PHILOSOPHICAL TRANSACTIONS B

royalsocietypublishing.org/rstb

CC BY

Research

Cite this article: Cook PA *et al.* 2026 Improving the representation of tropical peatland processes in the JULES land surface model using data from the central Congo Basin. *Phil. Trans. R. Soc. B* **381**: 20240487.

Received: 29 April 2025
Accepted: 7 May 2026

One contribution of 17 to a discussion meeting issue 'African tropical peatlands: function, value and vulnerability'.

Subject Areas:
environmental science

Keywords:
tropical peatlands, JULES-peat model, palaeoclimate simulations, vulnerability of peatlands

Author for correspondence:
Peter A. Cook
e-mail: P.A.Cook@exeter.ac.uk

Supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8558051.

THE ROYAL SOCIETY PUBLISHING

Improving the representation of tropical peatland processes in the JULES land surface model using data from the central Congo Basin

Peter A. Cook[1], Richard Betts[1,3], Eleanor J. Burke[3], Sarah Chadburn[2], Greta C. Dargie[4], Bart Crezee[4], Donna Hawthorne[5], Yannick Garcin[6], Enno Schefuß[7], Suspense Ifo[8], Nicholas Girkin[9], Mackline Mbemba[10], Yeto Emmanuel Wenina Mampouya[10], Dafydd Egryn Crabtree[11], Dylan M. Young[4], Paul J. Morris[4], Ian T. Lawson[12] and Simon L. Lewis[4]

[1]Global Systems Institute and [2]College of Engineering, Mathematics, and Physical Sciences, University of Exeter, Exeter, EX4 4QE, UK
[3]Hadley Centre, Met Office, Exeter, UK
[4]School of Geography, University of Leeds, Leeds, UK
[5]School of Natural and Built Environment, Queen's University Belfast, Belfast, UK
[6]CEREGE, Aix-Marseille University, Marseille, France
[7]MARUM—Center for Marine Environmental Sciences, University of Bremen, Bremen, Germany
[8]École Normale Supérieure, Marien Ngouabi University, Brazzaville, Congo
[9]Centre for Sustainable Agricultural Systems, University of Nottingham, Nottingham, UK
[10]École Normale Supérieure d'Agronomie et de Foresterie, Marien Ngouabi University, Brazzaville, Congo
[11]Centre for Ecology & Hydrology Bangor Site, Bangor, UK
[12]School of Geography and Sustainable Development, University of Saint Andrews, Saint Andrews, UK

PAC, 0000-0001-8877-1675; GCD, 0000-0002-1871-6360; BC, 0000-0002-1459-6402; DH, 0000-0002-0104-473X; NG, 0000-0001-7562-5775; DEC, 0000-0001-7502-8823; DMY, 0000-0002-6519-5473; SLL, 0000-0002-8066-6851

Tropical peatlands are not currently represented in large-scale terrestrial ecosystem models. Recent work in the central Congo Basin (CCB) measuring peatland processes and reconstructing peatland evolution and past climate provides a unique opportunity to further develop such models. Here, we modify the peatland scheme in the Joint UK Land Environment Simulator (JULES), the land surface component of the UK Earth System Model, in particular changing the vegetation litter composition and the dependence of peat decay on soil moisture. The modifications are informed by field measurements and by comparing the simulated peat accumulation and loss over 20 000 years with peat core records, including the 'Ghost Interval' period when reduced precipitation starting approximately 5000 years before the present (BP) resulted in significant peat loss. We drive JULES with a reconstruction of precipitation from peat core proxy data and other meteorological data from a global palaeoclimate model. The original JULES peatland scheme was unable to accumulate the observed quantities of peat or simulate the losses of peat suggested by palaeo records. Our updated version of JULES simulates peat increases until 3000 BP, when reduced precipitation results in substantial loss until 1000 BP. Correct representation of vegetation cover over time is also crucial for realistic peatland evolution. A French translation of this abstract is available in the supplementary material.

This article is part of the discussion meeting issue 'African tropical peatlands: function, value and vulnerability'.

© 2026 The Authors. Published by the Royal Society under the terms of the Creative Commons Attribution License http://creativecommons.org/licenses/by/4.0/, which permits unrestricted use, provided the original author and source are credited.

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

1. Introduction

Peatlands play important roles in the Earth system, including influencing potential feedback within the global carbon cycle [1] and also affecting hydrology. Since the existence of peatlands relies on sufficient levels of soil moisture, they are vulnerable to both climate change and the direct impacts of human land use, both of which have caused losses of peat carbon in the past. Numerical models can be used alongside data from observations and palaeo records to provide insights into the processes of change and make projections of future impacts of climate and land use change. However, none of the latest generation of Earth System Models (ESMs) in the 6th Coupled Model Intercomparison Project (CMIP6) included a representation of peatlands [2]. Although some global land surface models (LSMs) that could potentially be included in future ESMs do simulate peatland carbon stocks [3–5], they do not yet represent key processes involved in self-sustaining and threshold-type behaviours observed in peatlands. For example, the variation of thermal and hydraulic properties with the quantity of organic matter is not yet represented. Therefore, these models do not yet provide an accurate guide to the vulnerability of global peatland carbon stocks. Meanwhile, specialist peatland models [6,7] are not suitable for inclusion in global land surface schemes of ESMs owing to very different structures and approaches.

Development of peatland schemes in LSMs is underway. One such model is the Joint UK Land Environment Simulator (JULES), a land surface and terrestrial biosphere modelling system, designed primarily to operate at global scales [8,9]. One of the major applications of JULES is the simulation of large-scale processes of interaction between the land system and atmosphere in the Met Office's operational weather forecast model and the UK Earth System Model (UKESM) [10]. It is also commonly used outside of ESMs as a stand-alone terrestrial biosphere and hydrology model for global impacts studies, such as in the Inter-Sectoral Impacts Model Intercomparison Project (ISIMIP) [11] and for simulating historical changes in the terrestrial carbon cycle, for example, as part of the Global Carbon Budget [12]. JULES can either be used to simulate land processes at multiple points spatially distributed on a grid applied over a wide area (even global), or at a single point. A peatland scheme representing relevant processes has been developed for JULES [13] but so far only used the temperate/boreal zone. A globally applicable peatland scheme in a model such as JULES will need further attention and development of its ability to simulate tropical peatlands, with the representation of peatland processes being investigated and improved under different environmental conditions from those previously examined.

Recent observational and palaeoclimate/palaeocecological studies of the extensive peatlands of the central Congo Basin (CCB) [14–17] provide an opportunity to further develop the JULES peatland scheme (hereafter 'JULES-Peat') to represent tropical peatlands, and potentially to provide further insights into th e processes of peatland evolution. The Cuvette Centrale region, covering areas of both the Democratic Republic of the Congo and the Republic of the Congo, contains the most extensive peatland complex known in the tropics (supplementary material, figure S1). However, the extent and depth of the peat were only recently quantified [15], with an estimated area of 167 600 km^2 and total peat carbon content of 29 GtC (95% confidence interval, 26.3–32.2 GtC) [14]. This is approximately equivalent to 3 years of global anthropogenic CO_2 emissions at current rates [12]. The vulnerability of these globally relevant carbon stocks to climate change and the potential for land use change have only recently begun to be explored [16–18]. Process-based modelling can help to improve understanding of the drivers of past peat accumulation in the CCB and inform the assessment of current and future vulnerabilities.

By contrast with the peatlands of Southeast Asia, relatively little is known about the history and functioning of those in the CCB, but new evidence from radiocarbon dating suggests that in some locations, peat started to accumulate at least 20 000 years ago [16,17].

A key feature in the age–depth profiles of peat cores from across the CCB is the 'Ghost Interval': a long gap in the record where the peat is missing [16]. Proxy data suggest that there was a large reduction in precipitation from approximately 5000 years before the present (BP), peaking around 2000 BP, which caused drying out, oxidation and microbial decomposition of the peat. This suggests that a substantial thickness of previously accumulated peat was lost, as opposed to the build-up of peat having been halted [16,17]. A peatland model adapted to represent tropical peatlands, DigiBog_Congo, simulated the peat accumulation and loss in the CCB when driven by reconstructed precipitation and simulated temperatures over the past 20 000 years [19]. DigiBog_Congo reproduced the relationship between soil carbon age and depth obtained from the peat core, and the results suggested that as much as 55% of the peat thickness was lost during the period of drying that led to the 'Ghost Interval'.

Garcin *et al.* [16] suggest that the region may be close to a drought threshold, so, along with the evidence for past climate change having previously caused major losses of peat, this leads to concerns about the potential impacts of climate change on the CCB peatlands. Model projections of future climate change suggest a range of possible changes in mean precipitation, including both increases and decreases, but taken together, the models in the CMIP6 project an increasing likelihood of extreme drought in central Africa, including the CCB [20,21]. Young *et al.* [18] used a pattern-scaling approach to apply projected long-term trends in monthly mean climates from the CMIP6 ensemble to the Digibog_Congo model, and the projected range of impacts on the Central Congo peatlands, including both gains and losses of carbon. Assessments of the effect of the subsequent impacts on large-scale carbon and water cycles will require the inclusion of tropical peatland processes in land surface schemes of ESMs.

The unique palaeoecological and palaeoclimatic evidence for the peatland evolution and its climatic drivers, particularly the drought and soil carbon loss in the 'Ghost Interval', provides a rare opportunity to test and improve a model of peatland processes and their responses to past climate change as a step towards developing capability for assessing the impacts of future climate change. Here, we applied JULES-Peat for the first time to a tropical peatland and made further developments to broaden its global applicability with a view to potentially include peatland carbon feedback in UKESM. Along with palaeo information from a peat core and climate model simulations, we used new observations and studies of contemporary peatland behaviour to inform improvements to the model. We made a series of changes to the parameters in JULES-Peat so that the model better represented

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

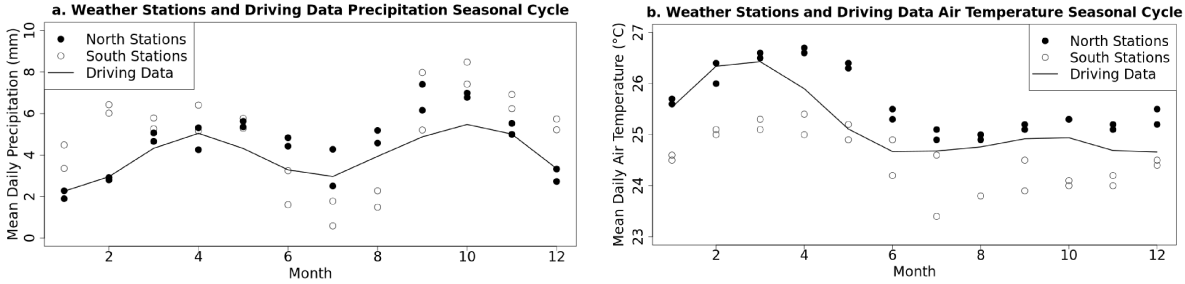


Figure 1. Seasonal cycles of (a) precipitation and (b) temperature from four weather stations in the CCB (circles) and from the dataset used to drive simulations with the JULES model (lines), for 1921–1940. Stations sited are sited at Impfondo (1.62° N, 18.07° E, 1932–1960) and Ouesso (1.62° N, 16.07° E, 1935–1960) in the north of the CCB (filled circles), and Gamboma (1.87° S, 15.88° E, 1936–1960) and Makoua (0.03° S, 15.58° E, 1953–1960) in the south (open circles). Measurements provided by the National Civil Aviation Agency of the Congo (personal communication between Ifo Suspense Averti and the National Civil Aviation Agency of the Congo, 2025).

the environment in the CCB, and carried out a new simulation after each change to determine the differences this made to the ability of the model to reproduce the evolution of the CCB peatlands in accordance with evidence and understanding from the palaeo record and other modelling.

