Global peatland initiation driven by regionally asynchronous warming

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Widespread establishment of peatlands since the Last Glacial Maximum represents the activation of a globally important carbon sink, but the drivers of peat initiation are unclear. The role of climate in peat initiation is particularly poorly understood. We used a general circulation model to simulate local changes in climate during the initiation of 1,097 peatlands around the world. We find that peat initiation in deglaciated landscapes in both hemispheres was driven primarily by warming growing seasons, likely through enhanced plant productivity, rather than by any increase in effective precipitation. In Western Siberia, which remained ice-free throughout the last glacial period, the initiation of the world's largest peatland complex was globally unique in that it was triggered by an increase in effective precipitation that inhibited soil respiration and allowed wetland plant communities to establish. Peat initiation in the tropics was only weakly related to climate change, and appears to have been driven primarily by nonclimatic mechanisms such as waterlogging due to tectonic subsidence. Our findings shed light on the genesis and Holocene climate space of one of the world's most carbon-dense ecosystem types, with implications for understanding trajectories of ecological change under changing future climates.

bioclimate | biogeography | deglaciation | basal date catalog | GCM

Peatlands are organic-rich wetlands that have developed mainly since the Last Glacial Maximum (LGM) (1) (ca. 26 ka B.P. to 19.5 ka B.P.), during which time they have sequestered between a sixth and a third of all global soil carbon in the form of poorly decomposed plant detritus (2, 3). Peatlands can be found across most latitudes and biomes (4, 5), and develop where local conditions promote a persistent excess of plant productivity over ecosystem respiration (6). A wide variety of theories has been proposed to explain peatland initiation in such diverse biogeographic regions, including changes in annual and seasonal metrics of precipitation and temperature to promote productivity and inhibit decomposition (5, 7–12), emergence of new land through isostatic readjustment (13, 14), and waterlogging due to tectonic subsidence (15–17).

The locations of most peatlands in Europe, North America, and Patagonia (Fig. 1A and Fig. S1) overlap with the former extent of continental ice at the LGM. However, peat initiation in many European and North American sites lagged local deglaciation by thousands of years (18–20). Hypothesized explanations for this lag include the slow dispersal of plant propagules, the development of leached podzols to inhibit drainage, the infilling of postglacial waterbodies with sediment and detritus, and the role of beaver dams in wetland development (18, 20). Moreover, the world's largest peatland complex in the Western Siberian lowlands (WSL), as well as important concentrations in the tropics, developed in areas that remained ice-free throughout the last glacial period.

The role of climate change in peatland initiation is particularly poorly understood. Several attempts have been made to use global or hemispheric temperature proxies such as those from ice cores to explain temporal trends in large, spatially extensive databases of peat initiation dates (1, 5, 7, 8). However, such proxies lack the spatial detail necessary to capture the complexity of climate change since the LGM (21) and are therefore unable to explain regional differences in timings of peat initiation (Fig. 1B). The two previous studies that have employed general circulation model (GCM) paleoclimate simulations (10, 22) have been restricted to specific geographical regions (Britain and the WSL) and have each considered only a single point in time rather than a time series of climate change.

We sought to determine whether the initiation of peatlands around the world occurred in response to any local climatic trigger. To this end, we compiled a catalog of published radiocarbon dates of peat initiation, the ages and locations of which we used as a basis to interrogate paleoclimate simulations from a coupled atmosphere–ocean–vegetation general circulation model. The use of such climate simulations is advantageous because it provides a combination of (i) global coverage, thereby enabling interregional comparisons; (ii) sufficient spatial and temporal detail to capture the complexity of postglacial climate change; and (iii) methodological consistency between regions.

