CLIMATE CHANGE

Past and future global transformation of terrestrial ecosystems under climate change

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Impacts of global climate change on terrestrial ecosystems are imperfectly constrained by ecosystem models and direct observations. Pervasive ecosystem transformations occurred in response to warming and associated climatic changes during the last glacial-to-interglacial transition, which was comparable in magnitude to warming projected for the next century under high-emission scenarios. We reviewed 594 published paleoecological records to examine compositional and structural changes in terrestrial vegetation since the last glacial period and to project the magnitudes of ecosystem transformations under alternative future emission scenarios. 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, terrestrial ecosystems worldwide are at risk of major transformation, with accompanying disruption of ecosystem services and impacts on biodiversity.

Terrestrial ecosystem function is governed largely by the 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 global greenhouse gas (GHG) emissions increase (*6*) and to understand the full potential magnitude of impacts should current GHG emission rates continue unabated.

Ecosystem transformation generally involves the replacement of dominant plant species or functional types by others, whether recruited locally or migrating from afar. Observations from around the globe indicate that current 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 under way in many forests and woodlands (*9*–*11*), with further mortality events predicted under increasing temperatures and drought (*3*, *9*, *10*, *12*). Replacement of predisturbance dominants by other species and growth forms has been widely documented (*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, models indicate ecosystem transformation under climate projections for the 21st century. These 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, the capacity for assessing the magnitudes 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 an independent means for gauging the sensitivity of ecosystems to climate change. High-precision time-series studies indicate 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. In this study, we used published reports to compile a global network of radiocarbon-dated paleoecological records of terrestrial vegetation composition and structure since the Last Glacial Maximum (LGM), ~21,000 years before the present (yr B.P.) (*24*). Most postglacial warming happened 16,000 to 10,000 yr B.P., although it commenced earlier in parts of the Southern Hemisphere (*25*, *26*). Global warming between the LGM and the early Holocene (10,000 yr B.P.) was on the order of 4 to 7°C, with more warming over land than oceans (*26*, *27*). These estimates are roughly comparable to the magnitude of warming that Earth is projected to undergo in the next 100 to 150 years if GHG emissions are not reduced substantially (*28*). The magnitudes of changes in vegetation composition and structure since the last glacial period (LGP) provide an index of the magnitude of ecosystem change that may be expected under warming of similar magnitude in the coming century (*29*). 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 (*26*), 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.

We reviewed and evaluated paleoecological (pollen and macrofossil) records from 594 sites

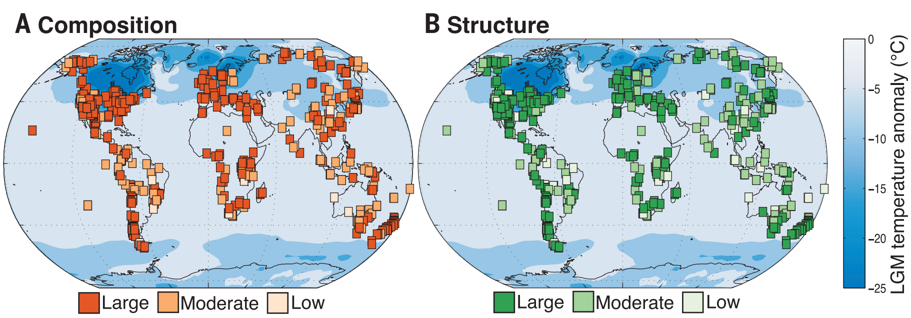

Fig. 1. Vegetation differences between the LGP and the present. Each square represents an individual paleoecological site. The color density indicates the magnitude of estimated vegetation change since the LGP (21,000 to 14,000 yr B.P.). Background shading denotes the estimated temperature anomaly between the LGM 21,000 years ago and today on the basis of assimilated proxy-data and model estimates (*27*). (**A**) Composition. (**B**) Structure.