2. Methods

(a) Region and site information

Within the CCB are regions of palm-dominated swamp forest (mostly species of Raphia palm), regions of hardwood-dominated swamp forest (mostly broadleaf evergreen tropical (BET) trees) and regions of terra firme tropical forest (mostly hardwood trees outside of the swamp, large areas of which are seasonally flooded but do not form peat) [15]. Peat forms when the addition of plant litter outpaces its decay under (usually) waterlogged anoxic conditions. The peatlands in the CCB are either rain-fed systems with peat filling shallow large-scale interfluvial basins or they occur in regions influenced by river flooding [15,22]. Profiles of carbon concentration and bulk age have been measured in many soil cores across the CCB. Using field data and modelling, Crezee *et al.* [14] estimated a mean peat thickness of 1.7 ± 0.9 m (5.6 m maximum) for the region, with a mean peat carbon density of 171.2 ± 63.4 kg C m^{-2} (397.0 kg C m^{-2} maximum).

The region has two wet seasons, peaking in February–April and October, and a seasonal cycle of temperatures with monthly averages peaking in April (figure 1). Here, we use weather station data from 1921 to 1940 because information on later dates is not available for this region. However, reanalyses of gridded datasets from recent decades using additional information from remote sensing have demonstrated that the seasonality of precipitation has remained similar over recent decades [23].

We focus here on modelling peatlands in rain-fed systems. The rain-fed systems in the CCB have a shallow interfluvial domed surface; LiDAR measurements show the centres to be approximately 1.8 m above the peat margins [17,24]. Our work with the JULES model draws heavily on information from the CEN-17.4 core [17], which contains the thickest peat sequence yet recovered from the CCB, at 5.99 m (deeper than the largest estimate of 5.6 m made by [14]). It has additionally been analysed to provide information on past vegetation and climate.

CEN-17.4 was collected in the middle of a 45 km-wide domed peatland on the interfluve between the Ubangui and Likouala Aux Herbes rivers, 1.1835° N, 17.6399° E [17]. The bulk age of the peat from radiocarbon dating increases with depth to 19 600 calibrated years before present (cal. yr. BP; taken as CE 1950), increasing sharply from around 2350 to 7520 years between 1.55 and 1.90 m—the 'Ghost Interval' feature [16,17]. Clay was found below the peat, and the deepest soil has 4–6 µm median particle size, which implies a silt-clay [17]. The bulk density profile was not measured in CEN-17.4 but was measured in another core, CEN-20, which was obtained 2.6 km from the CEN-17.4 core on the same transect. CEN-20 has a total organic carbon content of 59.7% ± 2.0% (between the surface and 4.9 m depth), which is comparable to that found in the CEN-17.4 core (56.4% ± 2.3%) for the same depth range.

The site of the CEN-17.4 core is currently covered by tropical swamp forest, which constitutes a mixture of hardwood species and palm [16], but palaeoecological reconstructions based on the CEN-17.4 core suggest that the vegetation was grasses and sedges until 12 500 cal. yr. BP [17].

The core also provides proxy data that can be used to infer aspects of the past climate at the site. Garcin *et al.* [16] used sedimentary isotope values (D/H) from leaf wax in the soil core to provide a reconstruction of annual precipitation from 19 600 cal. yr. BP to CE1940, based on empirical relationships between precipitation amount and rainwater isotopes at different locations in the CCB, with the isotope values at the top of the peat profile being scaled to modern precipitation isotope values. Modern precipitation data were not available from the site of the CEN-17.4 core, so instead were taken from datasets relating to alternative sites such as Bangui, which is several hundred km north of the CEN-17.4 site. For this reason, the reconstructed precipitation is not considered to be specifically representative of the CEN-17.4 core site. Hawthorne *et al.* [17] used the effects of long-term global ice volume and vegetation changes on the D/H isotope ratios to provide further corrections to the precipitation back to the Last Glacial Maximum. The precipitation reconstruction shows substantial variability on centennial and millennial

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

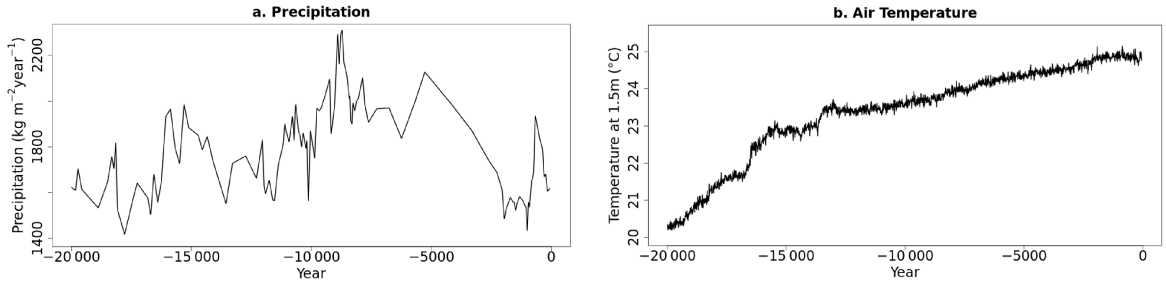


Figure 2. Palaeoclimate history in the central Congo Basin. (a) Precipitation reconstructed from isotopes in the CEN-17.4 peat core; (b) air temperature at 1.5 m above the surface, simulated by the HadCM3 climate model.

timescales, but generally demonstrates an increase to around 9000 cal. yr. BP, followed by a major decrease between about 5000 and 2000 cal. yr. BP (figure 2a).

The initial peat formation at 19 600 cal. yr. BP was around a millennium after the Last Glacial Maximum (approx. 21 000 BP). A simulation with the HadCM3 climate model driven by orbital forcing [25] suggests that near-surface air temperature rose by nearly 3°C between 20 000 and 15 000 cal. yr. BP, and then continued to rise but more gradually by approximately a further 2°C by around 2000 cal. yr. BP (figure 2b).

To provide an initial quantification of key peatland processes, we used field measurements that we had previously made in a one-hectare plot identified as EKG-02 in the hardwood-dominated peat swamp at roughly 1.2°N, 17.85°E, approximately 23 km east of the location of the CEN-17.4 peat core. Measurements here followed Global Ecosystem Monitoring (GEM) protocols [26]. Water table depth was measured every 20 minutes using a Solinst levelogger and Solinst barologger. Leaf litter was measured every 2 weeks using litter traps of area 0.25 m^2 in each of 25 sub-plots within the one-hectare plot, larger stem litter (coarse woody debris) collected in 50 m transects bordering the plot, and root inputs from minirhizotrons [27]. Respiration at the soil surface (which includes root respiration) was measured monthly using an EGM portable CO_2 gas analyser. Water table and litter measurements were taken from March 2019 to March 2021. Soil and root respiration measurements were taken from April 2019 to March 2021, with gaps in November 2019 and October–November 2020 because the site was inaccessible owing to flooding. Data from EKG-02 have previously been used with the DigiBog_Congo model [19].

(b) The JULES model and its existing peatland scheme, JULES-Peat

JULES represents the land surface energy balance, vegetation dynamics, soil biogeochemistry and heat, water, carbon and nitrogen fluxes [8,9,28–30]. It is used to simulate past and future changes in hydrology, and carbon and methane emissions/climate feedback [31–34]. JULES has been extensively used for studies focussing on several biomes, particularly forests, and also wetlands [35]. It has been used to simulate peatlands as part of permafrost regions.

JULES is driven by precipitation, downwelling shortwave and longwave radiation, temperature, humidity, surface pressure and wind speed, along with the local nitrogen deposition to plants and soil and the atmospheric CO_2 concentration. It simulates land–atmosphere exchanges of energy, water and carbon, with the latter determined by the simulated vegetation productivity, autotrophic and heterotrophic respiration, and litterfall. Each grid point can contain several different land-cover tiles, including plant functional types (PFTs) representing trees, grasses and scrub, as well as non-vegetated tiles (urban, water, ice and bare soil). The dynamic vegetation model can be used to simulate the vegetation distribution and its change over time, or the vegetation cover can be held fixed at a given distribution. There is input of carbon to the soil from vegetation via litter, including stem and root litter as well as leaf litter.

JULES includes a vertically resolved soil carbon and nitrogen scheme [28,30], which has four organic soil carbon pools and equivalent organic soil nitrogen pools for each soil layer, namely: decomposable plant material (DPM), resistant (recalcitrant) plant material (RPM), microbial biomass and humus. The DPM and RPM pools represent litter pools. The respiration in each soil layer depends on the carbon pool size, depth within the soil, soil moisture, temperature, vegetation cover fraction and nitrogen availability. In the standard JULES soil scheme, which represents mineral soils, there is diffusive mixing between the soil layers, which represents bioturbation (mixing of the soil owing to animals and plant roots) and, in cold regions, cryoturbation (soil mixing by frost heave and freeze–thaw processes) [28].

A key limitation of the standard vertically resolved soil carbon scheme in JULES and other LSMs for ESMs is that the soil layers are not allowed to grow or shrink. This means that carbon inputs from litter are continually added to the topsoil layer, so when decomposition is low, this results in an unrealistically high carbon content in that layer, and the increased carbon concentration does not extend far enough into deeper soil layers. These schemes therefore fail to recreate soil carbon profiles at sites with peat or a thick organic layer [32].