Growing Season Temperature as a Trigger for Peat Initiation

Our results indicate that peat initiation in midlatitudes and high latitudes of both hemispheres was driven primarily by rising
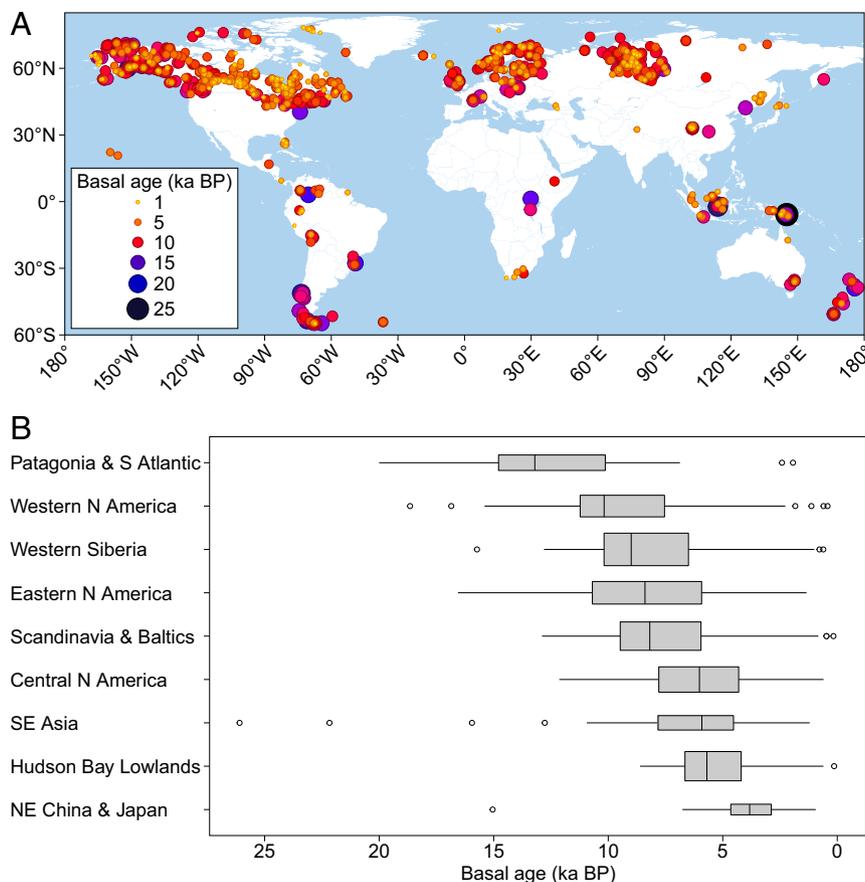
Fig. 1. Spatiotemporal patterns of peat initiation. (*A*) Global map of study sites, with continuous size and color scales to indicate calibrated dates of peat initiation. (*B*) Distributions of calibrated ages of peat initiation in selected geographical regions. Box widths indicate upper and lower quartiles; centerlines indicate medians. Whiskers extend to values no further than 1.5 times the interquartile range beyond the upper and lower quartiles; remaining observations are indicated by open circles. Box heights are proportional to the square root of the number of study sites per region.

growing season temperatures. Logistic regression models indicate that peat initiation is significantly predicted by local increases in the annual time integral of growing season temperature above 0 °C, GDD_0, in all northern peatland regions (those north of 30°N), as well as in Patagonia, Australia, and New Zealand ($P < 0.01$ in all cases; Table S1). Moreover, in most regions that were glaciated at the LGM, we find that the first major phases of peat initiation coincided with regional summer temperatures first rising above 0 °C (Fig. S2), leading to a rapid increase in GDD_0 (Fig. 2). The spatial heterogeneity of warming since the LGM (21) led to interregional differences in the timings of summer temperatures crossing the 0 °C threshold, and these differences explain much of the regional asynchrony in peat initiation. The earliest major phase of peat initiation in deglaciated terrain occurred in Patagonia, and coincided with local summer temperatures rising above 0 °C from ~17 ka B.P. onward. This was followed by maritime areas of eastern and western North America (~14 ka B.P.), the North Atlantic (~13 ka B.P.), Scandinavia and the Baltics (~12 ka B.P.), and the Hudson Bay Lowlands (HBL) (~8.5 ka B.P.) (Fig. 2) (see SI Materials and Methods and Fig. S1 for geographical extents of all regions).

As well as rising GDD_0, peat initiation in some northern regions is significantly associated ($P < 0.05$) with a reduction in the magnitude of seasonal temperature range, particularly in the continental interiors of Asia and North America (Table S1). This declining seasonality mainly reflects milder winters since the Early Holocene rather than cooler summers (Fig. 3C and Fig. S2), leading to a lengthening of viable growing seasons and so

increasing GDD_0. The effect of seasonal temperature range therefore appears to be secondary to, and covariant with, GDD_0. Other than in Scandinavia and the Baltics, seasonal temperature range is not a significant predictor of peat initiation in maritime regions (Table S1).

