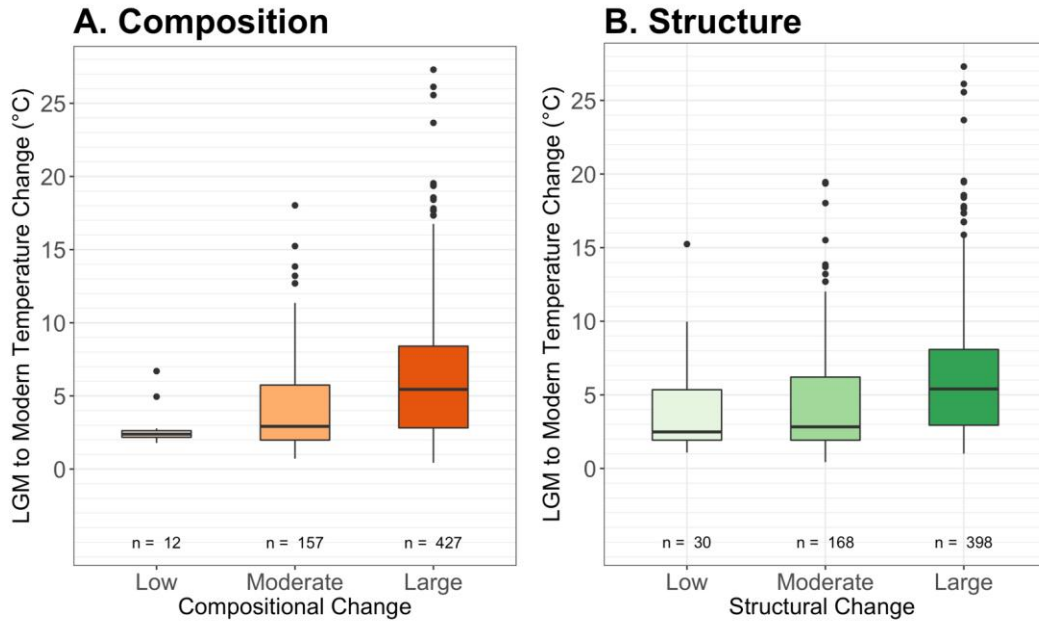
A. Composition

B. Structure

Fig. 2. Box plots of the estimated mean-annual temperature differences between the last glacial maximum and today in each of the three vegetation-change categories (low, moderate, large), for (*a*) composition and (*b*) structure. Sites showing low vegetational change are associated largely with relatively small temperature anomalies, while moderate and large changes are associated with larger post-LGM temperature differences, indicating that magnitude of temperature change plays an important role in the magnitude of vegetation change. The glacial temperature anomalies are based on (*26*). Analyses using the TraCE-21ka simulation show similar patterns (fig. S4).
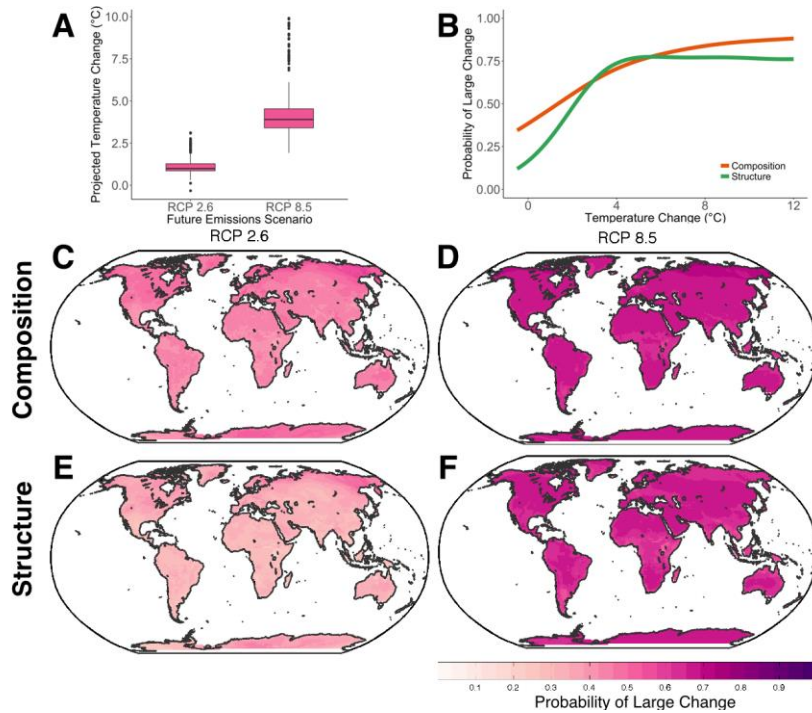
Fig. 3. *(a)* Box plots of the estimated mean-annual temperature differences between today and future-climate simulations for individual sites (using the nearest grid-point). Most sites show relatively small temperature change under the low-emissions scenario (RCP2.6), with substantially higher change under the high-emission scenario (RCP8.5). *(b)* Probability of large change in vegetation composition (orange) and structure (green) as a function of temperature change. *(c-f)* Estimated probability of large compositional and structural change by the end of the 21st century (average of 2081-2100) under RCP 2.6 *(c,e)* and RCP 8.5 *(d,f)*. Probabilities *(b-f)* are estimated from a logistic-spline regression model fit using LGM-to-modern temperature change as a predictor variable and observed LGP-to-modern vegetation changes (large *versus* not-large) as the response variable. Future temperature increases are calculated as an average of 2081-2100 under the model scenarios, minus an average of 1985-2005 from the CCSM4 historical simulation. Analyses using the TraCE-21ka simulation show similar patterns (fig. S7).

Supplementary Materials for

Past and future global transformation of terrestrial ecosystems under climate change

Nolan, Connor[1], Jonathan T. Overpeck[2,1], Judy R.M. Allen[3], Patricia M. Anderson[4], Julio L. Betancourt[5], Heather A. Binney[6], Simon Brewer[7], Mark B. Bush[8], Brian M. Chase[9], Rachid Cheddadi[9], Morteza Djamali[10], John Dodson[11], Mary E. Edwards[6], William D. Gosling[12], Simon Haberle[13], Sara C. Hotchkiss[14], Brian Huntley[3], Sarah J. Ivory[15], A. Peter Kershaw[16], Kim, Soo-Hyun[14], Claudio Latorre[17], Michelle Leydet[10], Anne-Marie Lézine[18], Kam-Biu Liu[19], Yao Liu[20], A.V. Lozhkin[21], Matt S. McGlone[22], Robert A. Marchant[23], Arata Momohara[24], Patricio I. Moreno[25], Stefanie Müller[26], Bette L. Otto-Bliesner[27], Caiming Shen[28], Janelle Stevenson[29], Hikaru Takahara[30], Pavel E. Tarasov[26], John Tipton[31], Annie Vincens[32], Chengyu Weng[33], Qinghai Xu[34], Zhuo Zheng[35], & Stephen T. Jackson[36*,1].

correspondence to: stjackson@usgs.gov

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> Supplementary Text
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> Instructions for assessors
> Captions for supplementary data table S1

Other Supplementary Materials for this manuscript includes the following:

> Additional Data Table S1

Materials and Methods

Paleoecological Inference and Expert Judgment

Sources of paleoecological inference concerning terrestrial ecosystem properties are diverse, and vary in level of detail, quality, and geographic coverage. For this study, we used pollen and plant macrofossil assemblages, which are widely applied, robust proxies that provide direct evidence for composition and structure of terrestrial vegetation. Our use of fossil pollen, plant macrofossils, or both, collectively provides broad geographic coverage within and among the vegetated continents and islands. Here, we discuss the characteristics of the paleoecological data we use, and justify our application of a transparent process of expert judgment that builds on more than a century of community experience in paleoecological inference and causal attribution. We describe specific procedures and protocols in the following section.

Pollen and plant macrofossil data derive from a wide variety of depositional settings, ranging from sediments of lakes and wetlands to land-surfaces buried under glacial and fluvial deposits to rodent middens stashed in caves. Pollen data can usually be expressed in a single numerical currency (percentages of a terrestrial taxon sum), but pollen percentages are influenced by site-specific processes (dependent on basin size, depositional environment, local vegetation, and regional topography, among others), and by differential pollen productivity and dispersal among taxa (*43-49*). Pollen accumulation rates and plant macrofossils, when available, can help inform and constrain interpretation of pollen percentages. Plant macrofossil data themselves lack a single universal currency beyond 'presence', so numerical comparisons among assemblages or sites are difficult and rare (*50,51*). No formal algorithm currently allows incorporation of information from macrofossils, pollen accumulation rates, or depositional context into interpretation of pollen percentages, and many macrofossil assemblages, particularly from buried land surfaces and rodent middens, lack associated pollen data. Numerical methods and formal tools have been developed to support vegetational inferences from paleoecological data, particularly pollen percentages (*20,47,48,52-54*). However, most of these tools are best suited for relatively uniform data and site types, and most require calibration or reference data sets from comparable modern sites. Such reference data sets do not exist in many regions. Furthermore, although the development of global databases for paleoecological inference is rapidly advancing (*55,56*), raw data for many sites and some entire regions remain unavailable, further hampering global application of numerical analyses.

The sole universal approach for inferring past vegetation composition and structure from these diverse data types remains the informed judgment of experts with relevant training and experience. Such expert judgment involves examining the available data with a particular question in mind, and weighing the evidence in context of broader knowledge and experience to arrive at a conclusion. Although often aided by formal numerical analyses, expert judgment is also informed by site-specific knowledge (basin morphometry, depositional environment, relevant taphonomic processes), region-specific knowledge (flora, vegetation, topography,

comparative modern pollen/vegetation datasets), taxon-specific knowledge (taphonomic and assemblage-representation properties), and general knowledge of the vegetation-sensing properties of fossil assemblages, including potential biases and distortions (*49,57*).