JULES-Peat is a development of the JULES soil carbon scheme to allow the representation of peatlands [13]. It does not follow the approach of specialized peat models such as DigiBog [6] and the Holocene Peat Model [7], which vertically resolve peatland structure by adding new peat as a separate layer on top of the soil column, because this produces a very large number of layers, which would be impractical for global modelling. Moreover, this approach is only applicable to peatlands so does allow modelling

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

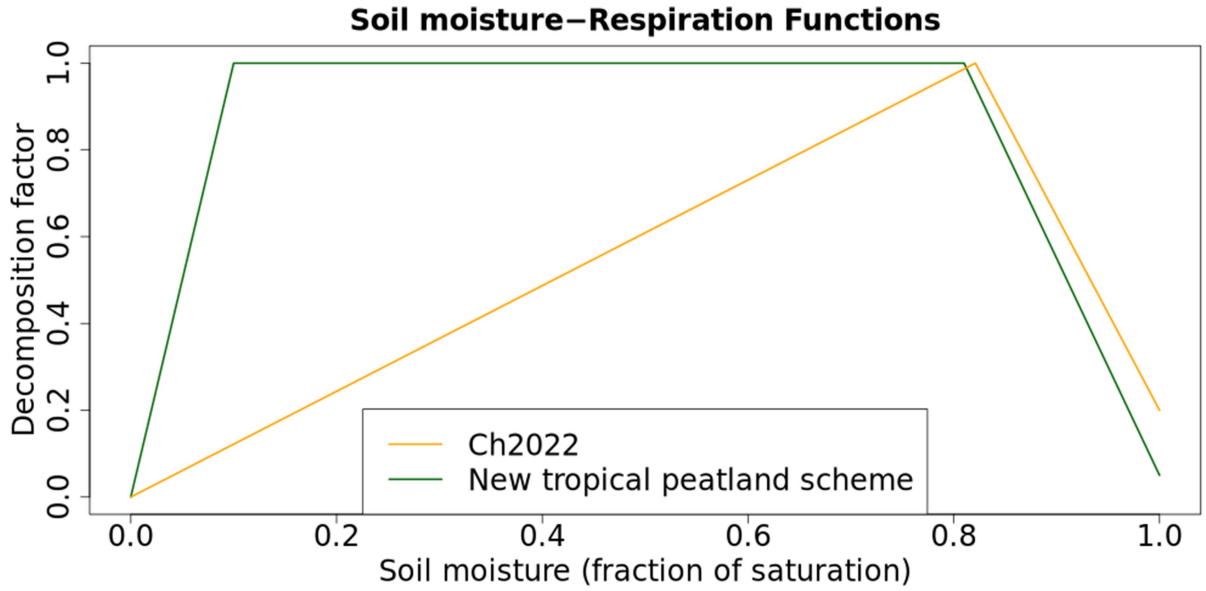


Figure 3. Old and new decomposition functions relating soil respiration to soil saturation in JULES-Peat.

of continuous transitions between mineral and organic soils. Instead, JULES-Peat modifies the existing vertically resolved soil carbon scheme to include soil organic matter accumulation and peatland formation and degradation.

JULES-Peat accounts for the volume of organic matter. Each soil carbon pool has an assumed density, with the litter pools (DPM and RPM) having a lower density than the decomposed carbon pools, which is used to determine the volume. The number of soil layers does not change as peat accumulates (or is lost); instead, as the soil carbon content changes, the carbon is re-interpolated across layers based on the volume of the organic matter that will fit within a layer. As the peat grows, the total depth of the soil column increases, with any extra depth required added to the bottom of the column. A major advantage of this scheme is that it not only maintains the thickness of soil layers used for the hydrology calculation within JULES but also allows for peat accumulation. JULES-Peat does not provide a precise total peat depth owing to the low vertical resolution and movement of carbon between soil layers. It simulates a rise in ground level owing to peat accumulation, which can be used as a broad indicator of peat accumulation, although it does not perfectly represent the total peat depth because carbon is mixed down into lower soil layers.

Chadburn *et al.* [13] also included an ecohydrological feedback between the soil organic matter content and the soil thermal and hydrological properties, such as hydraulic and thermal conductivity, porosity and saturated hydraulic suction. As the peat content changes, the soil hydraulic properties also change, for example, with hydraulic conductivity decreasing as carbon content increases. This means that peatlands' resilience to moderate drying owing to their maintaining wetter soil is included within JULES-Peat.

Another key aspect of JULES-Peat is the relationship between heterotrophic respiration and soil moisture in undecomposed organic soils (figure 3). This uses a scaling factor that is zero when soil moisture is zero (i.e. no respiration occurs in perfectly dry soil) [36] but that then increases to a maximum of 1.0 and subsequently—beyond a certain higher level of soil moisture related to the wilting point—decreases to 0.2 for fully saturated soil, reflecting understanding that respiration in anaerobic conditions is no more than 20% of the maximum rate for aerobic conditions [37]. Limited decomposition in saturated soil is key to peat formation. Several other models use a similar general form, although with wide variations, especially in the range of soil saturation levels at which the decomposition function is at 1.0, with particular uncertainty at medium to low levels of saturation [36,38].

JULES-Peat was developed for temperate and cold region peatlands but it has not yet been applied to a tropical peatland. Here, we further develop JULES-Peat to enable it to simulate the origin and development of the CCB tropical peatlands from 20 000 BP. As well as the simulation of peat accumulation, we particularly focus on the model's responses to the long period of reduced precipitation by simulating a substantial loss of peat and thereby recreating the observed age–depth profile of the CEN-17.4 core.

(c) JULES-Peat set-up for tropical peatlands in the CCB

We performed a series of JULES simulations under conditions representing those in the CCB peatlands over the past 20 000 years, introducing new changes to the model in each new simulation. This section presents details common to all simulations, and then §2d discusses the subsequent modifications required to make the configuration more suitable for tropical peatland. Section 2e describes the climate data used to drive the simulations.

In all simulations, which are one-dimensional (vertically resolved at a single location), the soil column is initially 7.2 m deep with 20 layers of increasing thickness with depth, from 0.05 m at the top to 0.64 m at the base, which is standard for JULES-Peat. The bottom layer increases in thickness as organic matter accumulates [13]. Each simulation starts with zero vegetation and zero carbon in the soil at 20 000 BP—the model is therefore not initialized with peat present, but instead creates peat when conditions

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

allow. The dynamic soil properties in JULES-Peat mean that the soil hydrology depends on the amount of peat that has built up, which then affects the soil moisture and hence how quickly the peat decays owing to microbial respiration.

We used the standard nine PFTs, which include hardwood BET trees. JULES does not include a PFT representative of palm, but since the site of the CEN-17.4 core is dominated by hardwood trees and the EKG02 site is also a hardwood swamp, the BET PFT is considered representative of these sites. The nine PFTs dynamically interact in JULES simulations, share the same soil column and all affect the water budget. Each simulation begins with bare soil, then as the vegetation grows, different PFTs come to dominate until a stable situation is reached. This results in mostly hardwood BET trees, with the exception of one simulation where we deliberately exclude trees for the earlier part of the simulation—this is discussed further in §2d, penultimate paragraph and table 1, final column.

The nitrogen cycle is enabled in the model, meaning that the vegetation can be nitrogen-limited. The responses of the simulated vegetation are complex owing to the feedback within the model. Plant productivity and therefore the amount of litter entering the soil are limited by the available nitrogen, and since decaying peat releases nitrogen, any increase in peat decay will stimulate plant productivity (and *vice versa*).

Clay soil was used as the starting soil type, as clayey silts underlie the peats [17]. Baseflow is turned off, which means there is no water flux out of the bottom of the soil profile because there would be little drainage through the clay; this increases the resilience of peat accumulation to moderate drying. Although simulations included the removal of excess rainwater by surface runoff, lateral flow into the grid box from outside is not considered, as the site is rain-fed as opposed to being influenced by river flooding.

(d) Improvements in JULES-Peat for the CCB

Our first simulation used the version of JULES-Peat that is hereafter denoted 'Ch2022' [13]. We then introduce a series of further changes to the parameters in order to better represent the processes in the CCB. We carried out a new simulation after each change to determine how this affected the ability of the model to simulate the peatland evolution.

In order to accumulate peat, the input to the soil carbon from the vegetation needs to be greater than the output from the soil respiration, which results from the decomposition of organic matter in the soil. Here, we discuss improvements made to both the simulation of vegetation inputs and the soil respiration output in order to simulate the processes of peat accumulation in a more appropriate manner for the tropical peatland under consideration.

In JULES, tropical broadleaf trees typically have rooting depths of approximately 3 m. However, in a swamp forest such as at the study site [17], trees typically have shallower roots than the tropical trees simulated in JULES, and fine root production decreases rapidly with depth [39]. To reflect this, here we reduced the rooting depth from 3.0 to 0.5 m. This means that more moisture is extracted from the soil for transpiration near the surface than at depth, and that a greater proportion of the litter is expected to go into the shallower soil layers. This will affect other vegetation responses such as Net Primary Productivity (NPP). Furthermore, since roots provide a source of litter input directly into the soil below the surface, we modified a key parameter determining this in order to increase the proportion of litter nearer the surface. In JULES, the vertical distribution of litter input into the soil is parameterized by an exponential function with an e-folding depth given by τ_lit. Here, we increased τ_lit from 3 (as in [13]) to 5. This pair of modifications is denoted 'R_d'.

In addition, the decomposability of the litter input from vegetation needs to appropriately represent the hardwood swamp forest. Chadburn *et al.* [13] prescribed a DPM/RPM ratio for tree litter of 0.25%, or 20% decomposable and 80% recalcitrant. However, evidence from measurements made on litter samples from the CCB field site indicates that the mean composition of the tree litter is 60% decomposable and 40% recalcitrant [19], so we updated the ratio to this in JULES-Peat for the CCB. In conjunction with this, we set bioturbation mixing to zero, consistent with shallower tree roots and an assumed lack of soil fauna below the water table. This eliminates diffusion of the soil carbon down the soil column. This set of modifications is denoted 'Q_{soil}', short for soil quality.

We also modified the decomposition factor determining the relationship between soil respiration and the level of soil saturation. As noted in §2b, there are large uncertainties regarding the range of soil saturation at which decomposition is at its maximum, and a range of forms of the function are used in different LSMs [38,40]. There are no field or laboratory data for soils in the CCB region to determine the form of this function. It is therefore quite possible that the existing function in [13] is not appropriate for the CCB, so in the absence of other data to constrain it, we explored a range of variations. Figure 3 shows the new form of the function used in the simulation presented in the results below, with soil moisture only limiting respiration in very dry and very wet conditions. Between these values, respiration is unaffected by soil moisture availability. Respiration falls to zero in completely dry soil, while in fully saturated soil, respiration reduces to 5% of its maximum value. Several alternative functions were tested, and the new function shown here produced the best balance between a strong build-up of peat and sensitivity to climatic change. The alternative soil moisture–respiration functions either produced a strong build-up of peat with insufficient sensitivity to climatic change, or had sensitivity to climatic change with a weaker build-up of peat (see supplementary material, figure S2). This new function is denoted 'R_θ'.

A final change concerned the nature of vegetation overlying the peatlands. JULES simulated forest for the entire 20 000-year period, whereas palaeoecological reconstructions suggest that the vegetation constituted grasses and sedges until 12 500 BP [17]. The nature of the vegetation cover can influence both carbon and water cycle processes in the peatlands, so it is important that the vegetation cover be realistic. We therefore performed a fifth simulation in which only grass was allowed to grow in JULES-Peat during this time. This was done by increasing the disturbance rates of all other PFTs so that the grass always out-competed them.

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

Table 1. Variables updated between each simulation. Bold values show the new parameterizations in each new simulation.