Peatlands initiated across a wide range of annual temperature and precipitation regimes (Fig. 3A), and the magnitudes of climate change they have endured since their formation (Fig. 3C) are modest compared to both those that preceded their initiation (Figs. S2–S6) and those projected for the 21st century (23). Although some arctic peatlands formed in annual average temperatures colder than −20 °C, peat initiation required mean temperature of the warmest month to be above freezing almost without exception (Fig. 3B). We interpret this apparent summer temperature threshold, along with the strong relationship between GDD_0 and peat initiation, to indicate that peat initiation in deglaciated landscapes was triggered primarily by warming growing seasons. In deglaciating landscapes of the Late Pleistocene and Early Holocene, a few weeks or even days per year of above-zero temperatures appear to have been sufficient to drive plant productivity and initiate peat accumulation. In the Northern Hemisphere, long, cold winters at the time would have protected nascent peat from decomposition in between short growing seasons (5, 8). As well as stimulating plant productivity, warming is likely to have caused changes in vegetation structure that allowed peat-forming species to establish, particularly in waterlogged areas (20).
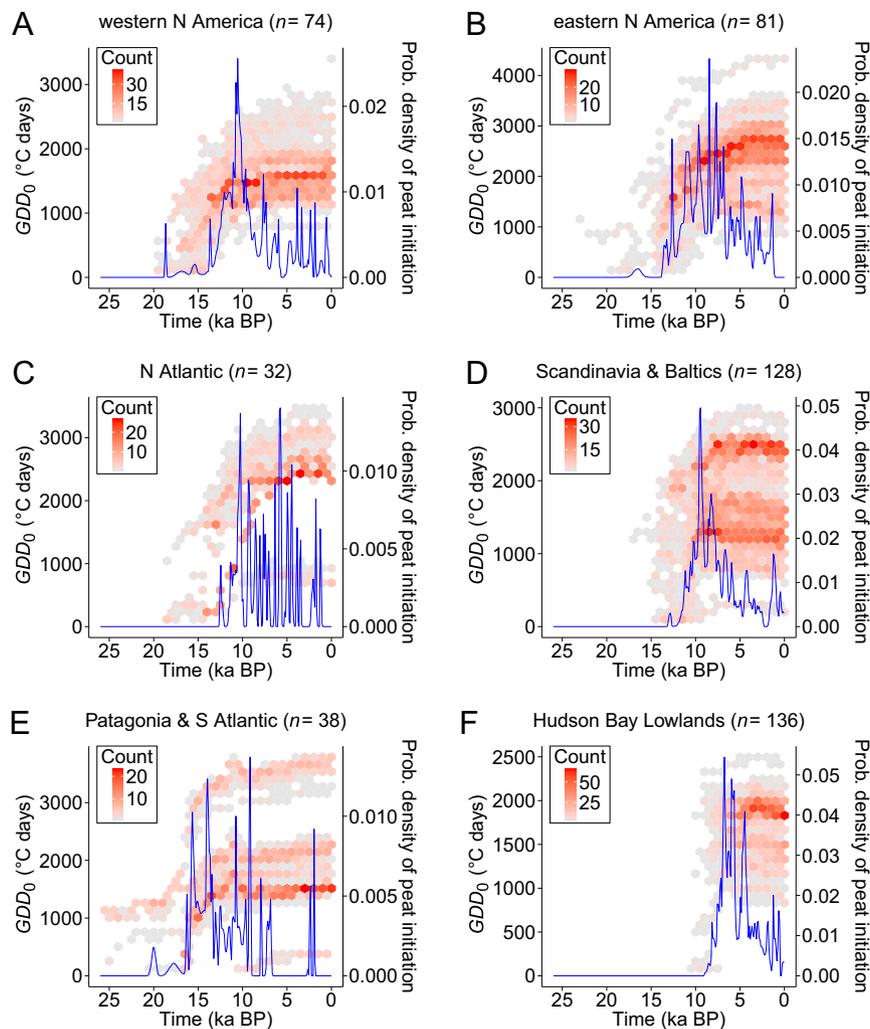
Fig. 2. Regional asynchrony of warming and peat initiation. Hexagonally binned point density plots showing long-term changes in annual growing degree days above 0 °C, GDD_0 (left-hand axes), in (A) western North America, (B) eastern North America, (C) the North Atlantic, (D) Scandinavia and the Baltics, (E) Patagonia and the South Atlantic, and (F) the HBL (see *SI Materials and Methods* and Fig. S1 for definitions of all regions). Count indicates the number of climatic data points per hexagonal bin; hexagons are scaled to represent 1,000 y. Solid blue lines show time series of summed probability functions of regional peat initiation in 100-y age bins (right-hand axes); *n*, number of study sites per region. Note differences in vertical scales between panels.