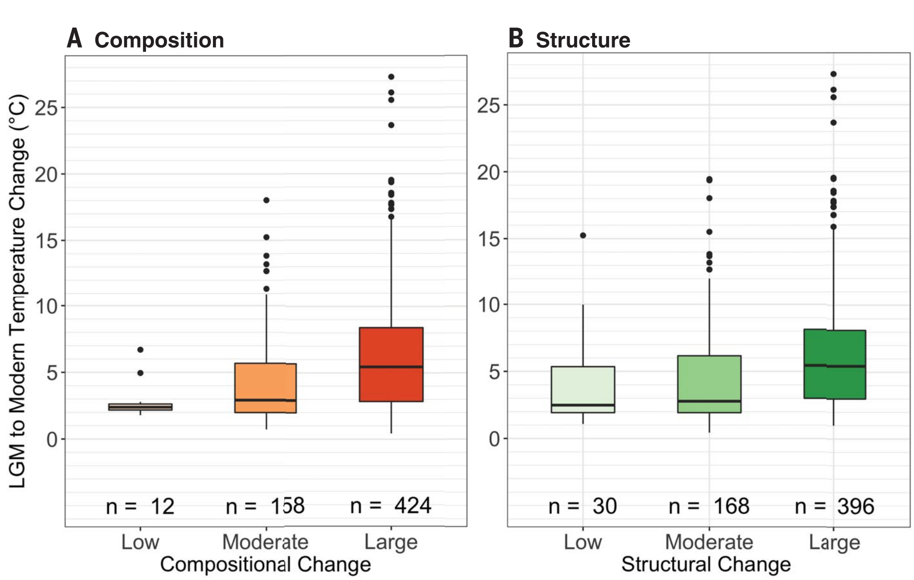

Fig. 2. Estimated temperature differences for different categories of vegetation response. Box plots of the estimated mean annual temperature differences between the LGM and today in each of the three vegetation change categories (low, moderate, and large) for (**A**) composition and (**B**) structure. Low vegetational changes are associated largely with relatively small temperature anomalies, whereas moderate and large changes are associated with larger post-LGM temperature differences, indicating that the magnitude of temperature change plays an important role in the magnitude of vegetation change. The glacial temperature anomalies are from data in (*27*). Analyses using the TraCE-21ka simulation show similar patterns (fig. S4).

worldwide (fig. S1), all drawn from peer-reviewed published literature, to determine the magnitude of postglacial vegetation change. We adopted an expert-judgment approach in which paleoecologists with relevant regional experience compiled published records (table S1); reviewed the data, diagrams, and accompanying papers; and inferred the composition and structure of the glacial-age and Holocene vegetation at each site (*24*). For the purposes of our analyses, we defined the LGP as the interval between 21,000 and 14,000 yr B.P. Although postglacial warming was under way in many regions by 16,000 yr B.P. (*25*), continental ice sheets were still extensive 14,000 yr B.P., and some climate regimes remained essentially "glacial" in nature, particularly in the Northern Hemisphere (*30*). Extending the LGP window to 14,000 yr B.P. provides a larger array of records for the assessment, both in glaciated and unglaciated terrains, and renders our analysis more conservative (climatic and vegetation contrasts with the Holocene are likely to decrease between 21,000 and 14,000 yr B.P.).

For each record, experts were asked to classify the magnitudes of compositional change and structural change since the LGP as large, moderate, or low and to provide detailed justification for their judgments (*24*) (table S2). This placed all the diverse records into a common framework for comparison. 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, postglacial CO_2 increase, and 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 (27% of sites) to large (71%), as well as moderate (28%) to large (67%) structural changes (Fig. 1 and 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

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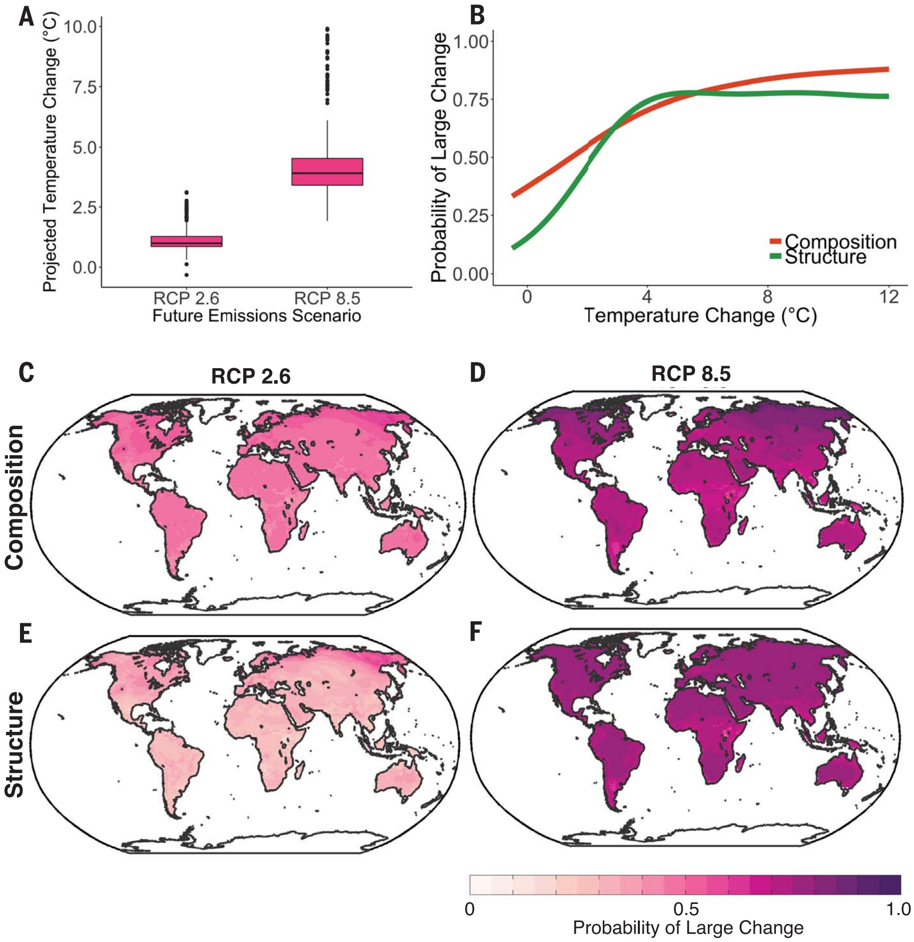