Attainment of expertise in paleoecology involves immersion in understanding the processes that intervene between source vegetation and fossil assemblages, in mastering the literature of paleoecological interpretation, and in identifying the idiosyncracies of individual sites and regions. Interpretation of fossil pollen percentages is based on a century of intensive study (*20,48,58,59*), and paleoecologists draw on a rich literature of theoretical and empirical studies to guide their interpretations (*43-49,52-54,57*). Interpretation of plant macrofossil assemblages from lakes, peatlands, and other 'wet' sites is also founded on theoretical and empirical understanding of the physical processes by which these assemblages are formed and what they do and do not record (*50,51,60-63*). Plant macrofossils in rodent (*Neotoma* and other genera) middens represent a particular case in which the behavior and foraging preferences of the animals need to be considered (*64-66*), along with other factors (*57*).

In the current study, scientists with experience in the various regions and data sources provided their best judgments concerning the degree of vegetational change between LGP and today for each site and their confidence in those judgments (see below). To ensure transparency and consistency, each expert also provided explicit justification for each assessment they made, noting the specific features of the LGP pollen or macrofossil assemblages, contrasting them with modern assemblages or modern vegetation, and identifying potential sources of uncertainty (e.g., taxonomic smoothing, depositional or dispersal processes). Judgments of the type used in this study are thus the same as those incorporated into the discussions and conclusions of virtually every paper in the paleoecological literature. Those judgments are often supported by numerical or other analytical tools, but they ultimately draw on skills and knowledge built on a century of paleoecological inquiry. Such informed judgment is at the heart of scientific inference, and applying it in our study allows us to maximize global coverage, using multiple data sources from diverse depositional settings, drawing on expertise from every region of the globe for which suitable pollen or macrofossil data exist.

Compilation of Last Glacial Period (LGP) paleoecological records

Teams of regional experts (Table S1) compiled 596 published paleoecological records (pollen, plant macrofossil, or both) from all vegetated continents and oceanic islands with data within the period 21,000-14,000 yr BP (Figure S1, Additional Data table S1), which we operationally define as the Last Glacial Period (LGP). The sole criterion for inclusion was that a site have pollen or macrofossil data (or both) reliably dating to the period between 21,000 and 14,000 yr BP.

Assessment of ecological change

Regional experts compared LGP records from each site with 'modern' vegetation or palaeoecological data. Magnitude of vegetational change in terms of composition and structure from LGP to 'modern' was qualitatively assessed as large, moderate, or low for each site. For 596 sites (85% of total), vegetational or paleoecological (pollen, macrofossil) data from the past-two centuries were used as the benchmark for comparison. In some cases, human land-use or lack of suitable paleoecological data required an earlier benchmark. The late Holocene (past 2000-3000 yr) was used for 57 sites (10% of total), and 33 sites (5% of total) used paleoecological data from the early or mid-Holocene. Typically, benchmark data from the same paleoecological site were used in the comparison, but experts also employed their knowledge of modern or natural vegetation of the respective region. If paleoecological data from a site did not extend into the Holocene, experts often used Holocene paleoecological data from other, comparable sites in the same region. No relationship was observed between the assessment of ecological change and the temporal benchmark used; each of the benchmarks used (modern, late Holocene, early-mid-Holocene) yielded a mix of low, moderate, and large changes in vegetation composition and structure.

The degree of confidence in the assessments of ecological change was rated as high, medium, or low. All assessments were based on the definitions in Table S2 and the instructions in the Instructions for Assessors (see Other Supplementary Materials). Authors provided succinct but informative justifications for each individual assessment of compositional and structural change, sufficient to allow a paleoecologically literate reader to understand the empirical basis for their assignment. A complete list of sites with accompanying metadata, assessments, and justifications, is provided in Additional Data table S1.

Attribution of Vegetational Change

Climate change is among many mechanisms potentially capable of driving vegetational change. For each site where ecological changes were assessed as moderate or large, the role of climate in driving those changes was also assessed (large, moderate, or none). For this decision, expert judgment drew from multiple considerations, including understanding of modern ecosystems and communities and their controls, independent paleoclimatic evidence from multiple proxies (paleontological, geochemical, lithological) deriving from multiple sources (ice-cores, marine sediments, lake sediments, paleosols, glacial deposits, fossil groundwater, boreholes) (67) and climate-model simulations (68,69). The inclusion of 'none' as a choice, although rarely used, was to ensure that experts considered alternatives to climate as a primary driver (including succession, neutral assembly, ecological drift, human activities, soil development, biogeochemical changes, migration, and evolution). The degree of confidence in assessments of the role of climate was rated as high, medium, or low.

Estimates of temperature change since LGP

Site-level changes in mean annual temperature since LGP were estimated based on two different datasets: the model/proxy integration of Annan and Hargreaves (2013) (26) and the TraCE-21ka transient climate model run (32). For each dataset the estimate of temperature change for the single closest grid box to each site was used. The distribution of temperature

changes is shown in box plots, in subsets according to degree of assessed ecological change (figure 2, figure S4).

The main paleoclimate dataset used is the last glacial maximum (LGM) temperature anomaly reconstruction from Annan and Hargreaves (2013) (*26*). This reconstruction uses fully coupled GCMs from the PMIP3/CMIP5 set of models run with LGM boundary conditions and proxy data in a multiple linear regression framework to obtain an estimate of the surface air-temperature anomaly from LGM to pre-industrial on a 2.5° x 2.5° grid. The proxy data include marine sea-surface temperature reconstructions from Multiproxy Approach to Reconstructing Global Oceans (*70*), the multiproxy deglaciation synthesis (*71*), and pollen-derived LGM temperatures from selected continental sites (*72*).

Estimated LGM-to-preindustrial temperature change based solely on the models is 3.1-5.9°C (*26*). With the data constraints, the final resulting LGM cooling estimate relative to preindustrial temperatures is 4.0±0.8°C. Application of the proxy data in this framework reduced uncertainty by arbitrating disagreements between the nine individual models and by improving spatial skill (*26*). The influence of proxy data on the mean estimates of temperature change between LGP and the preindustrial period was very small (*26*).

As an independent check on the temperature estimates and analyses, we also used the TraCE-21ka (simulation of the transient climate evolution over the last 21,000 years) (*32,33*), a 21,000 year run of the National Center for Atmospheric Research's Community Climate System Model version 3 (CCSM3) with time-evolving forcing including atmospheric CO_2 concentrations, insolation, and land ice sheets. This is the only fully-coupled, moderately high-resolution transient simulation of the LGM to Holocene climate evolution. We estimated the LGP to late Holocene temperature change from TraCE by subtracting the average temperature for 0-6ka from the average temperature from 14-21ka. These large windows were chosen with the intention of smoothing out noise in the transient simulation and getting a coarse estimate of temperature change at each grid point. The estimate of LGM-to-late-Holocene temperature change from TraCE at the grid point nearest to each paleoecological site is plotted in figure S4, an expanded version of Figure 2.

The boxplots suggest a relationship between the degree of ecosystem change and temperature change. We tested for statistical significance of this relationship using the Wilcoxon rank-sum test. The temperature change experienced by sites with Large ecological change was statistically significantly different from that at sites with Moderate and Low ecological change (table S3). The temperature differences between sites with Moderate versus Low ecological change were not statistically significant. Results were similar for the paleo-temperature estimates from the Annan and Hargreaves reconstructions and from TraCE (Table S3).

Projections of future temperature change

For each LGP paleoecological site we also obtained estimates for the projected future mean annual temperature change under various emissions scenarios. We used the difference between the average temperature for the last 20 years (2081-2100) of the future simulations under four different representative concentration pathway (RCP) scenarios and the average temperature for the last 20 years of the historical simulations (1985-2005) at the nearest grid point using

simulations of the Community Climate System Model version 4 (CCSM4) run for CMIP5 and included in IPCC AR5 (*35,73*). All four RCPs – RCP 8.5, 6.0, 4.5, and 2.6 (also known as RCP 3.0-PD) – were used in our analysis.

These RCPs represent net radiative forcing of 8.5, 6.0, 4.5, and 2.6 W/m^2 at the end of the 21st century (*35*). RCP 8.5 is a "business-as-usual" scenario that ends up with ~1370 ppm CO_2 equivalent and global average temperature increase of approximately 5°C. RCP 6.0 is a stabilization scenario where radiative forcing is stabilized shortly after 2100. The CO_2 equivalent at 2100 is 936 ppm and the resulting global average temperature increase is 3-4°C. The RCP 4.5 and 2.6 scenarios represent aggressive emissions cutting. RCP 4.5 results in 650 ppm CO2 equivalent and a global average temperature increase of 2.4°C by 2100. This scenario represents aggressive emission stabilization without overshoot. The most aggressive mitigation pathway is RCP 2.6. This scenario results in 490 ppm CO2 equivalent and a global average temperature increase of 1.5°C at 2100. The emissions in this scenario peak at a radiative forcing of 3.0 W/m^2 in the mid-21st century and decline to 2.6 W/m^2 by 2100 (*35*).

The distributions of projected temperature change at our LGP paleoecological sites are shown as box plots in main text figure 3A and figure S5.

Estimating risk of future ecological change

We used our database of LGM-to-modern ecological change and associated temperature change to project the risk of future ecosystem transformation under different emission scenarios (see above). We developed a regression model between temperature change and ecological change using a logistic spline regression, also known as a generalized additive model (GAM). These models were fit in R using the mgcv package (*36,74*). We fit one model for compositional change and one for structural change. For both models the independent variable was the temperature change from the LGM to present at the closest grid box to each site from Annan and Hargreaves 2013 (Fig. 3) or TraCE-21ka (fig. S7). Ecological change served as the dependent variable. We used the ordered categorical family of GAMs where Small/No change is coded as 1, Moderate change is coded as 2, and Large change is coded as 3. The smooth terms of both models are highly significant (p<0.001).

We used these regression models to predict the probability of large, moderate, and low compositional and structural change for the full range of LGM-to-present temperature changes (0-30°C) and for the full range of future projected temperature changes (0-12°C) (fig. S7). The results in figure S7 are from the same GAM plotted on different x-axes. We also mapped these probabilities spatially for all of the representative concentration pathways (Figure 3, fig. S6).