It has previously been proposed (13, 14) that the pacing of peat initiation in the HBL, the world's second-largest peatland complex, was driven by isostatic emergence from the postglacial Tyrrell Sea. However, our results indicate that first peat initiation in the HBL coincided with summer temperatures rising above 0 °C (Fig. 2F) and is significantly predicted by rising GDD_0 ($P < 0.001$). Peat initiation in the HBL was therefore limited before ~8.5 ka B.P. not only by the availability of land but also by low temperatures. Unlike previous suggestions (13) that peat initiation in the HBL occurred despite cold, dry climatic conditions at the time, our paleoclimate simulations indicate that peat formed in response to local warming. This disagreement may be explained, in part, by the fact that the nearest long-term pollen reconstructions are from northern Quebec (13, 24), centered on a location ~1,000 km northeast of the center of the HBL peat complex in Ontario, and include data from as far north as Baffin Island. Our paleoclimate simulations show a steep gradient in summer temperatures between the HBL peat complex and northern Quebec during the main phase of HBL peat initiation (8.5 ka B.P. to 4.0 ka B.P.), with June and July temperatures in the HBL often exceeding those in northern Quebec by more than 10 °C.

Role of Precipitation

In the WSL, which were not glaciated at the LGM (25, 26), our results indicate that peat initiation did not possess the same growing season temperature trigger as in formerly glaciated landscapes. Although rising GDD_0 is a significant predictor of peat initiation in the WSL ($P = 0.003$), average temperature of the warmest month remained above 5 °C in all WSL study sites, and, in many cases, above 10 °C, since before the LGM. The forest and grassland communities that occupied the region before extensive peat initiation (27, 28) seem unlikely to have been converted into peat-forming wetlands by further warming alone. First peat initiation in the WSL around 11.5 ka B.P. coincided closely with a pronounced increase in effective precipitation (total precipitation minus evapotranspiration) ($P < 0.001$) (Fig. 4A). The WSL are a low-gradient, poorly drained landscape where extensive peatland cover is maintained in part by widespread river flooding during summer months that promotes soil anoxia (27). The climatically driven increase in available water since 11.5 ka B.P. may have been sufficient to inundate preexisting plant communities and cause a shift to peat-forming vegetation. Waterlogged conditions would also have aided peat accumulation by suppressing soil respiration. Increasing effective
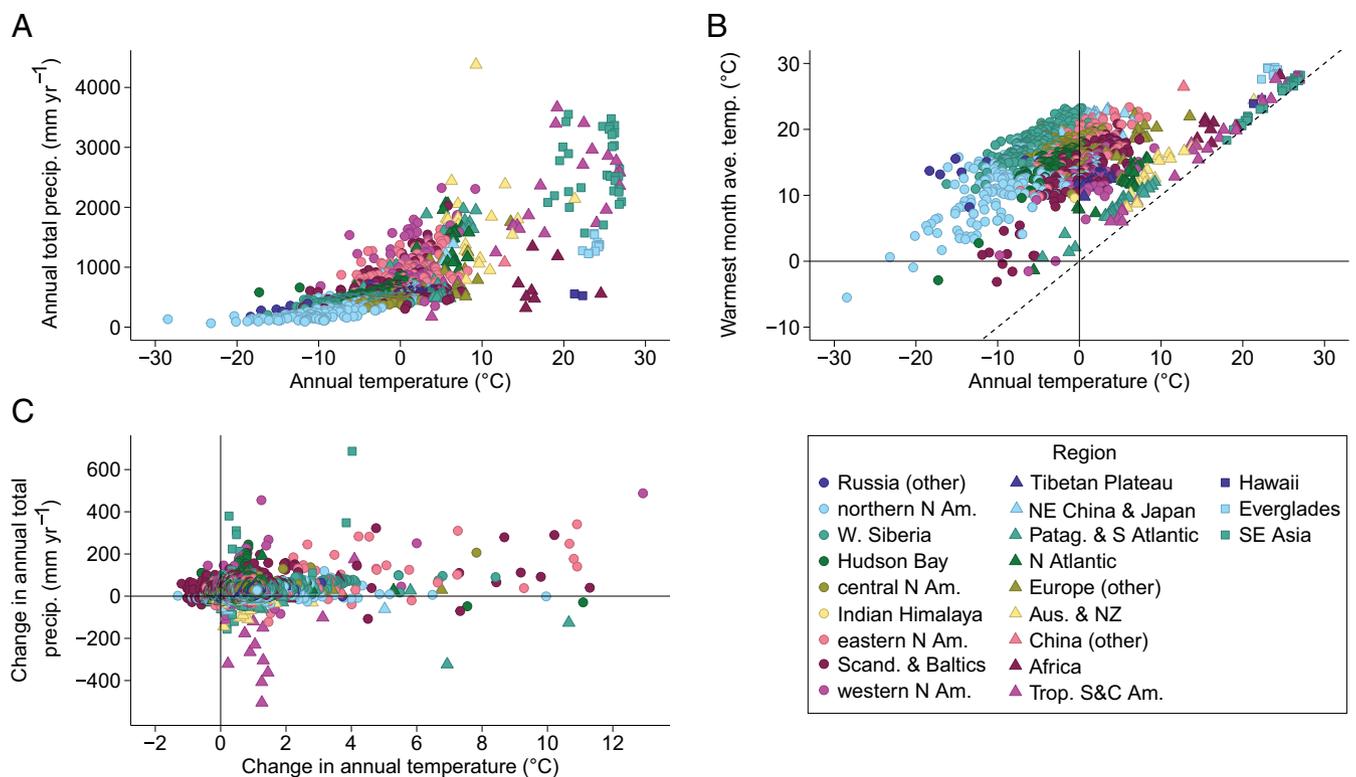
Fig. 3. Climate space of peatland development. (*A* and *B*) Annual and seasonal climate metrics at times of formation of our 1,097 study sites. Broken diagonal line in *B* is 1:1 line, height above which indicates seasonality of temperature. (*C*) Change in annual average temperature and annual total precipitation in each of our 1,097 study sites between the times of peat initiation and a preindustrial 1950 CE (0 ka B.P.). See Fig. S1 and *SI Materials and Methods* for definitions of all regions.