	Ch2022	R_d	R_dQ_{soil}	$R_dQ_{soil}R_\theta$	$R_dQ_{soil}R_\theta$-grass
tree rooting depth (m)	~3	**0.5**	**0.5**	**0.5**	**0.5**
τ_*lit*	3	**5**	**5**	**5**	**5**
decomposable proportion of litter (%)	20	20	**60**	**60**	**60**
recalcitrant proportion of litter (%)	80	80	**40**	**40**	**40**
bioturbation	yes	yes	**no**	**no**	**no**
soil respiration vs. soil moisture	original function in figure 3	original function in figure 3	original function in figure 3	**new function in** figure 3	**new function in** figure 3
vegetation cover during simulation	mostly broadleaf evergreen tropical (BET) trees (driven by climate)	mostly BET trees (driven by climate)	mostly BET trees (driven by climate)	mostly BET trees (driven by climate)	**grass only for the first 7500 years (prescribed), then mostly BET trees (driven by climate)**
common set-up for all simulations	20 soil layers between surface and 7.2 m depth. use clay soil. baseflow (drainage) turned off. start with zero soil carbon (no peat layer). run with dynamic soil properties. start with zero vegetation (bare soil). run with dynamic vegetation. nitrogen limitation of the vegetation is enabled.				

After 7500 years, the disturbance rates were reset to those typically used by JULES-Peat and the vegetation was allowed to grow unimpeded, and the conditions then led to vegetation dominated by BET trees as in the other simulations. This new vegetation cover time series is denoted 'grass'.

Using the described driving data, we performed five different simulations starting with the version of JULES-Peat derived from [13] and then making additional changes for each subsequent simulation. Table 1 lists the parameterizations that were changed between the simulations. The bold values represent the new values. The new parameterizations were added sequentially in order to understand the impact of each change.

(e) Climatic data to drive JULES-Peat

We drove JULES-Peat at a single point with palaeo-meteorological data (3 hourly values) covering approximately 20 000 years (18 000BCE–1940). Precipitation was scaled so that annual means match the reconstruction from the CEN-17.4 core [16,17]. Since the palaeo reconstruction cannot resolve sub-annual timescales, seasonal cycles remained as simulated by the model. The other meteorological variables needed to drive JULES are not available from palaeo records, so were taken from a global palaeoclimate simulation with a variant of the Hadley Centre Coupled Model version 3 (specifically HadCM3M2.1aD [25]). We used data from a single grid box of spatial resolution 3.75° longitude by 2.5° latitude at the centre of the CCB (0°N, 18°E). The HadCM3M2.1aD simulation followed the Palaeoclimate Modelling Intercomparison Project phase 4 (PMIP4) deglaciation protocol [40–42]. The time series of simulated surface air temperature is shown in figure 2b, and those of the other variables (shortwave and longwave radiation, humidity, surface air pressure and wind speed) are shown in supplementary material, figure S3.

The model-derived precipitation has large seasonal cycles in the early part of the simulation (not shown), but smaller cycles in later years, which are closer to the measured values of precipitation (figure 1). Given that there is very little proxy record information about the seasonal cycle over palaeo timescales, we set the seasonal cycle of precipitation in each year to the mean cycle from the past 1000 years. The final precipitation for the last two decades of the reconstruction (1921–1940) compares well with measurements from weather stations at Impfondo (1.62°N, 18.07°E, 1932–1960) and Ouesso (1.62°N, 16.07°E, 1935–1960) in the north of the CCB, and Gamboma (1.87°S, 15.88°E, 1936–1960) and Makoua (0.03°S, 15.58°E, 1953–1960) in the south (figure 1a).

The downwelling shortwave radiation was also scaled to vary with the new values of precipitation (supplementary material, figure S3a), since less precipitation means less cloud cover and more shortwave radiation (and *vice versa*). This was done

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

Table 2. Comparison of key quantities resulting from the initial, final and intermediate variants of the JULES-Peat simulations with annual mean measurements at the EKG02 site, total soil carbon in the CEN-20 core and peat depth from across the CCB and the CEN-17.4 core.

	Ch2022	R_d	R_dQ_{soil}	$R_dQ_{soil}R_\theta$	$R_dQ_{soil}R_\theta$-grass	measurements
annual mean water table depth (m)	−0.17	−0.12	−0.22	−0.19	−0.18	−0.05
annual mean litter flux (kg C m^{-2})	1.06	1.06	1.14	1.02	1.04	1.07
annual mean soil respiration (kg C m^{-2})	1.07	1.07	1.13	1.02	1.06	1.34
final total soil carbon (kg C m^{-2})	232	298	70	275	337	171 (mean) 397 (maximum)
final ground level or peat depth (m)	3.09	2.90	0.78	3.22	4.27	1.70 (mean) 5.60 (maximum)

according to the approximately linear relationships between monthly downwelling shortwave radiation and monthly precipitation seen in the HadCM3 data for each month of the year.

The air temperatures in the HadCM3 data are higher than observed, so all the modelled temperatures were lowered by 1.1°C to match the measurements. The resulting seasonal cycle of air temperatures in the CCB from the model (1921–1940) and from the weather stations is shown in figure 1b, the two peaks and two troughs being typical of equatorial regions.

The associated palaeo CO_2 concentrations and nitrogen depositions used in HadCM3 [25] were also used in JULES-Peat. CO_2 was lower at the start of the simulation at around 200 ppm, rising gradually throughout the Holocene to around 280 ppm in the eighteenth century, then more rapidly owing to anthropogenic emissions to reach 312 ppm in 1950.

3. Results

We first assess the impact of the model parameter updates on the performance of JULES-Peat by comparing the results at the end of individual simulations with: (i) the field measurements of litter fall, water table depth and soil respiration at the EKG02 site; (ii) the measured total soil carbon content in the CEN-20 core; and (iii) the measured peat depth in the CEN-17.4 core. Alongside this, we analyse the time series of the individual simulations to understand the simulated processes of peat evolution resulting in the different final results, in the context of understanding of the peatland evolution processes gained from previous analysis of peat cores. These simulations all allow the JULES model to compute its own vegetation cover throughout the process, resulting in forest cover estimations for the whole period. We then examine the impact of applying the correct vegetation cover—grassland—for the first 7500 years of the simulation. Next, we compare the evolution of the profiles of soil carbon content and age with depth relative to the CEN-20 and CEN-17.4 cores, respectively. Then, focussing on the final simulation, we assess the sensitivity to a quantifiable aspect of uncertainty in the palaeoclimate simulation. In §4, we compare our final simulation with the previously published results from DigiBog_Congo to assess how our updated version of a model designed as an ESM land surface scheme compares with those of a specialist peatland model.

(a) Impact of model parameter updates

Ideally, to assess the performance of our model against field measurements, we would have driven the model with observed meteorological variables from the same site. However, for practical reasons, it was not possible to make meteorological measurements there, so instead we make the comparison using the mean seasonal cycle of the final 20 years of our JULES-Peat simulations (1920–1940), with the end dates being determined by the end date of the precipitation reconstruction. The 20-year mean climatology is used since the model and field data are not available for the same individual years. We are not considering our results to be truly representative of the specific EKG02 site because: (i) the precipitation reconstruction uses isotope records from the CEN-17.4 core site approximately 20 km away and modern isotope information from Bangui, approximately 350 km away, and (ii) the other meteorological variables are from a model simulation at grid resolution 3.75° by 2.5°. Instead, both the model results and field measurements are taken to be broadly representative of the region as a whole.

Figure 4 shows the 20-year mean seasonal cycles of (a) evapotranspiration, (b) litter carbon flux, (c) water table depth and (d) microbial respiration in the soil at the end of the simulations (1921–1940), with the latter three variables compared with measurements for 2019, 2020 and 2021. Table 2 shows the annual means. Figure 5 shows the full simulations over 19 940 years, and table 3 shows the values at key periods in time, and observations of soil carbon and peat depth. We compare the measured peat depth to the model rise in ground level because JULES-Peat does not provide a precise depth of the peat layer owing to the low vertical resolution and movement of carbon between soil layers. However, we note this is not a perfect comparison. The following section discusses the results of the different model variants in the context of the measurements from these various sources.

2020 is the only year with measurements covering the full seasonal cycle and shows seasonality in water table depth and soil respiration. The water table is deeper, and soil respiration is higher in January–April, which is the warmest time of year in the regional climatology (figure 1b) and also a period of transition from a dry to wet season (figure 1a). Water table measurements began in March 2019 and did not show a deeper water table at this time, and soil respiration measurements did not begin until

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

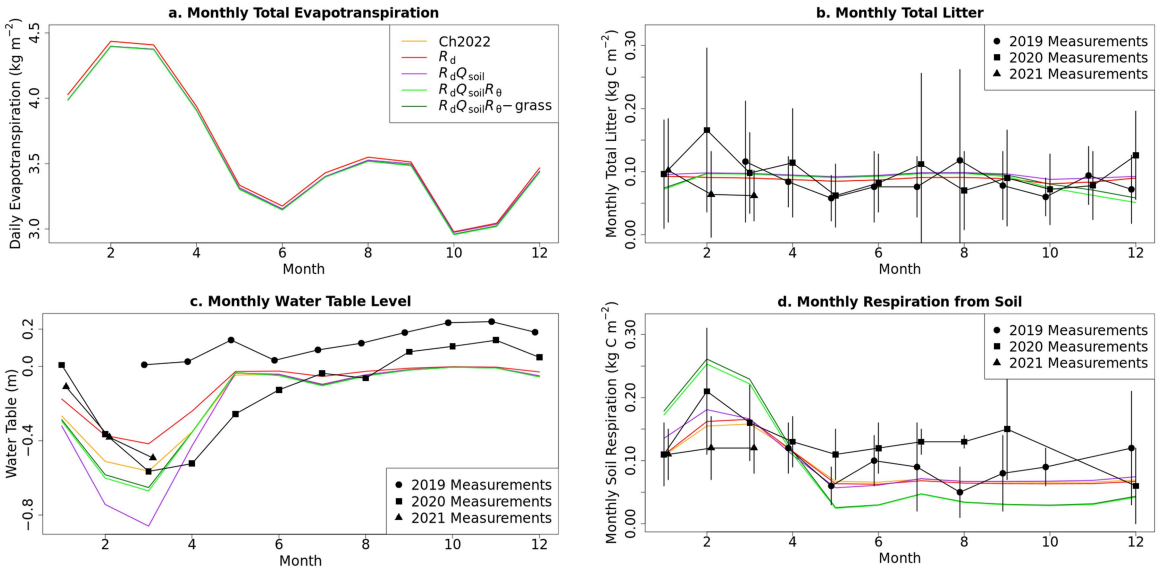


Figure 4. Seasonal cycles of (a) evapotranspiration, (b) total monthly carbon in litter inputs to the soil, (c) water table depth and (d) respiration from the soil. Colours: monthly mean values from the 20 years at the end of the JULES-Peat simulations (table 1). Black: measurements at the EKG02 site, with symbols showing means across sub-plots and whiskers showing the standard deviation across sub-plots for litter and soil respiration. Water table depth was only measured at one point in the plot. Note that measured respiration will also include autotrophic respiration from roots as well as heterotrophic respiration from the soil, whereas modelled respiration only includes the latter, and that the JULES-Peat simulations are not driven with meteorological data from the EKG02 site and are merely considered broadly representative of the region.