Supplementary Text

Confidence by region

In fig. S2 we plot the confidence (low, medium, high) for assessment of compositional and structural change for the entire data set and for each individual region. Confidence for large compositional and structural change was high for nearly all regions; confidence was lower for sites assessed as having moderate and (especially) low change. The lower confidence associated with moderate to low change derived largely from poor taxonomic resolution in pollen assemblages, and from uncertainties associated with long-distance pollen transport, which may respectively mask vegetational changes and confound interpretations (*43-49*). These pollen considerations also resulted in moderate confidence for many high-latitude Northern Hemisphere pollen sites (Northern Eurasia, North America). (In unforested vegetation (particularly tundra, but also some grassland and steppe) low pollen productivity (low NPP, prevalence of insect-pollinated plants with poor pollen dispersal) renders pollen assemblages susceptible to high relative influx of pollen (particularly tree pollen) from distant sources. Vegetation in such regions is also often dominated by grasses (Poaceae), sedges (Cyperaceae), composites (Asteraceaea), chenopods (Chenopodiaceae), and other taxa that cannot be differentiated palynologically below the family level.)

Many North American sites were assessed as having medium confidence for structural change (in contrast to high confidence for compositional change); most of these were rodent-midden sites from the western United States. Middens primarily sample floristic composition, not relative or absolute abundance, and are thus more reliable indicators of vegetation composition than structure (*57,65*).

Temperature change by region

In fig. S3 we plot the frequency distributions of the estimated mean-annual temperature differences between the last glacial maximum and today for each region of the globe (*26*), in each of the three LGP-to-modern vegetation-change categories (low, moderate, large) for composition and structure. Although some regions (North America, Europe, New Zealand, Japan) have very high sampling density (figs. S1, S2), they do not dominate the patterns observed in Figure 2. Furthermore, although regions in proximity to continental ice sheets (North America, Europe) have many sites with extreme temperature anomalies (>10°C) between LGM and today, large vegetation changes are associated at many sites (typically further from ice sheets) with smaller temperature anomalies. Observed vegetational changes at sites near ice sheets may have occurred with much smaller temperature differences.

Comparing estimates of LGM-to-modern temperature change

In fig. S4 we plot the frequency distributions of the mean-annual temperature change from LGM to present vs. vegetation change using two different products for the temperature change: Annan and Hargreaves 2013 (*26*) and TraCE-21ka (*32*), as described above.

The Annan and Hargreaves estimate may overestimate the temperature change required to drive the observed ecological changes, because not all the paleoecological records extend to LGM. Our temperature-change estimates using TraCE (LGP to late Holocene) provide an independent check, with a bias opposite that of Annan and Hargreaves 2013. TraCE may underestimate the temperature change necessary to drive the observed vegetation change because of its cold Holocene bias (*34*) and because of the broad time ranges used to estimate the temperature change (particularly including the post-LGM warming trend observed in many regions between 21,000 and 14,000 yr BP). TraCE is based solely on climate model forcings and physics, and thus provides independent validation of our inferences, free of any possible bias from pollen and other paleoclimate proxy data. (As noted above, such bias is small even for the Annan and Hargreaves 2013 dataset.)

The range of temperature estimates and the general pattern in which greater vegetation change is associated with higher temperature change are consistent between the two LGM temperature products (fig. S4; table S3)). We repeated the GAM modeling of ecological change as a function of estimated temperature change using the TraCE temperature-change estimates. Results were consistent with those obtained using the Annan & Hargreaves 2013 estimates (fig. S7).

Role of climate and confidence

For all cases in which compositional or structural change were judged to be moderate or large, assessors were asked to judge the role of climate in driving the observed changes, as well as their confidence in that judgment (table S4). Climate was assessed with high confidence to have played a large role in the observed changes in composition and structure for 85% of the sites, and was judged as having a large role with medium or high confidence for 88% of sites. Climate was assessed to have played a low role in driving ecological change at less than 1% of sites (6 out of 584 for composition and 1 out of 566 for structure).

Role of Carbon Dioxide in Forcing Vegetational Changes

Some studies suggest that atmospheric CO_2 concentrations may be a primary driver of vegetation change, particularly in savanna and grassland regions (*75*), even overriding changes in climate (*76*). This hypothesis is based on advantages conferred by increased CO_2 concentrations on C_3 plants relative to C_4 plants in terms of quantum yield, wherein reduced transpiration raises soil moisture and water-use efficiency (*77-79*), increases woody-plant resprouting rates (*75*), or both.

Global temperature and atmospheric CO_2 concentrations are strongly linked (*80*); both increase significantly across the last glacial-interglacial transition (*81*), and both are predicted to rise in the future (*73*). Our conclusion that substantial changes in vegetation are likely to occur in the future does not require that the relative importance of these two controls be disentangled. The

spatial scale of our study does, however, allow for some degree of insight regarding the role of CO_2 versus climate in driving vegetation changes observed in the past.

At the global scale, atmospheric CO_2 levels are essentially homogeneous; when CO_2 rises in one part of the globe, it rises everywhere else proportionally. In contrast to CO_2, climate change is much more heterogeneous; increasing global temperature may manifest itself climatically in any number of ways across the globe (*39*), and climatic changes since the LGM have been spatially heterogenous (*25*). Although temperatures have increased globally since the LGM - and as a result the hydrological cycle has been invigorated, resulting in wetter conditions in many regions - the degree of change varies significantly between regions, and in some parts of the world the LGM was in fact more humid than the Holocene (*82-86*). Thus, although certain ecosystems may be particularly sensitive to CO_2 forcing (*87*), or may exhibit threshold responses to changing CO_2 levels (*88*), if CO_2 was a dominant global driver of postglacial vegetation change, it would be expected to override, or strongly modify, climatic influences, and a widespread deglacial trend towards more arboreal taxa would be observed.

Paleoecological records indicate, however, that several regions show a clear decline in arboreal taxa during the deglacial period, in spite of increasing CO_2, but consistent with increasing drought stress as a result of reduced precipitation and/or increasing temperatures (fig. S8). In other regions, where a deglacial increase in arboreal taxa is recorded, the variability observed is much more tightly coupled to changes in hydroclimate than CO_2 (fig. S8; see also (*89*)). These disparities do not mean that CO_2 is unimportant in vegetation change, but suggest instead that CO_2 changes may modulate vegetational responses to climate change, rather than being the sole or dominant driver.

Rate-of-Change Differences Between the Past and the Future

Although the last deglaciation included periods of rapid global, regional, and local climate change, the future rates of climate change projected under RCP 4.5, 6.0, and 8.5 are far greater, by at least an order of magnitude (*25*). We focus on the past and future magnitude of change, which is more directly comparable. Our analysis indicates that, all else being equal, the magnitude of climate change anticipated in coming decades under high-emission scenarios is by itself sufficient to effectively 'lock in' major vegetational transformations over most of the globe. Thus, our analysis may represent a relatively conservative estimate of the magnitude of ecological change expected in the future, owing to the anticipated higher rate of future climate change, and to the compounding factors of land-use, human disturbance, landscape fragmentation, invasive species, and other contemporary influences.

We acknowledge some critical differences between past and future. The warming between LGP and the Holocene occurred within the range of previous glacial/interglacial temperatures, while projected future changes will exceed those experienced over the past 2 million years (*25*). Also, under higher rates of environmental change, migration lag and

ecological disequilibrium are likely to be more severe than in the past. Even in the past, migrations have sometimes lagged climate change, and some ecosystems have been in transient disequilibrium with climate (e.g., *38*). Habitat fragmentation, invasive species, harvesting, biogeochemical disruptions, and other novel factors will also play important roles in the future (*41*). However, our study demonstrates that the magnitude of projected global temperature change is sufficient to drive large ecological changes. Undoubtedly, inertial processes (incumbency, local seed sources, ecological legacies) will allow many ecosystems to at least temporarily 'resist' effects of climate change (*90*). But climate extremes and widespread mortality events (*15*) are likely to accelerate ecosystem transformation, and other factors (fragmentation, invasives, harvesting, etc.) are likely to amplify and accelerate, rather than dampen, ecological change.