precipitation is also a significant predictor of peat initiation in Scandinavia and the Baltics ($P = 0.036$), although this wetting trend began ~10 ka before peat formation (Fig. 4*B*) and the effect size is less than a tenth of that in the WSL (Table S1). Although peat initiation in Scandinavia and the Baltics was likely aided by this increase in effective precipitation, our results indicate that the subsequent rise in growing season temperatures was the primary driver, as in other deglaciated regions.

Other parts of Asia and much of the interior of North America exhibited temperature-driven increases in total annual precipitation around the first major phases of peatland initiation (Fig. S2). However, these were more than outweighed by concomitant increases in evapotranspiration, meaning that peat initiation in the HBL ($P = 0.020$) and much of northern North America ($P < 0.001$) occurred despite decreasing effective precipitation (Fig. 4 *C* and *D* and Table S1). Most other biogeographic regions represented in our peatland database displayed no clear trends in either total or effective precipitation around the time of peat initiation (Figs. S2 and S3 and Table S1). Peat initiation in deglaciated landscapes therefore does not appear to have required any increase in effective precipitation to promote waterlogging.

Saturated, anaerobic soil conditions are clearly important to the establishment and persistence of peat through the suppression of soil respiration, so it is perhaps surprising, at first, that peat initiation in most regions displays no relationship to effective precipitation. However, the development of peat across such a broad range of precipitation regimes (Fig. 3*A*) implies that the climatic availability of water is rarely a limiting factor at the spatial scale of our GCM grid, and that more localized factors such as topography, drainage network topology, and near-surface permeability control the spatial distribution of saturated conditions,

and, in turn, the precise locations of individual peatlands at the subgrid scale. The vast peat complexes of the WSL and HBL represent special cases where large portions of the landscape were susceptible to waterlogging, and where favorable climatic changes triggered widespread peat initiation.

Of the major northern peatland regions, peat initiation in the WSL is the most closely linked to climate, as indicated by high accuracy, informedness, and markedness of the fitted logistic regression model. Lower explanatory power of models in European and North American regions (Table S1) may indicate the roles of previously hypothesized nonclimatic factors in deglaciated landscapes, such as drainage network development and infilling of waterbodies (14, 18, 20), particularly in central and northern North America where first peat initiation noticeably lagged summer warming (Figs. S2, S5, and S6). Warming in maritime areas of eastern and western North America preceded that in the rest of the continent (Fig. 2 and Figs. S2, S5, and S6), meaning that the gradual inland spread of peat across the continent (Fig. 1) likely reflects a combination of climatic (current study) and nonclimatic (18, 20) drivers.