April 2019. In January–March 2021, when the measurements ended, the water table dropped to lower levels comparable with early 2020, and soil respiration was higher than December 2020 but not as high as early 2020.

In all simulations, the vegetation does not seem to be water-limited, and carbon slowly accumulates in the soil. The simulations with dynamic vegetation establish stable vegetation with 70%–80% BET trees after a few centuries (initially, shrubs are dominant). The fifth simulation starts with grass alone and still accumulates carbon in the soil. This is despite the reconstructed precipitation levels prior to 17 000 cal. yr. BP being similar to or lower than those between about 3000 and 1000 cal. yr. BP, when substantial volumes of carbon were lost (figure 2a), leading to the 'Ghost Interval' in the peat cores. Crucially, the evapotranspiration simulated by JULES-Peat was substantially lower in that early period (figure 5a) owing to the colder climate of the glacial period (figure 2b). The precipitation–evapotranspiration balance (figure 5b) was therefore such that the soil could remain at a relatively high level of saturation (figure 5g), allowing peat to accumulate. Considerable variations in the net precipitation (figure 5b) are inferred from the empirical data, with a particularly strong reduction between 3000 and 1000 BP. These variations are also seen in the fraction of saturated soil and the net increase (annual accumulation) in soil carbon. Saturation is lowest between 3000 and 1000 BP, and there is peat loss during this period.

(i) Original JULES-Peat scheme

The end of the simulation with the original scheme [13] agrees with the observed seasonality in water table depth in 2020 and 2021, but not in 2019, which did not see a lower water table in March and April (figure 4c). It also agrees with soil respiration, within the uncertainty ranges (figure 4d). Peatland development begins early in the simulation, with both soil carbon (figure 5j) and ground level (figure 5i) building up from the outset. The simulated litter agrees well with that measured in the litter traps (figure 4b). However, the long-term build-up of soil carbon and ground level does not reach present-day levels, nor is there a substantial loss during recent millennia as would be needed for consistency with the Ghost Interval. This suggests that the scheme [13] is not responsive enough in a tropical peatland, either for peat accumulation or loss.

(ii) Effects of shallower rooting depths and increased proportion of litter near the soil surface

The end of the R_d simulation simulates a smaller increase in water table depth in January–April and slightly larger increases in soil respiration in February and March. However, both are still within the ranges of the field measurements. Over the full simulation, R_d simulates higher rates of both NPP (figure 5d) and soil respiration (figure 5f) in the early part of the simulation, with net carbon accumulation being close to that in the scheme until around 10 000–9000 years ago when the net accumulation becomes higher in the R_d simulation, resulting in a larger build-up of soil carbon in the second half of the simulation [13]. Although this results in more soil carbon at the end of the simulation, there is still only a slight response to the drying climate in recent millennia, with relatively little loss of carbon in the Ghost Interval.

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

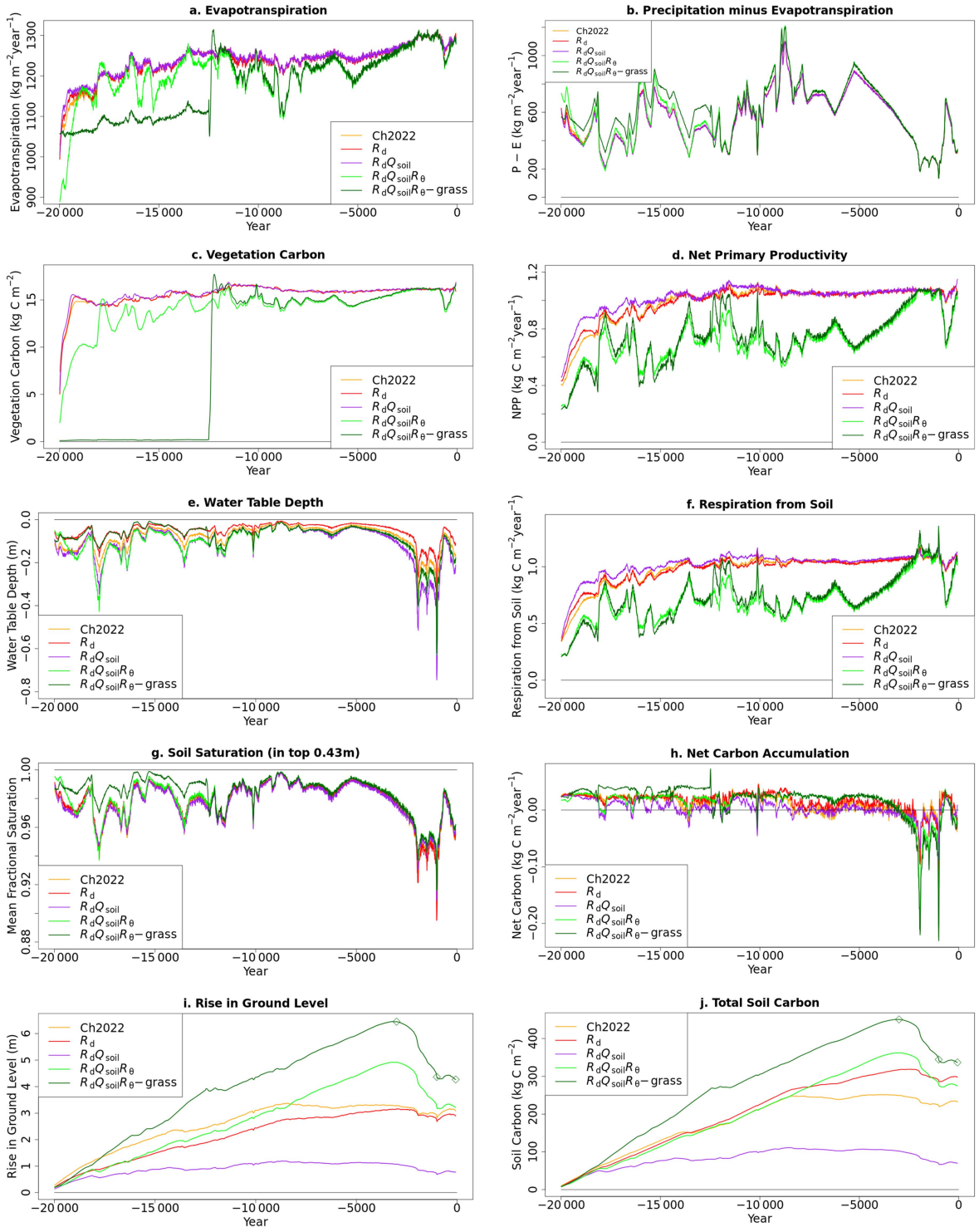


Figure 5. Evolution of the central Congo Basin peatlands in the five simulations, the variants of the JULES-Peat model (table 1): (a) evapotranspiration, (b) precipitation − evapotranspiration ($P - E$), (c) carbon in vegetation, (d) net primary productivity, (e) water table depth, (f) respiration from soil, (g) fractional soil saturation (top 0.43 m), (h) net annual increase in soil carbon, (i) rise in the ground level and (j) total carbon in the soil. The diamonds in the top traces of (i) and (j) mark 3000 BP (when there was the greatest depth of peat), 1000 BP (following the large loss of peat) and the end of the simulation, and the profiles from these times are shown in figure 6.

(iii) Effects of changes in the ratio of decomposable to recalcitrant litter

Compared with field measurements, the end of the R_dQ_{soil} simulation shows a much larger increase in water table depth in January–April. The increases in soil respiration are larger in January and February than in R_d, but still comparable with field measurements. These changes are reflected throughout the simulation, with a deeper water table, generally drier soil and further increases in soil respiration compared with R_d from the start of the simulation. R_dQ_{soil} also shows further increases in NPP, but the net impact of the NPP and soil respiration changes was lower rates of net carbon accumulation, resulting in a much slower build-up of soil carbon and ground level.

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

Table 3. Simulated changes in soil saturation, net carbon fluxes, carbon stock and ground level in the initial, intermediate and final periods of the JULES-Peat simulations.

	years	Ch2022	R_d	R_dQ_{soil}	$R_dQ_{soil}R_\theta$	$R_dQ_{soil}R_\theta$-grass
mean fractional saturation in soil (in top 0.43 m)	20 000–10 000 BP	0.977	0.978	0.976	0.980	0.987
	10 000–3000 BP	0.988	0.989	0.987	0.990	0.990
	3000–1000 BP	0.955	0.955	0.957	0.960	0.960
mean net carbon accumulation (g C m^{-2} $year^{-1}$)	20 000-10 000 BP	20.5	22.1	9.3	20.6	30.0
	10 000–3000 BP	5.3	14.5	0.5	21.9	22.0
	3000–1000 BP	−14.5	−15.5	−17.1	−42.2	−53.4
total carbon in soil (kg C m^{-2})	10 000 BP	214	226	100	213	305
	3000 BP	249	318	102	362	450
	1000 BP	221	288	68	278	344
	reduction between 3000 and 1000 BP	11%	9%	33%	23%	24%
	present	232	298	70	275	337
ground level (m)	10 000 BP	3.10	2.44	1.09	2.88	4.35
	3000 BP	3.28	3.15	1.07	4.92	6.45
	1000 BP	2.85	2.70	0.69	3.21	4.36
	reduction between 3000 and 1000 BP	13%	14%	36%	35%	32%
	present	3.09	2.90	0.78	3.22	4.27

(iv) Effects of changes in the soil moisture–respiration relationship

In the $R_dQ_{soil}R_\theta$ simulation, the seasonal increase in water table depth in January–April returns to agreement with the field measurements and is largely unchanged in the rest of the year compared to previous simulations. The seasonal increase in soil respiration in January–March is larger in this latest simulation and agrees with the field measurements for 2020. From May onwards, simulated soil respiration is lower than in the previous simulations and also lower than in the EKG-02 measurements. However, we note that the measurements will include root respiration, whereas the model variable examined here is just heterotrophic respiration from the soil.