Our primary goal is to provide an independent perspective on climate-driven ecological change that complements other approaches such as real-time observations and modeling efforts. Our approach is built on an entirely different combination of assumptions, strengths, and shortcomings than the other approaches, and convergent predictions of these various approaches strengthens the inference that projected climate changes will drive major ecosystem transformations.
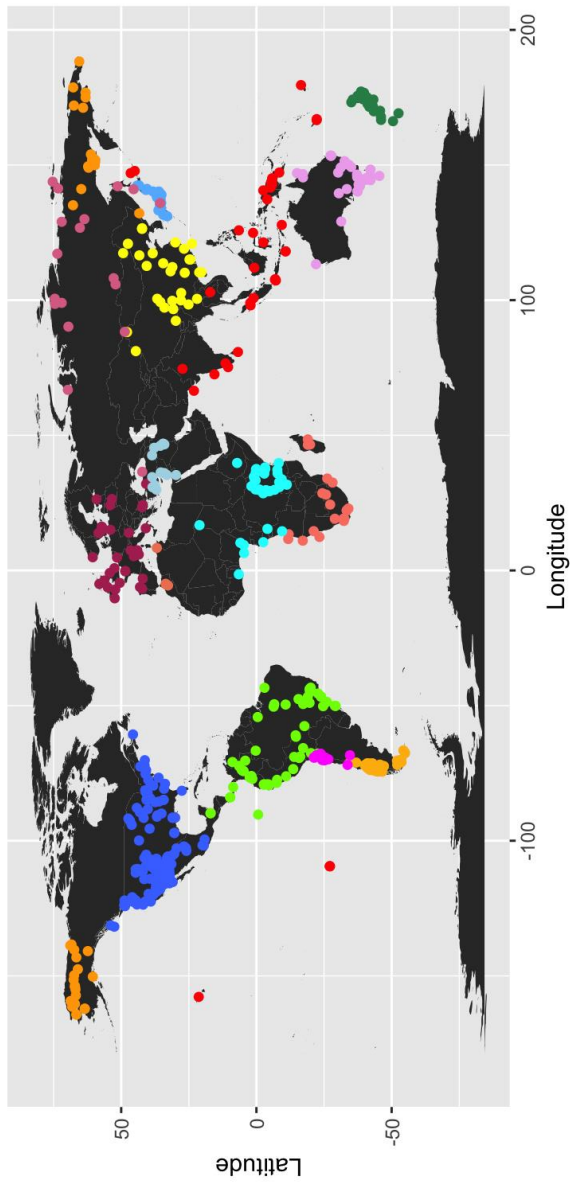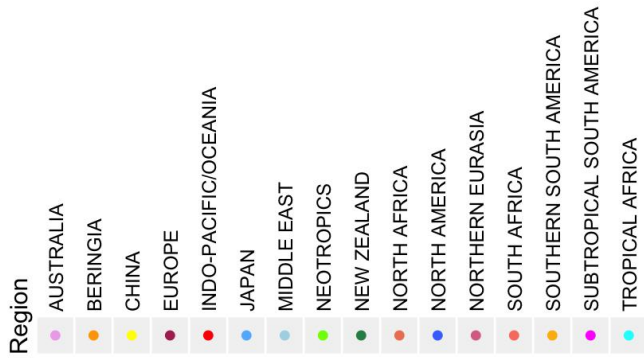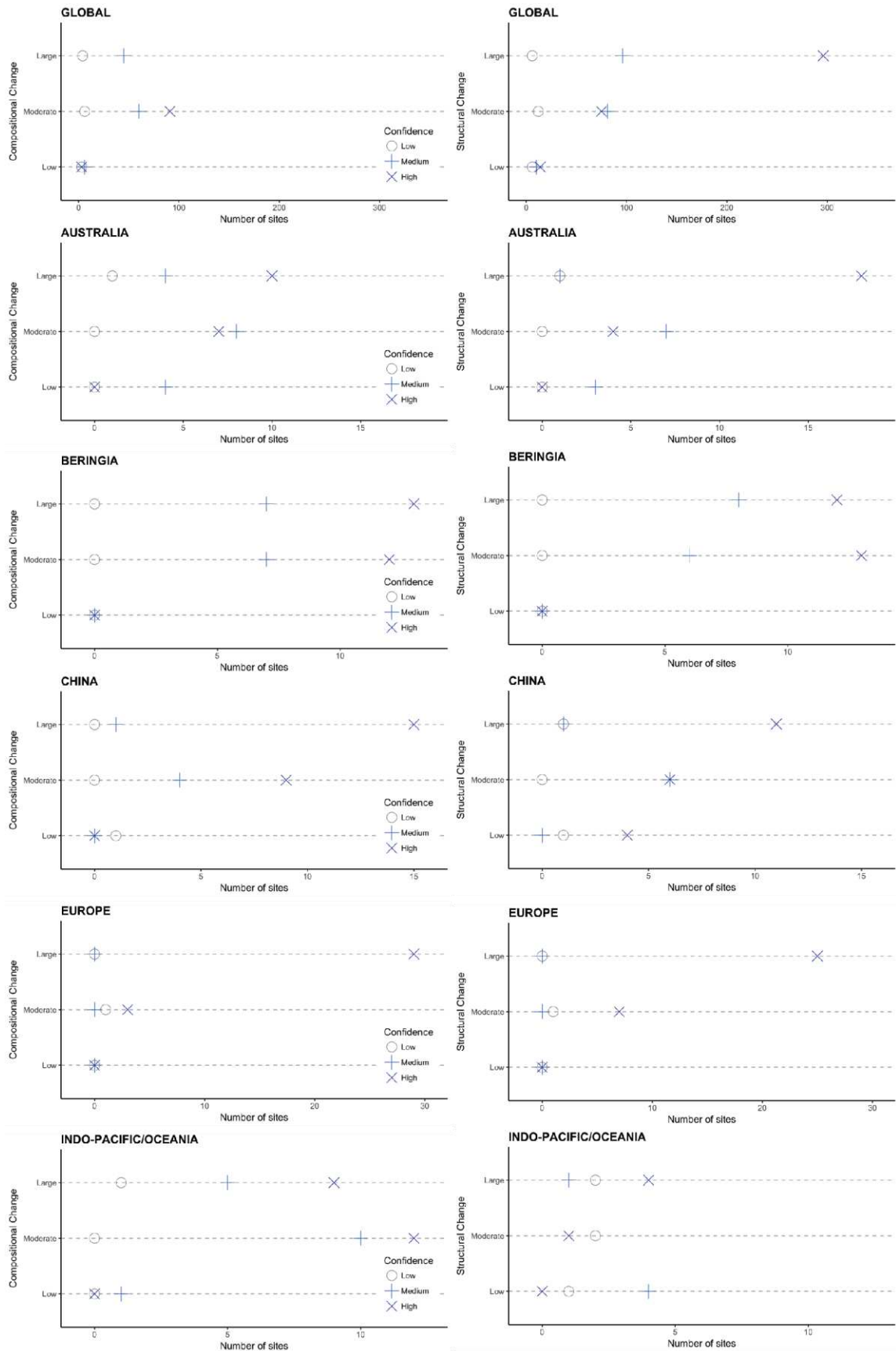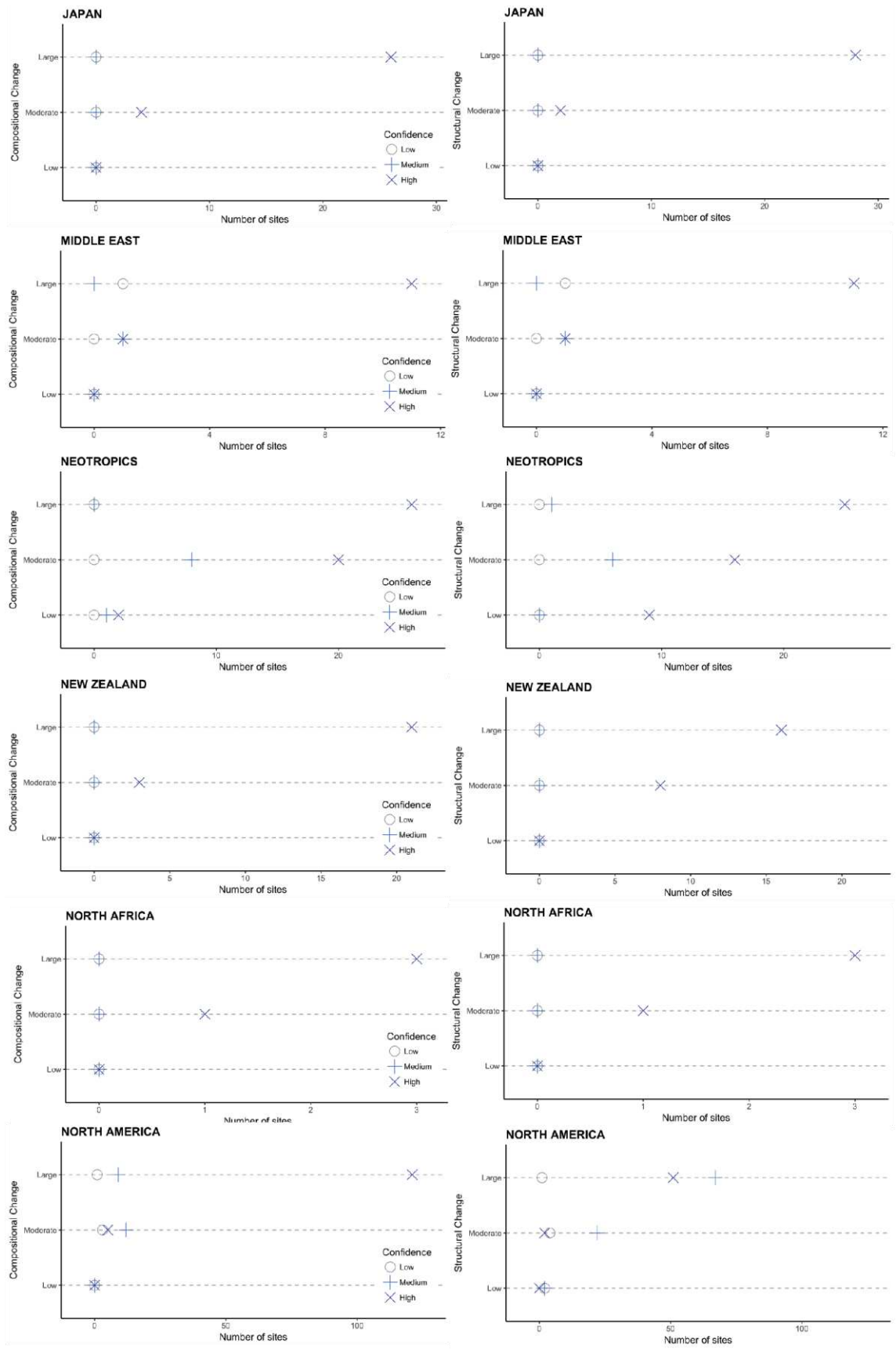
Fig. S1. Distribution of paleoecological sites used in the assessment. Site dots colored by region.
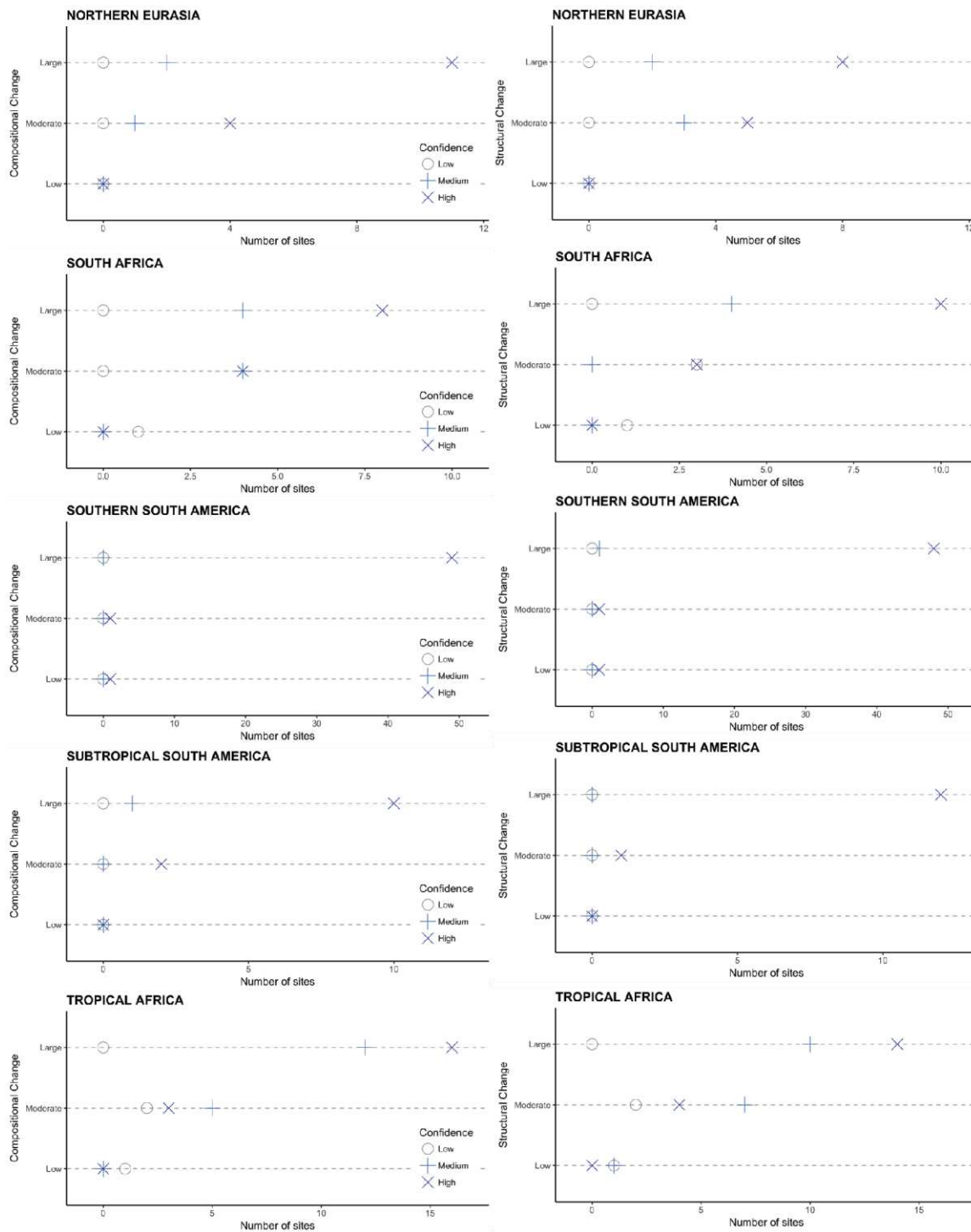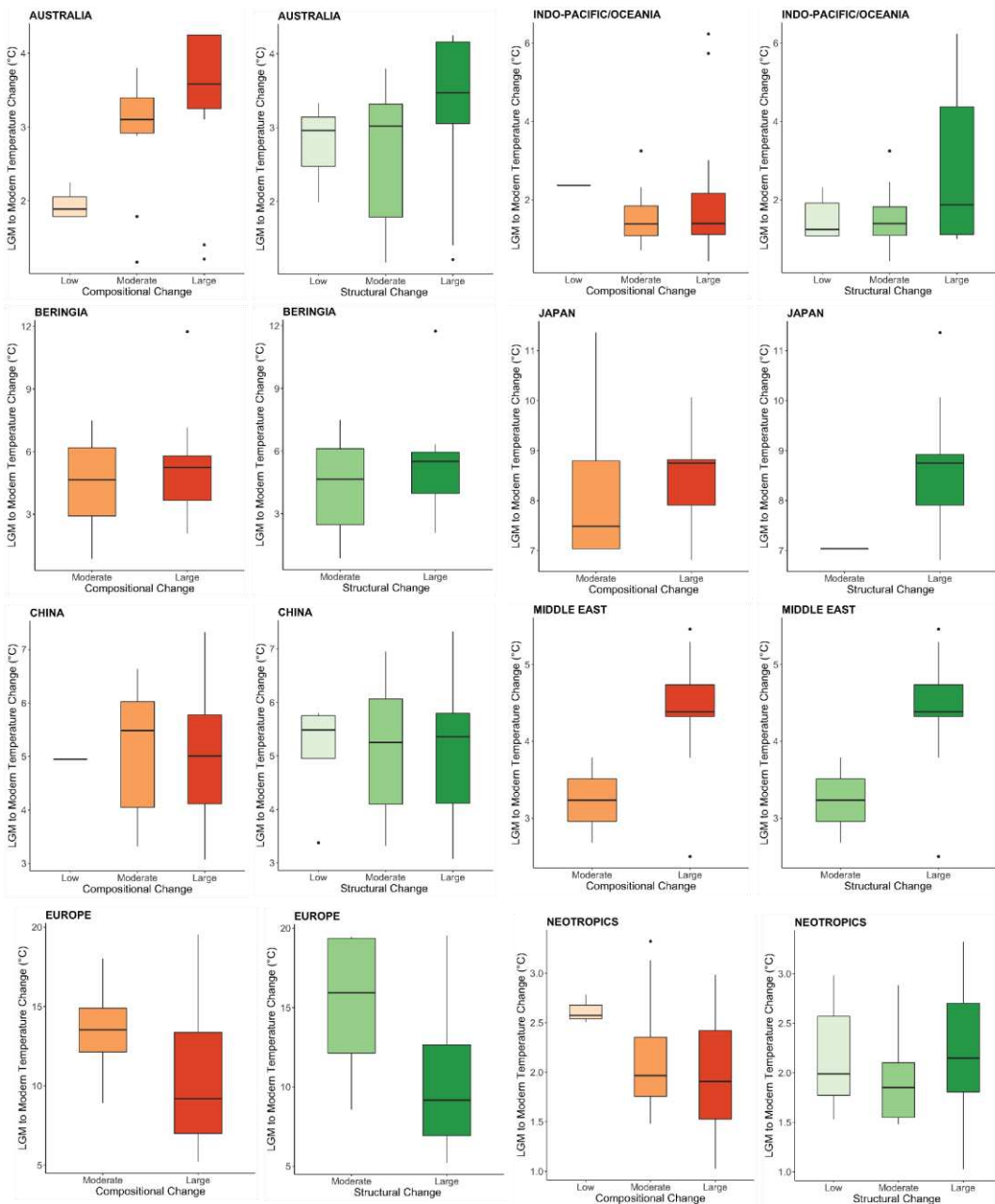
Fig. S2
Confidence (high, medium, low) of individual assessments for each category of vegetation change (low, moderate, large), across the entire data set (Global) and individually for each region.
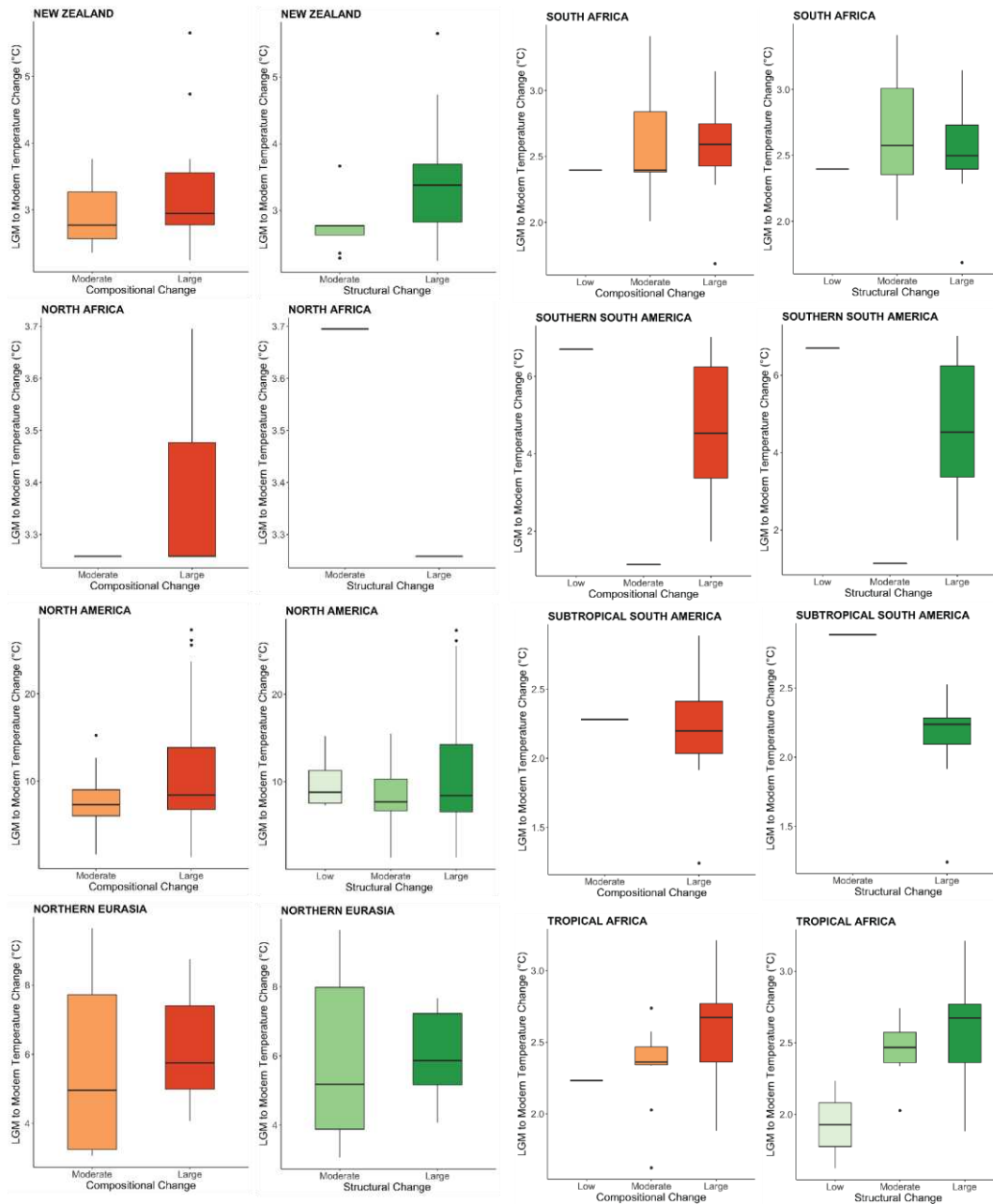
Fig. S3