Climate Drivers for Tropical and Subtropical Peat Initiation

The role of climate in tropical and subtropical peat initiation is less clear than in higher latitudes. In SE Asia and the Florida Everglades, peat initiation is significantly predicted by rising annual temperatures and declining seasonality of both temperature and effective precipitation ($P < 0.05$); rising annual effective precipitation is significant in the Everglades only ($P < 0.001$). High accuracy, informedness, and markedness all indicate that climate change reliably predicts peat presence/absence in these two regions (Table S1). However, all tropical and subtropical regions represented in our database remained more
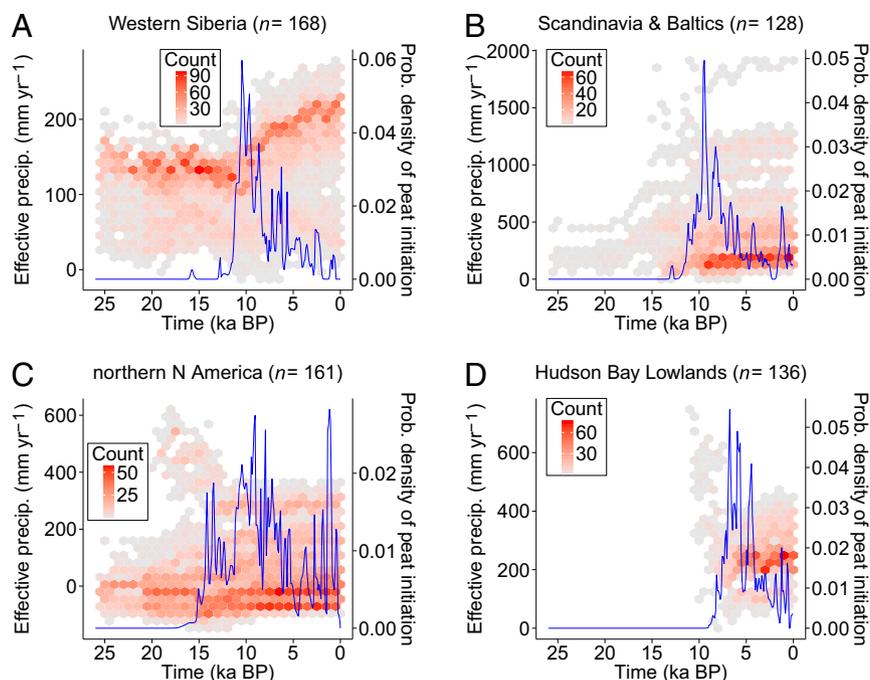
Fig. 4. Role of effective precipitation in peat initiation. Hexagonally binned point density plots showing long-term changes in annual effective precipitation (left-hand axes), in (*A*) the WSL, (*B*) Scandinavia and the Baltics, (*C*) northern North America, and (*D*) the HBL (see *SI Materials and Methods* and Fig. S1 for definitions of all regions). Count indicates the number of climatic data points per hexagonal bin; hexagons are scaled to represent 1,000 y. Solid blue lines show time series of summed probability functions of regional peat initiation in 100-y age bins (right-hand axes); *n*, number of study sites per region. Note differences in vertical scales between panels.

than warm enough to allow vigorous ecosystem productivity throughout the LGM (Figs. S2, S5, and S6), meaning that a temperature trigger such as that proposed for deglaciating landscapes is unlikely. In Africa and tropical South and Central America, peat presence/absence is not significantly predicted by any paleoclimate variable, and performance of the logistic regression models is little better than random (Table S1). Inundation resulting from tectonically driven hydrological changes (16, 17, 29, 30) remains the most plausible general explanation for peat initiation in many low-latitude regions, although our results indicate that this may have been aided by favorable climatic changes in SE Asia and the Everglades.