Feedback within JULES-Peat may also be involved here, with the increased peat decay early in the year releasing more nitrogen that boosts vegetation growth, then reduced peat decay later in the year that means less available nitrogen for growth. Over the full simulation, vegetation cover, soil respiration, NPP, evapotranspiration and water table depth are all much more sensitive to changes in precipitation, with much higher millennial-scale variability. Vegetation cover is also lower, as indicated by lower vegetation carbon (figure 5c). Vegetation seems to be strongly influenced by the feedback within JULES-Peat that involves the nitrogen cycle, as accumulating peat locks away nitrogen while decaying peat releases nitrogen for vegetation to use. Net carbon accumulation is similar to that in the original scheme until around 8000 cal. yr. BP [13], after which the accumulation remained at higher rates until around 3000 cal. yr. BP when all simulations show accumulation becoming negative. After that, net carbon accumulation is more negative in $R_dQ_{soil}R_\theta$, that is: a faster loss of carbon, leading to a substantial decrease in total carbon content and ground level. The total carbon stock therefore reaches a greater peak amount and then has a much greater loss owing to the stronger dependence of soil respiration on soil moisture. The relationship between soil saturation and respiration therefore appears key to the simulation of the long-term evolution of the CCB peatlands, including the substantial loss of carbon in the Ghost Interval. However, the present-day soil carbon and the increase in ground level remain lower than the measured values.

(b) Role of vegetation history in peatland evolution

In $R_dQ_{soil}R_\theta$-grass, evapotranspiration is similar to $R_dQ_{soil}R_\theta$ at the end of the simulation but substantially lower in the period when vegetation cover was forced to be grass until 12 500 cal. yr. BP. This results in higher levels of near-surface soil saturation and a shallower water table, leading to higher net carbon accumulation rates. After that, carbon accumulation returns to similar

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

rates to the previous simulation, with the result that the overall build-up of soil carbon and ground level by 3000 cal. yr. BP was the highest of all simulations. The subsequent loss of soil carbon and changes in ground level follow that of the previous simulation, and the final values are close to those measured at the present-day.

In the $R_d Q_{soil} R_\theta$-grass simulation, evapotranspiration is much smaller during the first 7500 years when vegetation cover is a grass-only, leading to wetter soil, shown by the larger values of $P - E$ (figure 5b) and soil saturation, a shallower water table and reduced microbial respiration in the soil. Hence, there is a much stronger build-up of carbon during this time, as shown by the higher values of net carbon (annual accumulation). This simulation has the greatest peak amount of carbon and the greatest loss near the end, shown in the ground level and total soil carbon stock.

(c) Sensitivity to uncertainty in the palaeoclimate reconstruction

Since the modern isotope values for the rainfall reconstruction were taken from data at Bengui rather than the site of the CEN-17.4 core, it is important to test the sensitivity of the results to possible differences in isotope ratios. Two further reconstructions of the palaeo annual precipitation had been made using the CEN-17.4 core data to reconstruct past variability, but using modern precipitation isotope values (D/H) from two other locations (Kisangani and Kinshasa), which, like Bengui, are several hundred kilometres from the CEN-17.4 site but to the east and south, respectively [16]. We carried out further JULES-Peat simulations with the $R_d Q_{soil} R_\theta$-grass set-up and the two new precipitation reconstructions. Figure S4 in the supplementary material shows that the results from these three new simulations are very similar to those of the original $R_d Q_{soil} R_\theta$-grass simulation, all having a substantial build-up of peat followed by a substantial loss. The final carbon stocks simulated using precipitation reconstructions with the Bengui, Kisangani and Kinshasa isotope ratios are 337, 372 and 326 kg C m^{-2}, with ground levels of 4.28, 4.55 and 3.65 m, respectively. This suggests that the simulated peatland evolution is not very sensitive to the choice of source data for the isotope ratios for the precipitation reconstruction. It should be noted that this is not a full exploration of the palaeoclimate uncertainty because only one source of information on rainfall variability was available.

(d) Comparison with depth profiles of carbon content and age

Figure 6a shows the carbon concentration with soil depth from the five simulations, compared with the measured concentrations from the CEN-20 core, which is only 2.6 km from the CEN-17.4 core and has very similar total organic carbon [16,17]. The final simulation has an acceptable mean concentration; the carbon concentrations obtained from the other simulations are shown to be too small, but the profiles are too smooth owing to the coarse vertical resolution of JULES-Peat. Figure 6b shows how the profile develops during the final simulation (which has the greatest amount of carbon), results at 3000 BP (greatest depth of peat), at 1000 BP (following a large loss of peat) and at the end of the simulation (the times marked by diamonds on figure 5i,j).

Figure 6c shows the age–depth profiles from the five simulations, alongside the empirical age–depth model based on radiocarbon dating of the CEN-17.4 core [17]. The model updates with the new soil moisture–respiration function show greater bulk at all depths, consistent with more carbon having accumulated over time. However, JULES-Peat does not capture the observed shape of the age–depth profile, presumably as a result of the method of interpolating changes in carbon content across existing soil layers. Figure 6d shows the development of the profile in the final simulation, where carbon ages increase between 3000 and 1000 BP as peat is lost and the profile is compressed.

4. Discussion

In this first attempt to use JULES-Peat to simulate tropical peatlands, the step-by-step comparison of the successive model updates with field observations and inferences from peat core records reveal the importance of the various processes in simulating peatland evolution in a way that is consistent with data and previous understanding. The simulated accumulation of soil carbon before 3000 BP followed by the significant loss of carbon during the long period of reduced precipitation between 3000 and 1000 BP is the dominant characteristic of the final simulation. It is consistent with previous conclusions that the 'Ghost Interval' feature of CEN-17.4 and other peat cores was a result of secondary decomposition (loss of previously accumulated peat) as opposed to a reduced build-up of peat.

To further assess whether the updated version of JULES-Peat represents tropical peatland evolution in ways consistent with current understanding, it can be compared with the results of the specialist peatland model, DigiBog [6,19]. This provides a representation of the same system using a different approach, again in one dimension at a single point in the peat dome. Not being constrained by the need to work within the existing framework of a general LSM, DigiBog simulates the build-up of peat layer-by-layer in a way that is more directly analogous to the real-world process than the approach required in JULES-Peat, and is able to generate a very large number of layers in the soil. It is therefore more suitable for direct comparison with profiles of carbon content and age derived from peat cores. The variant of DigiBog established for this region, DigiBog_Congo, has previously been used to simulate the peatland evolution in the CCB with a similar experimental design to that used here with JULES-Peat [19]. DigiBog_Congo was driven with monthly mean precipitation from the combination of annual precipitation reconstructed from the CEN17.4 peat core and seasonal cycle from the HadCM3 climate model, along with temperatures from HadCM3 and potential evapotranspiration (PET) calculated with the Penman–Monteith method [43] using temperature, humidity, wind speed and net radiation from HadCM3.

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

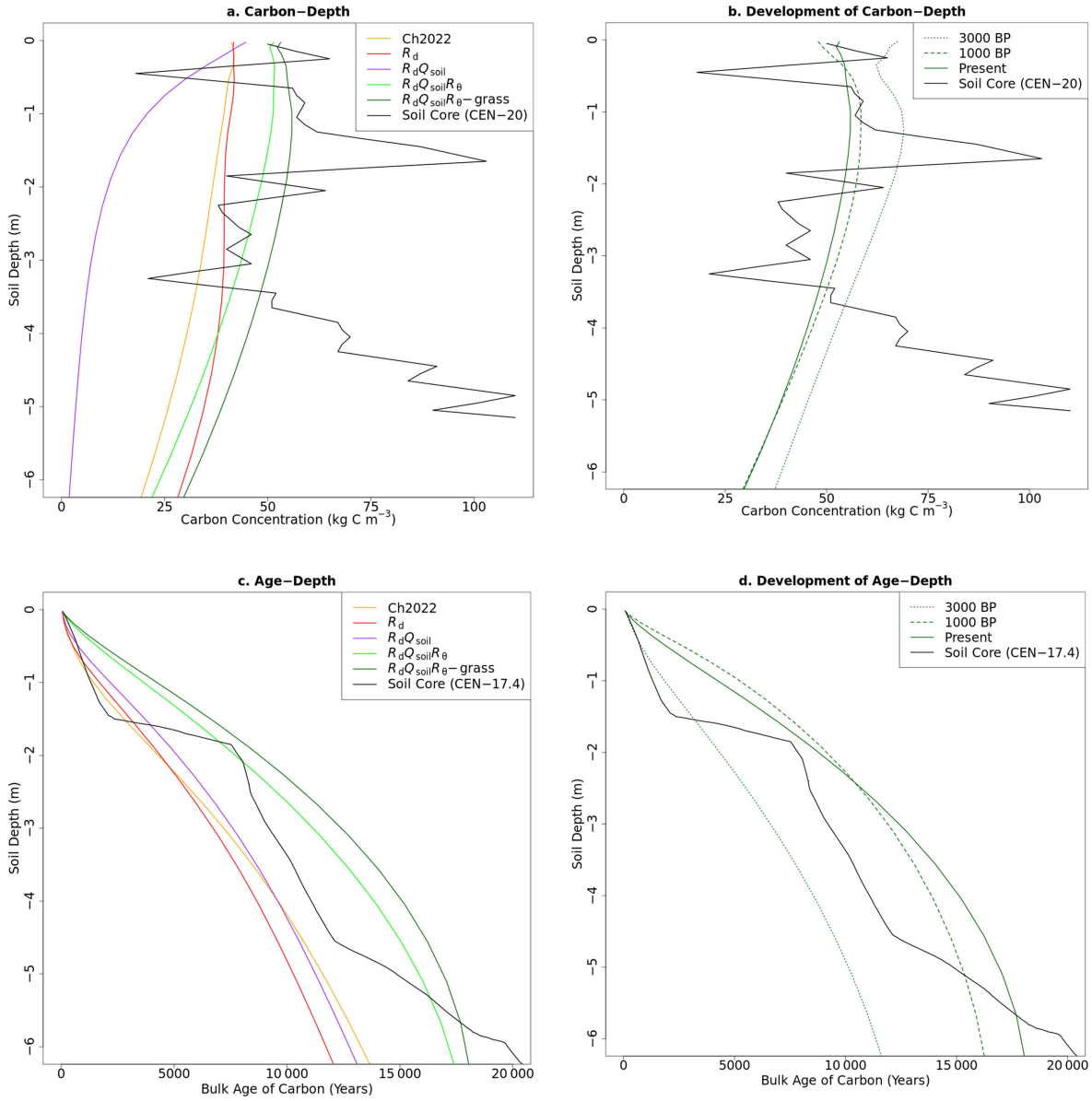


Figure 6. (a) Carbon concentration profiles from JULES-Peat at the end of all five simulations compared with the measurements obtained from the CEN-20 core; (b) carbon concentration profiles at 3000 BP (greatest depth of peat), 1000 BP (following large loss of peat) and the end of the final simulation (times marked by diamonds on figure 5i,j) compared with CEN-20; (c) carbon bulk age profiles from JULES-Peat at the end of all five simulations, with radiocarbon dates obtained from the CEN-17.4 core; (d) development of the carbon bulk age profile in the final simulation with CEN-17.4.