Regional decomposition of Figure 2. Box plots show the estimated mean-annual temperature differences between the last glacial maximum and today in each of the three vegetation-change categories (low, moderate, large), for composition and structure.
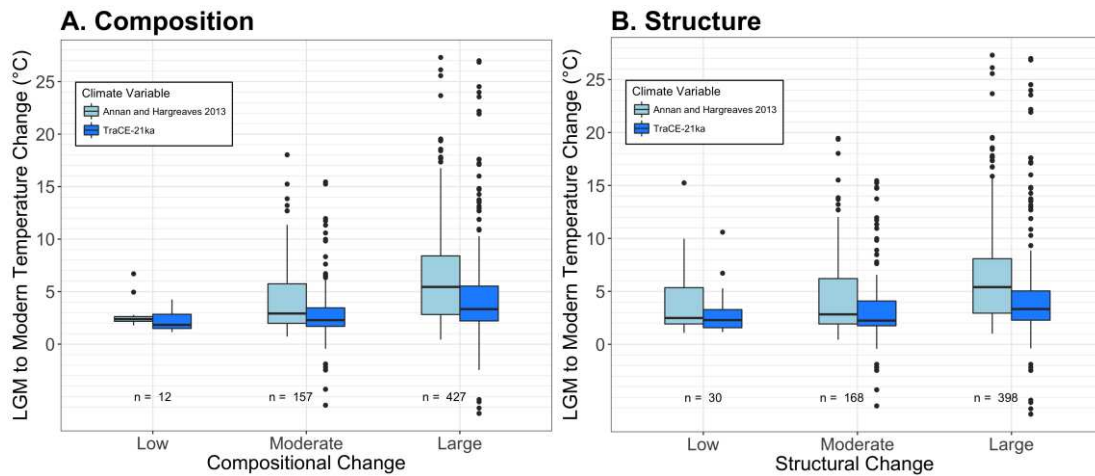
Fig. S4