Fig. 3. Estimated vegetation change under future climate scenarios. (**A**) Box plots of the estimated mean annual temperature differences between today and future climate simulations for individual sites (as determined by using the nearest grid point). Most sites show relatively small temperature change under the low-emission scenario (RCP 2.6), with substantially greater change under the high-emission scenario (RCP 8.5). (**B**) Probabilities of large changes in vegetation composition and structure as a function of temperature change. (**C** to **F**) Estimated probabilities of large compositional and structural changes by the end of the 21st century (the average of the period from 2081 to 2100) under RCP 2.6 (C and E) and RCP 8.5 (D and F). Probabilities (B to F) are estimated from a logistic spline regression model fit by 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 for 2081 to 2100 under the model scenarios, minus an average for 1985 to 2005 from the CCSM4 historical simulation. Analyses using the TraCE-21ka simulation show similar patterns (fig. S7).

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 (*31*, *32*). For nearly all sites that experienced moderate or large ecological change, climate change since the LGP was judged to be sufficient to explain the observed changes with high confidence (table S4). Atmospheric CO_2 concentrations also increased from 190 to 280 parts per million during the deglaciation, interacting with and in some cases modulating ecological responses to climate change. However, CO_2 changes alone cannot account for postglacial vegetation changes (supplementary text).

Independently of the expert-judgment process, we used the estimated anomaly in mean annual temperatures between the LGM and the present (preindustrial) as a proxy for the overall magnitude of climate change since the LGP (*24*). LGM temperature estimates were derived using an assimilated data–model integration (*27*). 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 estimated 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 substantial 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 (*33*, *34*), which yield a lower magnitude of LGP-to-Holocene climate change (*35*); despite the potential conservative bias, results for compositional and structural changes (fig. S4) were similar to those in Fig. 2. Temperature differences between the LGP and the present were substantially greater for sites with large ecological change than for those with low to moderate change, by both paleoclimate estimates (*27*, *33*) (table S2).

We also used our database of ecological change since the LGM to assess the global distribution of the probabilities of large compositional and structural changes given GHG emission scenarios [representative concentration pathways (RCPs) 2.6, 4.5, 6.0, and 8.5, each as simulated by the Community Climate System Model version 4 (CCSM4)] (*24*, *36*). 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 and fig. S5). We quantified the relationship between temperature and ecological change by using a logistic spline regression with ordered categories (*37*). We fit models for compositional and structural change by 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. 3, C to F) 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). By contrast, under the business-as-usual emissions scenario, RCP 8.5, the probabilities of large compositional change and large structural change are both greater than 60% (Fig. 3, D and F). 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 to 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*, *38*, *39*), and ecological responses will often be episodic or nonlinear (*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 (*26*, *40*, *41*)—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 RCP 8.5 scenario, the rate of warming will be on the order of 65 times as high as the average warming during the last deglaciation (*26*). Furthermore, the warming between the LGP and the Holocene occurred within the range of previous glacial and interglacial temperatures, whereas projected future changes will exceed those experienced over the past 2 million years (*26*). Although many ecological responses (e.g., species migration, colonization, and succession) will likely lag behind climate changes, ecosystem transformations will often 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 changes in the absence of markedly 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 (*42*), 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*, *43*). Structural transformation will have particularly large consequences for ecosystem services (*4*), including the achievement of nature-based development solutions under the United Nations' Sustainable Development Goals (*44*). 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 will increase substantially with increasing GHG emissions, particularly if warming exceeds that projected by the RCP 2.6 emission scenario (1.5°C).

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/361/6405/920/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S8
Tables S1 to S4
References (*45*–*95*)
Data S1

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Future predictions from paleoecology

Terrestrial ecosystems will be transformed by current anthropogenic change, but the extent of this change remains a challenge to predict. Nolan *et al.* looked at documented vegetational and climatic changes at almost 600 sites worldwide since the last glacial maximum 21,000 years ago. From this, they determined vegetation responses to temperature changes of 4° to 7°C. They went on to estimate the extent of ecosystem changes under current similar (albeit more rapid) scenarios of warming. Without substantial mitigation efforts, terrestrial ecosystems are at risk of major transformation in composition and structure.

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