Figure 7 shows the results from DigiBog_Congo compared with our $R_dQ_{soil}R_\theta$-grass simulation and the observed age–depth profile from the CEN-17.4 core. The general profiles of net carbon accumulation/loss and changes in ground level are qualitatively similar in shape in the two models. However, DigiBog_Congo appears to be more sensitive than JULES-Peat to the environmental changes. Prior to approximately 7000 BP, DigiBog simulated higher net carbon accumulation than JULES-Peat, but with periods of smaller accumulation or even net loss (figure 7a). Moreover, in DigiBog_Congo, the net carbon accumulation starts to decline at approximately 5000 BP and soon becomes a net loss, closely following the decline in reconstructed precipitation. In JULES-Peat, this does not occur until precipitation becomes much lower. Consequently, DigiBog_Congo simulates a faster and larger rise in ground level than JULES-Peat, then simulates a much larger decline in ground level that also began earlier than in JULES-Peat (figure 7b). In DigiBog_Congo, ground level rises by over 12 m and then reduces to less than 6 m above the initial state—a reduction in peat thickness of about 55% (figure 7b). In JULES-Peat, the rise in the ground level as peat accumulates is less than the total peat depth because the soil composition is changed as carbon is mixed down into it.

DigiBog_Congo broadly recreates the observed age–depth profile, showing the substantial discontinuity of the 'Ghost Interval' period owing to loss of previously accumulated peat during the extended drought period. Although JULES-Peat is not able to reproduce this feature of the age–depth curve owing to the model formulation requiring interpolation of soil between existing soil layers, the qualitative agreement in periods of soil carbon accumulation and loss with DigiBog_Congo suggests that those patterns in JULES-Peat are also consistent with the evidence from the peat core.

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

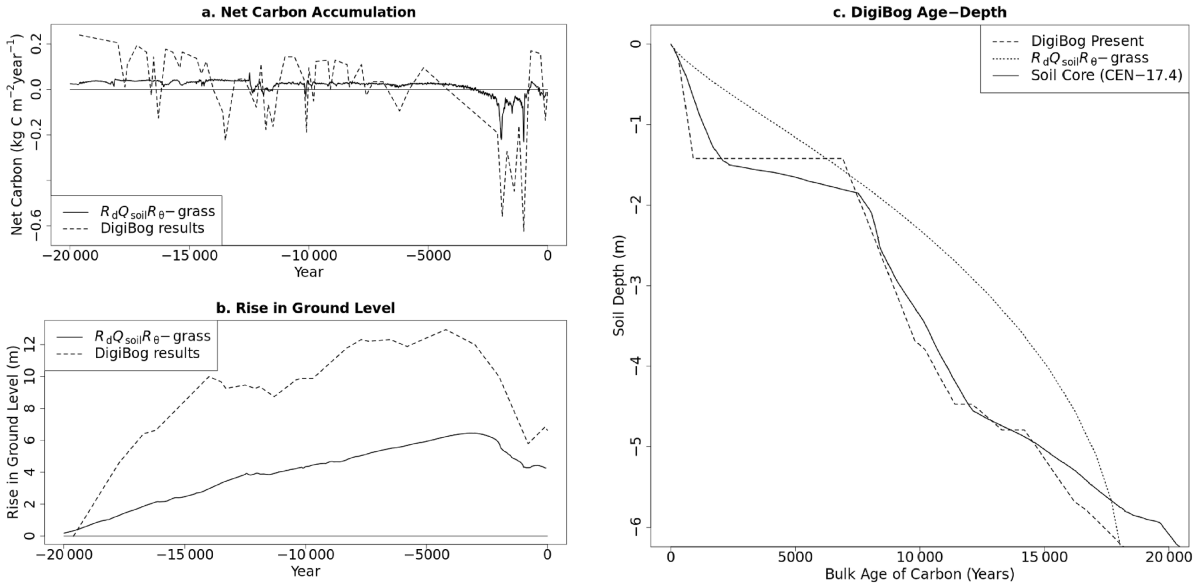


Figure 7. Comparing the results from the final JULES-Peat simulation to DigiBog: (a) net carbon accumulation, (b) rise in ground level and (c) age–depth profiles compared with the CEN-17.4 core.

Although DigiBog_Congo is more suitable for comparing against the peat core records owing to its design, and hence it can be assessed against a wider range of data with more confidence than JULES-Peat, the additional processes included in the wider JULES model can provide further insight into wider environmental processes that may be relevant to developing further understanding of peatland evolution. Here, we briefly discuss some of these as a motivation for future lines of research.

A key difference between DigiBog_Congo and JULES-Peat is that the former takes prescribed values of litter as an input, whereas the latter simulates the vegetation process as an integral part of the simulation. Vegetation grows during the drier periods, as shown by the resulting evapotranspiration and net primary productivity. This is in response to variations in the shortwave radiation, which mirror the variations in precipitation, since with less precipitation, there is less cloud and more shortwave radiation. In the CCB, precipitation is always enough for photosynthesis to be radiation-limited rather than water-limited. However, soil carbon accumulates during the wetter periods with greater soil saturation and less microbial respiration, as shown by the net carbon increase.

Responses to changes in the climate have been amplified by the changes made here to JULES-Peat. The change in the composition of the litter from 80% to 40% recalcitrant material, based on field measurements, resulted in faster responses of the soil carbon to drier conditions, although on its own, this change leads to greater losses of carbon and less peat accumulation overall. However, combined with the change in the response of microbial respiration to soil saturation, it reduces the loss of carbon from fully saturated soil and leads to more peat accumulation overall.

These changes in the litter composition and the response of respiration in the soil to saturation also influence the vegetation by means of the feedback within JULES-Peat that involves the nitrogen cycle. Accumulating peat locks away nitrogen and so limits growth, while decaying peat releases nitrogen for vegetation to use.

Perhaps counterintuitively, the periods with the greatest vegetation growth and litterfall see losses of peat, whereas peat accumulates when there is the least growth and litter. Although more litter is added to the soil during the dry periods with greater shortwave radiation and more available nitrogen for the vegetation, the loss of carbon owing to respiration in the drier soil is as great as or greater than the gain from the litter. Conversely, less litter is added during the wet periods with less shortwave radiation and less available nitrogen, but carbon builds up as respiration in the wetter soil is even less than the added litter.

We also found the nature of the vegetation cover in the CCB to be an important factor in the simulated development of the peatlands. In simulations beginning with grassland before forest had been allowed to develop later, the soil is wetter owing to lower rates of evaporation, so more carbon accumulates and the resulting peat layer remains substantially thicker at the end of the simulations.

Given the challenges of comparing JULES-Peat with carbon and age profiles from peat cores, and accurately quantifying the simulated peat depth, it is worth reflecting on whether improvements can be made within the constraints of JULES being a global LSM representing multiple ecosystems and needing to interact with an atmosphere model. The key difference with DigiBog appears to be the number of soil layers (there are many more in DigiBog) and the method for introducing new litter input. Although using exactly the same approach as DigiBog in adding a new layer every year would be impractical in JULES, it would be valuable to explore alternative methods to add litter preferentially near the surface while retaining the physical soil layer structure for thermal and hydrological processes.

There are several valuable next steps and future directions for the ongoing development of JULES-Peat in tropical peatlands. For example, while we have used as many relevant sources of data as are available at present, there is clearly a need for additional data to provide additional constraints. In particular, the absence of long-term CO_2 or CH_4 flux data limits the ability to evaluate

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

carbon-balance dynamics and seasonal variability comprehensively. As well as aiming to establish further measurement activities in the region, it would be worth exploring the potential for incorporating multi-source or longer-term datasets from other regions, if appropriate.

The sensitivity to additional sources of uncertainty in the palaeoclimate reconstructions also needs further investigation. As noted in §3c, so far we have only been able to explore the sensitivity to the isotope ratios used in the rainfall reconstruction, and have been limited to information on the past rainfall variability from a single peat core. Information from other cores would be extremely valuable. Moreover, we have only been able to use one palaeoclimate model simulation, so alternative simulations with other models would also be valuable.

There are also important next steps in the modelling. Our step-by-step method does not isolate the independent contribution of each process, and we recognize that alternative sequences of steps may yield different outcomes owing to path dependency. Some changes may simply be compensating for biases introduced in previous iterations. Furthermore, parameter uncertainty and the robustness of internal feedback processes have yet to be explored. Although we have demonstrated that it is possible to create a version of JULES-Peat that successfully reproduces the peatland evolution as it is currently understood, further work is needed to establish the level of confidence that can be assigned to this.

A further process in the CCB peatlands that has not yet been explored is the role of fluvial flooding. This work has focussed only on a rain-fed system in a specific region. Inundation processes in peatlands will be a further focus of future work. More generally, the performance of JULES-Peat also needs to be investigated in comparison with data from other locations in the wider region, and indeed in other tropical peatland areas globally.

5. Conclusions

This is the first time that JULES-Peat has been tested in a tropical environment. Our results suggest that the previous version of JULES-Peat, developed for temperature and cold region peatlands, was not sufficiently sensitive to soil moisture availability to simulate a forested tropical peatland accurately. It required further development to reproduce the empirical pattern of peat accumulation in the CCB, such that peat accumulation responds strongly to climatic change, accumulating under wetter climatic conditions and being lost under drier conditions. The principal modifications required consisted of a change in the composition of the vegetation litter and a new curve linking microbial respiration in the soil to the soil saturation.

Simulating a tropical peat swamp site with JULES-Peat provides an opportunity to test its performance in conditions outside of its original design scope. We adapted the model to improve its performance in this tropical environment. This modified version of JULES-Peat successfully recreates a substantial loss of peat during the mid- to late Holocene. This is a further step towards a generic peatland scheme that can be meaningfully applied in a global configuration of JULES for use in large-scale carbon budget calculations and climate impact assessments and potential inclusion in a future ESM.

The most important update for enabling JULES-Peat to recreate the expected evolution of the CCB peatlands was to the relationship between soil moisture and respiration. Although it was not possible to constrain this directly with observations, and the final chosen form was arrived at on the basis of the model's ability to represent peatland evolution suggested by other evidence, this nevertheless demonstrates that the existing JULES-Peat scheme can be modified to give an acceptable performance in tropical peatlands through changes that are within uncertainty ranges in the literature. This is encouraging in that it suggests a globally applicable version of JULES-Peat may be possible. Further work is needed to develop such a robust version suitable for future projections.

Despite these large uncertainties, the qualitative conclusion that soil moisture is the most important factor determining the balance between simulating accumulation and loss of peat is in line with previous research [16,19] and it supports previous concerns that the CCB peatlands remain vulnerable to any future decrease in soil moisture. If the peatlands are to continue to function as a carbon store, they need to remain highly saturated. It is particularly important to note that early in our simulations, peat began to accumulate even when precipitation was relatively low, because evapotranspiration was also low in the cooler climate of the glacial period; when the reconstructed precipitation returned to low levels in a warmer climate with higher rates of evapotranspiration, the reduction in soil moisture was greater, leading to a loss of peat instead of an accumulation. Hence, reduced precipitation and/or increased evapotranspiration owing to future climate change could result in peat loss.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All figure panels (.pdf or .png format) plus the NetCDF data files and R-script programmes used to make them can be downloaded from: [44]. The code for JULES-Peat is available from the Met Office web pages at: https://code.metoffice.gov.uk/trac/jules/browser/main/branches/dev/eleanorburke/vn6.2_accumulate_soil.