Comparison of the estimated temperature change obtained from the Annan and Hargreaves 2013 data and the TraCE simulations, in each of the vegetation-change categories. The Annan and Hargreaves 2013 plots are as in Figure 2; the corresponding TraCE-21ka estimates are plotted for comparison. The TraCE plots show smaller temperature differences than the Annan and Hargreaves 2013 plots, but show a similar pattern of increasing magnitude of vegetational change with increasing temperature change.

Fig. S5
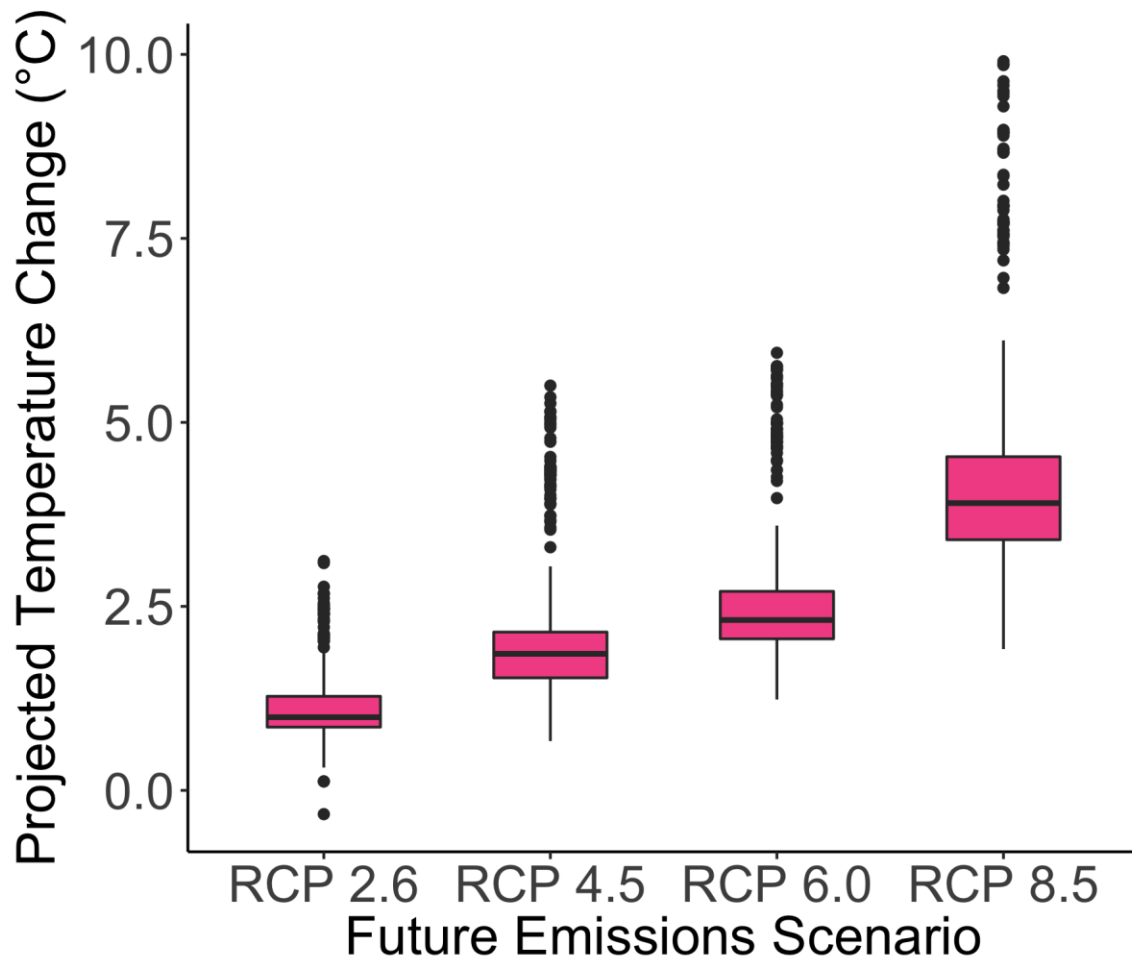
Box plots of the estimated mean-annual temperature differences between today and future-climate simulations for individual sites (using the nearest grid-point). RCP2.6 and RCP8.5 are as in Fig. 3a; this figure includes RCP4.5 and RCP6.0 for comparison. Projected temperature changes generally increase with higher radiative forcing.