Linking Past, Present, and Future Climate Change

Recent climatic warming of the Antarctic Peninsula has caused widespread stimulus of biological activity, including accelerated peat accumulation beneath thin, previously slow-growing moss banks (31, 32). The Antarctic moss banks may provide an instructive modern analog for temperature-triggered peat initiation in deglaciating landscapes of the Late Pleistocene and Early Holocene. Successional chronosequences on Icelandic lava flows (33) and long-term monitoring of deglaciating Alaskan fjords (34) indicate that pioneering mosses can be replaced by more structured communities of higher plants within a few centuries or even decades of initial colonization. Both of these locations experience subarctic maritime climates that are comparable to that projected for the Antarctic Peninsula by the end of the 21st century (23). It remains to be seen what proportion of the Antarctic moss banks, if any, will develop into mature peatlands with valuable carbon sink functions in response to continued warming, and how many will be outcompeted by faster-growing communities once more mature hydrological and biogeochemical cycles are established. Any such transformation from aerobic moss bank to mature peatland would likely require favorable

local hydrogeological conditions to promote waterlogging and preserve peat in rising temperatures.

The conversion of the WSL from grassland and forest into the world's largest peatland complex in the Early Holocene illustrates the potential for rapid, widespread ecological change at high latitudes in response to climatic wetting. Multimodel projections of future changes in precipitation patterns contain less agreement than those for temperature, but most models agree on increased annual effective precipitation in the peat-rich high latitudes of North America and Asia during the 21st century (23). Such climatic wetting may provide opportunities for the establishment of new peat, particularly in areas of impeded drainage. However, the majority of this increased precipitation at high latitudes is projected to fall as snow during winter months (23). Any role of this increased precipitation in driving new peat initiation may therefore be limited to short-lived melt during shoulder seasons, outweighed during summer by temperature-driven increases in evapotranspiration.

Concerns about the stability of water table regimes and carbon stocks in Southeast Asian peatlands under projected future drying (35, 36) should be considered in the context of our paleoclimate simulations. The region as a whole has seen gradual climatic wetting since the LGM (Figs. S3 and S4), although this wetting trend is highly variable between individual sites (Fig. 3*C*). On the one hand, a long-term regional wetting trend may be taken to indicate that SE Asian peatlands have endured, and, in many cases, initiated during, periods of considerably lower annual total and effective precipitation than they now experience. On the other hand, the rates and magnitudes of future drying projected in the region, particularly during dry seasons, are without precedent since the LGM.

Conclusions

The initiation of peatlands in formerly glaciated landscapes of both hemispheres was driven primarily by warming growing

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seasons, and was not dependent on climatic wetting. The development of viable growing seasons above 0 °C occurred asynchronously between geographic regions, and first peat initiation in deglaciating landscapes tracked this warming trend. In landscapes that were not glaciated during the last glacial period, peat initiation appears to have required an increase in available water. In the large peatland complex of the WSL, waterlogging arose from an increase in effective precipitation. Peat initiation in the tropics was no more than weakly related to climate change, and waterlogging probably occurred through tectonic subsidence. As well as explaining the genesis of one of the world's most carbon-dense ecosystem types, our results also provide context for projected future changes in climate and their possible implications for both extant and nascent peatlands.

Materials and Methods

We compiled a catalog of basal radiocarbon dates from 1,097 extant peatlands around the world (Fig. 1 and Fig. S1), screened using published protocols (37) to ensure that they represent genuine dates of peat initiation rather than other landscape processes such as lateral peat expansion. We combined these dates with paleoclimate simulations from a coupled ocean–atmosphere–vegetation general circulation model, the Hadley Centre Coupled Model, version 3 (HadCM3), at intervals of 500 y (21 ka B.P. to 0 ka B.P.)

and 1,000 y (26 ka B.P. to 21 ka B.P.). The model's outputs were regionally bias-corrected and downscaled to 0.5 × 0.5° resolution (~50 × 50 km at midlatitudes) to provide local estimates of paleoclimate before, during, and after peat initiation at each site. We used geologically constrained ice sheet reconstructions to estimate dates of deglaciation at the 644 study sites that were glaciated at the LGM, and dates of emergence at the 137 sites that were submerged in shallow postglacial oceans before peat initiation. We omitted climate simulation data from times and locations that we estimated to be covered in continental ice or submerged before peat initiation. We grouped the 1,097 sites into 21 distinct biogeographical regions (SI Materials and Methods and Fig. S1) and considered the role of climate in peat initiation separately for each region. We fitted logistic regression models in each region to predict the presence or absence of peat on the basis of our simulated climate data. We assessed the reliability of the logistic regression model in each region using the metrics accuracy, informedness, and markedness. Details are provided in SI Materials and Methods.

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