Fig. S6

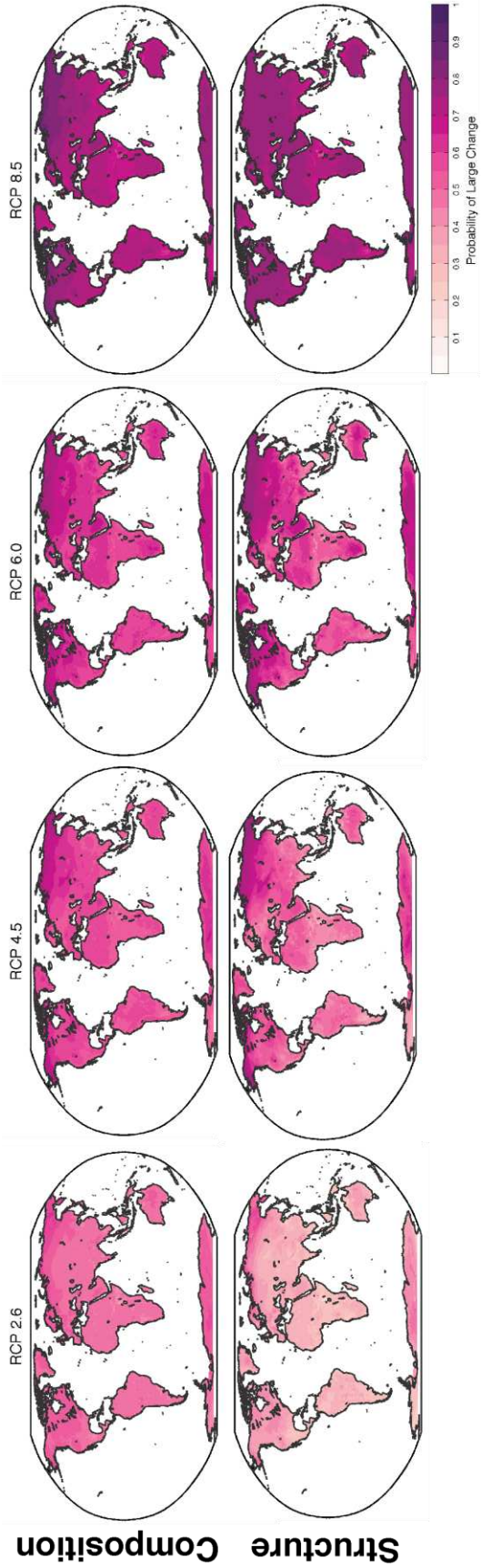Estimated probability of large compositional and structural change by the end of the 21st century (average of 2081-2100) under the four representative concentration pathway (RCP) scenarios: RCP2.6, RCP4.5, RCP6.0, and RCP 8.5. Results for RCP2.6 and RCP8.5 are as in Fig. 3c; RCP4.5 and RCP6.0 are added for comparison. Global risk of large vegetational change increases with magnitude of radiative forcing.
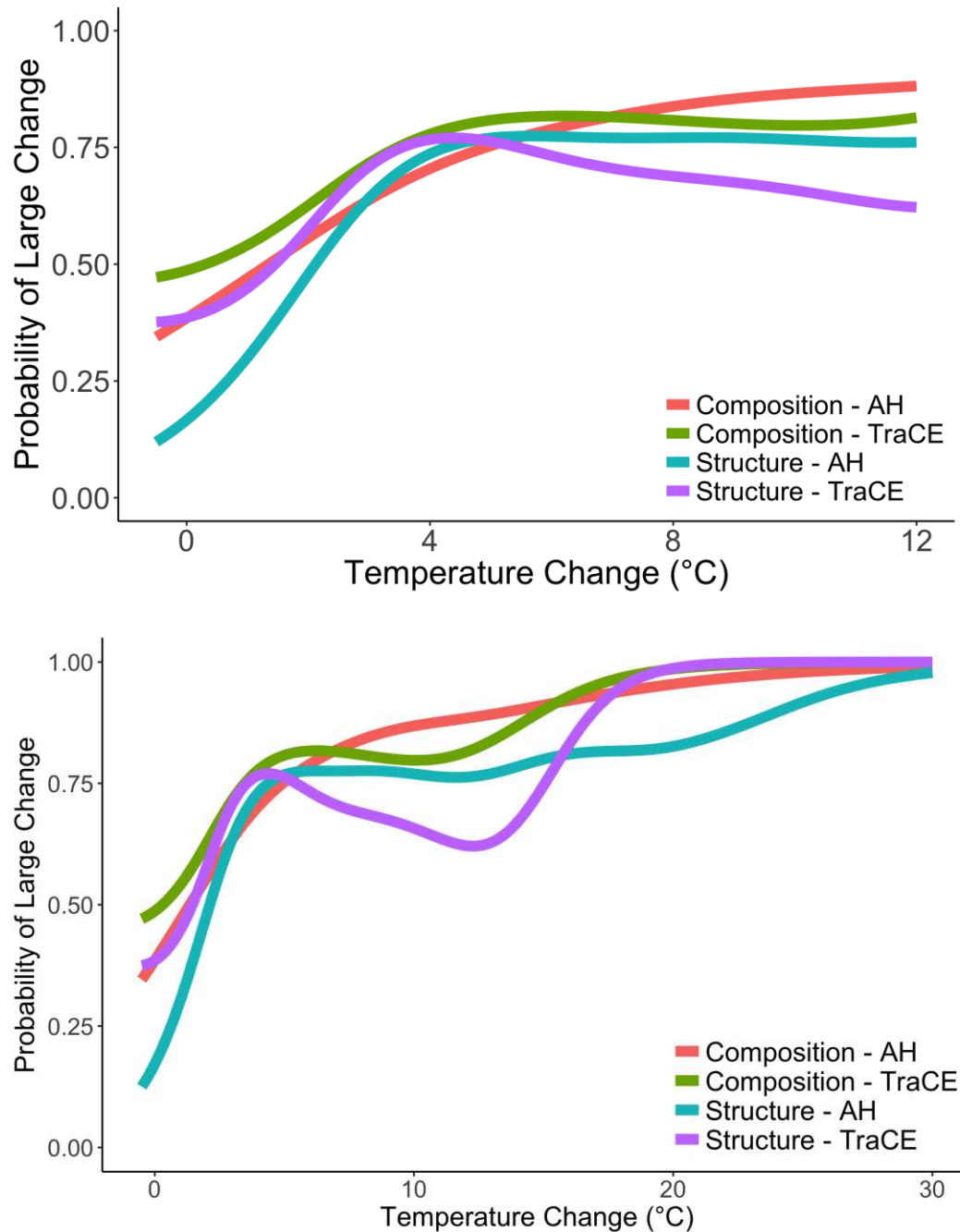
Fig. S7

Probability of large change in vegetation composition and structure as a function of temperature change, based on the generalized additive models (GAMs) using two sets of temperature-difference estimates as the independent variable: Annan and Hargreaves 2013 LGM to pre-industrial temperature change (as in Fig. 3b), and the TraCE-21ka LGP to late Holocene temperature change. Although the shape of the function differs between the two data sets, both show sensitivity of vegetation change to temperature change. Upper figure shows the model within the range of projected future temperature change for the 21st century. Lower figure shows results of the same models with an expanded x-axis to show the entire range of temperatures

used in developing the model. The excursion for 'Structure-TraCE' response between 10 and 18 is driven by several sites in Europe within this temperature range that were assessed as having moderate compositional change.

Fig. S8
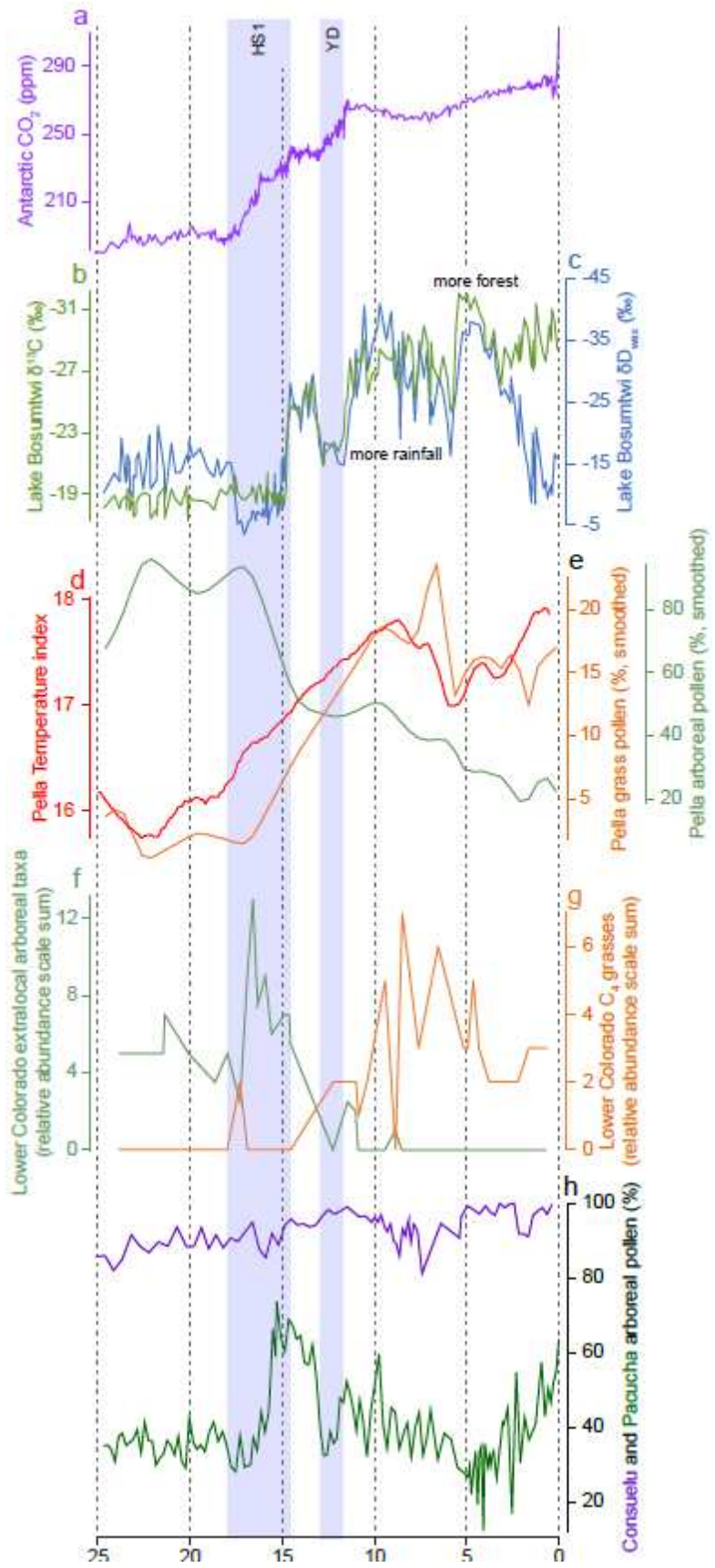
Comparison of atmospheric CO_2 concentrations as measured from Antarctic ice cores (a) (*91*) with a selection of records that highlight the relative importance of CO_2 and climatic factors as drivers of vegetation change. At Lake Bosumtwi, Ghana, $\delta^{13}C$ data (woody C_3 plants versus C_4 grasses) indicate an increase in forest cover since the Last Glacial Maximum (LGM) (b, c) (*88*). While this is not inconsistent with the broad changes in atmospheric CO_2, vegetation change is much more tightly linked to changes in hydroclimate, as indicated by δD data (rainfall amount/intensity) from the same site. While the late Holocene persistence of forest at the site may be enabled by high CO_2 levels (*88*), it may also, or alternatively, be related to a mid-Holocene establishment of a stable forest state that is naturally resistant to perturbation (*92*). At Pella, on the southern margin of the Namib Desert, fossil pollen data indicate that arboreal vegetation was dominant during the LGM, contrary to predictions based on CO_2 forcing, and grasses became an important feature of the vegetation only during the CO_2-rich Holocene (d, e) (*85*). A similar pattern is observed in the North American southwest, with macrofossil data from the Lower Colorado River Basin revealing that significant C_4 grass cover only became established during the Holocene, with the decline of extra-local arboreal taxa (f, g) (*84*). In South America, records from the Andes indicate no significant change in forest cover at higher elevations sites such as Consuelo, and vegetation change at lower elevations is driven by climatic drivers, with no post-glacial increase in forest cover that can be clearly linked to changes in CO_2 (h) (*93,94*).

Table S1. Team members responsible for compilation and assessment of specific regions.

REGION	TEAM MEMBERS
North America	Jackson, Nolan, Betancourt, Overpeck
Neotropics	Bush, Gosling
Subtropical South America	Latorre
Southern South America	Moreno
Europe	Huntley, Allen
Northern Eurasia	Tarasov, Muller, Binney
Japan	Takahara, Momohara
Beringia	Edwards, Lozhkin, Anderson, Binney
China	Y. Liu, Xu, Zheng, Shen, K.B. Liu, Weng
Middle East	Djamali, Cheddadi, Brewer
North Africa	Cheddadi, Djamali, Brewer
East and Tropical Africa	Ivory, Lezine, Marchant, Vincens
South Africa and Madagascar	Chase
Indo Pacific and Oceania	Stevenson, Hotchkiss, Soo-Hyun
Australia	Kershaw, Haberle, Dodson

New Zealand	McGlone

Table S2.
Working definitions used in assessments of paleoecological records.

Term	Definition
Composition	The species composition of the dominant vegetation in the record (Note: Although pollen records do not support species level discrimination, species turnover can be inferred from genus- and family-level changes)
Physiognomy/Structure	The physical structure of the dominant vegetation (e.g. coniferous forest, grassland, steppe, deciduous woodland, etc)
Large change	Complete or nearly complete replacement of dominant species or growth forms. (Note: does not imply complete biogeographic turnover; former dominants may remain in region, but not as dominants. Conversely, current dominants may be present at LGM , but not as dominants)
Moderate change	Partial replacement of dominant species or growth forms
Small change	Little or no replacement; dominant species and growth forms of today are unchanged at LGM
High confidence	Few or no substantial uncertainties, high quality data, inferences clear and unequivocal
Medium confidence	Some substantial uncertainties related to questions of data quality or clarity of inference
Low confidence	Significant uncertainties in the quality or interpretation of the data

Table S3.

Summary of the results of the Wilcoxon rank sum test for statistically significant difference in temperature change from LGM to modern between different levels of ecological change. The table shows the test statistic, W, and the p-values for different pairs of ecological change groups using two different estimates of the temperature change from LGM to modern.

Ecological Change Group 1	Ecological Change Group 2	Climate Variable	W	P-Value
Large Composition	Moderate Composition	Annan and Hargreaves	20985	4.108e-12
Large Composition	Moderate Composition	TraCE	22916	4.479e-9
Large Composition	Low Composition	Annan and Hargreaves	1015.5	0.003612
Large Composition	Low Composition	TraCE	1275.5	0.003005
Moderate Composition	Low Composition	Annan and Hargreaves	769.5	0.2924
Moderate Composition	Low Composition	TraCE	754.5	0.2523

Ecological Change Group 1	Ecological Change Group 2	Climate Variable	W	P-Value
Large Structure	Moderate Structure	Annan and Hargreaves	22174	2.39e-10
Large Structure	Moderate Structure	TraCE	24720	9.501e-7
Large Structure	Low Structure	Annan and Hargreaves	3288	4.052e-5
Large Structure	Low Structure	TraCE	3735.5	0.006269
Moderate Structure	Low Structure	Annan and Hargreaves	2275	0.3977
Moderate Structure	Low Structure	TraCE	2309.5	0.4676

Table S4.

Summary of assessments, ordered by confidence, of the role of climate in driving observed moderate or large compositional change (top) or structural change (bottom). Columns represent the assessed role of climate in driving the observed ecological changes. Rows are the confidence assigned to those judgments by the assessors. The numbers are the number of sites in each combination of role of climate and confidence. The role of climate was not assessed for sites for which the ecological change was assessed as low (12 sites for composition and 30 sites for structure).

Composition	Large Role of Climate	Moderate	Low	N/A
High Confidence	514	11	0	0
Medium	39	13	1	0
Low	3	1	2	0
N/A	0	0	0	12
Total	556	25	3	12

Structure	Large Role of Climate	Moderate	Low	N/A
High Confidence	502	8	0	0
Medium	21	26	0	0
Low	5	3	1	0
N/A	0	0	0	30
Total	528	37	1	30

Instructions for Assessors

The following document was sent to all assessment team members, along with templates for data compilation and submission.

Assessment:

- Based on expert evaluation of all available and reliable paleoecological records from individual sites, in all regions of the planet.
- Our primary focus is on climate-driven vegetational change. Vegetation has, of course, been altered greatly by human activities in many regions. Thus, an important subsidiary question is whether substantial vegetational changes happened (or would have happened) in the absence of human activities.
- Assessments in this initial analysis will be based on "expert judgment" by paleoecologists who have experience in collection, analysis, and interpretation of the relevant data.
- Assessment will be qualitative, based on judgment of degree of contrast between glacial-age vegetation states and modern or Holocene vegetation states
- Assessments will be categorical, typically involving three classes (see below)
- Assessments will require judgment of confidence (also three classes)

Central Operational Questions (to be asked for each individual record):

1. What has been the magnitude of vegetational change, *in terms of vegetational composition,* since the last glacial period? *Choose from three outcomes:*
    a. Large
    b. Moderate
    c. None
2. What is the level of confidence for this assessment? *Choose from three outcomes:*
    a. High confidence
    b. Medium confidence
    c. Low confidence
3. If the answer to Question 1 was "Large" or "Moderate", what role did climate change since the last glacial period play in driving change of this magnitude? *Choose from three outcomes:*
    a. Large
    b. Moderate
    c. None
4. What is the level of confidence for this assessment? *Choose from three outcomes:*
    a. High confidence
    b. Medium confidence
    c. Low confidence

5. What has been the magnitude of vegetational change, *in terms of vegetation physiognomy*, since the last glacial period? *Choose from three outcomes:*
    a. Large
    b. Moderate
    c. None
6. What is the level of confidence for this assessment? *Choose from three outcomes:*
    a. High confidence
    b. Medium confidence
    c. Low confidence
7. If the answer to Question 5 was "Large" or "Moderate", what role did climate change since the last glacial period play in driving change of this magnitude? *Choose from three outcomes:*
    a. Large
    b. Moderate
    c. None
8. What is the level of confidence for this assessment? *Choose from three outcomes:*
    a. High confidence
    b. Medium confidence
    c. Low confidence

N.B. concerning Questions 3 and 7: Assessments should focus on judging whether climate change since the last glacial period was *sufficient* to drive vegetation change of "large" magnitude. Climate change as an explanation of high-magnitude vegetational change is not mutually exclusive of other processes (e.g., human activity, post-glacial CO_2 increase, megafaunal decline, etc.). In some regions with a strong human signature (e.g., Europe), judgment can be facilitated by examining the magnitude of change that is recorded before extensive human land-clearance. Thus, comparison of glacial-age with early Holocene assemblages may be useful in many cases.

N.B. concerning coverage: In some regions, some sites with temporal coverage to >14 ka may occur on land surfaces formerly occupied by continental or montane ice-sheets. *These sites should be included in the analysis, as long as they have records extending more than ~1000 years after site inception.* Thus, for example, a lake on glaciated terrain with basal pollen assemblages dating to 17 ka might be included, whereas a lake with basal sediments dating to 14.5 ka should be excluded. The purpose of the 1000-year rule is to ensure that sufficient time elapses after deglaciation to allow primary successional processes to play out.

Provisional Operational Definitions:

Vegetation terms:

Composition: The species composition of the dominant vegetation in the record. Although most pollen records do not support species-level discrimination, species turnover can of course be inferred from genus- and family-level changes. Macrofossils can also support such inferences, particularly among dominant types.

Physiognomy: The physical structure of the dominant vegetation (e.g., coniferous forest, grassland, steppe, tundra, deciduous woodland, etc.).

Magnitude of vegetation change:

Large: Complete or nearly complete replacement of dominant species or growth-forms. (This does not imply complete *biogeographic* turnover; former dominants may remain in the region, but not as dominants. Conversely, current dominants may have occurred at the locale during LGM, but not as dominants.)

Moderate: Partial replacement of dominant species or growth-forms

None: Little or no replacement; dominant species or growth-forms today are unchanged

Role of climate change:

Large: Climate change since the last glacial period is by itself sufficient to explain the magnitude of observed vegetation change. (Other factors may well have played a role, but in the absence of those factors, a similar magnitude of vegetation change would have been observed.)

Moderate: Climate change since the last glacial period explains at least part of the observed magnitude of vegetation change. (Other factors, in addition to climate change, are necessary to explain the magnitude of vegetation change).

None: Climate change is entirely insufficient to explain the magnitude of vegetation change observed since the last glacial period. Other factors are wholly responsible for the magnitude of change.

Level of confidence:

High: Few or no substantial uncertainties; high-quality data, inferences clear and unequivocal

Medium: Some substantial uncertainties arising from questions of data quality or clarity of inferences from the data

Low: Significant uncertainties in quality or interpretation of data

Additional Data table S1 (separate file)

List of paleoecological sites used in analysis with data and metadata:

Region:	Region in fig. S1, S2, S3, and Table 1.
Site:	Site name
Sitelats:	Latitude
Sitelons:	Longitude
CompChange:	Compositional change since LGP
CompConf:	Confidence of compositional change assessment
CompClim:	Role of climate change since LGP in driving compositional change
CompClimConf:	Confidence of climate-change role for composition
StructureChange:	Structural change since LGP
StructureConf:	Confidence of structural change assessment
StructureClim:	Role of climate change since LGP in driving structure change
StructureClimConf:	Confidence of climate-change role for structure
CompJustification:	Description of the ecological change the underlies the composition change assessment
StructureJustification:	Description of ecological change that underlies the structure change assessment
Sitetemps_ah:	Temperature difference since LGM (Annan&Hargreaves2013)
Sitetemps_trace1:	Temperature change since LGP (TraCE21ka)
Sitetemps_ccsm4rcp85:	Projected temperature change (RCP8.5)
Sitetemps_ccsm4rcp26:	Projected temperature change (RCP2.6)
Sitetemps_ccsm4rcp45:	Projected temperature change (RCP4.5)
Sitetemps_ccsm4rcp60:	Projected temperature change (RCP6.0)
ReferenceDOI:	Digital Object Identifier (DOI) for the site's reference
Reference:	Citation for paleoecological site