Supplementary material is available online [45].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. P.A.C.: data curation, formal analysis, investigation, software, writing—original draft, writing—review and editing; R.B.: supervision, writing—review and editing; E.J.B.: data curation, resources, software, supervision; S.C.: software; G.C.D.: conceptualization, methodology, project administration, resources; B.C.: methodology, resources; D.H.: methodology, resources; Y.G.: methodology, resources; E.S.: methodology, resources; S.I.: resources; N.G.: resources; M.M.: resources; Y.E.W.M.: resources; D.E.C.: resources; D.M.Y.: software; P.M.: software; I.T.L.: methodology, resources; S.L.L.: conceptualization, funding acquisition, project administration, resources.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

Funding. The CongoPeat project was funded by the Natural Environment Research Council of the UK, grant number NE/R016860/1 CongoPeat, to S.L.L. The CEN-17.4 and CEN-20 cores were collected using funding from a NERC Open CASE studentship to G.C.D., S.L.L., I.T.L. and Susan E. Page, and a Philip Leverhulme Prize to S.L.L. E.J.B. was supported by the Met Office Hadley Centre Climate Programme funded by the Department for Science, Innovation and Technology. We also acknowledge support from Agence Nationale de la Recherche (ANR) grant ANR-19-CE01-0022 to Y.G. and Deutsche Forschungsgemeinschaft (DFG) grant SCHE903/19-1 to E.S.

Acknowledgements. We thank Corneille Ewango and his team at the University of Kisangani in the Democratic Republic of the Congo, and the communities who facilitated our research in the central Congo Basin, especially in the villages of Ekolongouma and Itanga. We thank the National Civil Aviation Agency (ANAC) of the Congo for providing weather station measurements and the Ministry of Environment in the Republic of the Congo for assistance. We also thank Paul Valdes and his team at the University of Bristol School of Geographical Sciences for providing the palaeometeorological simulation outputs, and George Burningham and Dean Jones for design work on supplementary material, figure S1.

References

1. Loisel J *et al.* 2021 Expert assessment of future vulnerability of the global peatland carbon sink. *Nat. Clim. Change* **11**, 70–77. (doi:10.1038/s41558-020-00944-0)
2. Arora VK *et al.* 2020 Carbon–concentration and carbon–climate feedbacks in CMIP6 models and their comparison to CMIP5 models. *Biogeosciences* **17**, 4173–4222. (doi:10.5194/bg-17-4173-2020)
3. Bechtold M *et al.* 2019 PEAT-CLSM: a specific treatment of peatland hydrology in the NASA Catchment Land Surface Model. *J. Adv. Model. Earth Syst.* **11**, 2130–2162. (doi:10.1029/2018MS001574)
4. Müller J, Joos F. 2020 Global peatland area and carbon dynamics from the Last Glacial Maximum to the present—a process-based model investigation. *Biogeosciences* **17**, 5285–5308. (doi:10.5194/bg-17-5285-2020)
5. Qiu C *et al.* 2018 ORCHIDEEPEAT (revision 4596), a model for northern peatland CO_2, water, and energy fluxes on daily to annual scales. *Geosci. Model. Dev.* **11**, 497–519. (doi:10.5194/gmd-11-497-2018)
6. Baird AJ, Morris PJ, Belyea LR. 2012 The DigiBog peatland development model 1: rationale, conceptual model, and hydrological basis. *Ecohydrology* **5**, 242–255. (doi:10.1002/eco.230)
7. Frolking S, Roulet NT, Tuittila E, Bubier JL, Quillet A, Talbot J, Richard PJH. 2010 A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation. *Earth Syst. Dyn.* **1**, 1–21. (doi:10.5194/esd-1-1-2010)
8. Best MJ *et al.* 2011 The Joint UK Land Environment Simulator (JULES), model description Part 1: energy and water fluxes. *Geosci. Model. Dev.* **4**, 677–699. (doi:10.5194/gmd-4-677-2011)
9. Clark DB *et al.* 2011 The Joint UK Land Environment Simulator (JULES), model description part 2: carbon fluxes and vegetation dynamics. *Geosci. Model. Dev.* **4**, 701–722. (doi:10.5194/gmd-4-701-2011)
10. Sellar AA *et al.* 2019 UKESM1: description and evaluation of the UK Earth System Model. *J. Adv. Model. Earth Syst.* **11**, 4513–4558. (doi:10.1029/2019MS001739)
11. Mathison C *et al.* 2023 Description and evaluation of the JULES-ES set-up for ISIMIP2b. *Geosci. Model Dev.* **16**, 4249–4264. (doi:10.5194/gmd-16-4249-2023)
12. Friedlingstein P *et al*. 2026 Global carbon budget 2025. *Earth Syst. Sci. Data*. **18**, 3211–3288. (doi:10.5194/essd-18-3211-2026)
13. Chadburn SE *et al.* 2022 A new approach to simulate peat accumulation, degradation and stability in a global land surface scheme (JULES vn5.8_accumulate_soil) for northern and temperate peatlands. *Geosci. Model Dev.* **15**, 1633–1657. (doi:10.5194/gmd-15-1633-2022)
14. Crezee B *et al.* 2022 Mapping peat thickness and carbon stocks of the central Congo Basin using field data. *Nat. Geosci.* **15**, 639–644. (doi:10.1038/s41561-022-00966-7)
15. Dargie GC, Lewis SL, Lawson IT, Mitchard ETA, Page SE, Bocko YE, Ifo SA. 2017 Age, extent and carbon storage of the central Congo Basin peatland complex. *Nat. Res. Lett.* **542**, 86–90. (doi:10.1038/nature21048)
16. Garcin Y *et al*. 2022 Hydroclimatic vulnerability of peat carbon in the central Congo Basin. *Nature* **612**, 277–282. (doi:10.1038/s41586-022-05389-3)
17. Hawthorne D *et al*. 2023 Genesis and development of an interfluvial peatland in the central Congo Basin since the Late Pleistocene. *Quat. Sci. Rev.* **305**, 107992. (doi:10.1016/j.quascirev.2023.107992)
18. Young DM *et al*. 2026 Land-use change causes rapid carbon losses in Congo basin peatlands across climate scenarios, whereas the effects of climate change alone are uncertain. *Phil. Trans. R. Soc. B*. **381**, 20240486. (doi:10.1098/rstb.2024.0486)
19. Young DM *et al.* 2023 Simulating carbon accumulation and loss in the central Congo peatlands. *Global Change Biol.* **29**, 6812–6827. (doi:10.1111/gcb.16966).
20. Caretta MA *et al.* 2022 *Water*. In *Climate change 2022: impacts, adaptation and vulnerability* (eds H-O Pörtner *et al.*), pp. 551–712. Cambridge, UK and New York, NY: Cambridge University Press. (doi:10.1017/9781009325844.006)
21. Cook BI, Mankin JS, Marvel K, Williams AP, Smerdon JE, Anchukaitis KJ. 2020 Twenty-first century drought projections in the CMIP6 forcing scenarios. *Earth's Future* **8**, e2019EF001461. (doi:10.1029/2019EF001461)
22. Georgiou S *et al.* 2023 Mapping water levels across a region of the cuvette centrale peatland complex. *Remote Sens.* **15**, 3099. (doi:10.3390/rs15123099)
23. Dyer ELE, Jones DBA, Nusbaumer J, Li H, Collins O, Vettoretti G, Noone D. 2017 Congo Basin precipitation: assessing seasonality, regional interactions, and sources of moisture. *J. Geophys. Res. Atmos.* **122**, 6882–6898. (doi:10.1002/2016JD026240)
24. Davenport IJ *et al*. 2020 First evidence of peat domes in the Congo Basin using LiDAR from a fixed-wing drone. *Remote Sens.* **12**, 2196. (doi:10.3390/rs12142196)
25. Valdes PJ *et al*. 2017 The BRIDGE HadCM3 family of climate models: HadCM3@Bristol v1.0. *Geosci. Model Dev.* **10**, 3715–3743. (doi:10.5194/gmd-10-3715-2017)
26. Malhi Y *et al*. 2021 The Global Ecosystems Monitoring network: monitoring ecosystem productivity and carbon cycling across the tropics. *Biol. Conserv.* **253**, 108889. (doi:10.1016/j.biocon.2020.108889)
27. Sciumbata M. 2022 Measuring fine root production in tropical peatlands: assessing ingrowth cores and minirhizotrons in the central Congo Basin. *MSc thesis*, Vrije Universiteit, Amsterdam, The Netherlands.
28. Burke EJ, Chadburn SE, Ekici A. 2017a A vertical representation of soil carbon in the JULES land surface scheme (vn4. 3_permafrost) with a focus on permafrost regions. *Geosci. Model. Dev.* **10**, 959–975. (doi:10.5194/gmd-10-959-2017)

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026

29. Harper AB *et al.* 2016 Improved representation of plant functional types and physiology in the Joint UK Land Environment Simulator (JULES v4.2) using plant trait information. *Geosci. Model. Dev.* **9**, 2415–2440. (doi:10.5194/gmd-9-2415-2016)
30. Wiltshire AJ *et al.* 2021 JULES-CN: a coupled terrestrial carbon–nitrogen scheme (JULES vn5.1). *Geosci. Model. Dev.* **14**, 2161–2186. (doi:10.5194/gmd-14-2161-2021)
31. Burke EJ, Ekici A, Huang Y, Chadburn SE, Huntingford C, Ciais P, Friedlingstein P, Peng S, Krinner G. 2017b Quantifying uncertainties of permafrost carbon-climate feedbacks. *Biogeosciences* **14**, 3051–3066. (doi:10.5194/bg-14-3051-2017)
32. Chadburn SE, Burke EJ, Essery RLH, Boike J, Langer M, Heikenfeld M, Cox PM, Friedlingstein P. 2015b Impact of model developments on present and future simulations of permafrost in a global land-surface model. *Cryosphere* **9**, 1505–1521. (doi:10.5194/tc-9-1505-2015)
33. Comyn-Platt E *et al.* 2018 Carbon budgets for 1.5 and 2 C targets lowered by natural wetland and permafrost feedbacks. *Nat. Geosci.* **11**, 568. (doi:10.1038/s41561-018-0174-9)
34. Gedney N, Huntingford C, Comyn-Platt E, Wiltshire A. 2019 Significant feedbacks of wetland methane release on climate change and the causes of their uncertainty. *Environ. Res. Lett.* **14**, 084027. (doi:10.1088/1748-9326/ab2726)
35. Gedney N, Rudorff C, Betts RA. 2024 Future Amazon Basin wetland hydrology under projected climate change. *PLoS Water* **3**, e0000225. (doi:10.1371/journal.pwat.0000225)
36. Yan Z, Bond-Lamberty B, Todd-Brown KE, Bailey VL, Li S, Liu C, Liu C. 2018 A moisture function of soil heterotrophic respiration that incorporates microscale processes. *Nat. Commun.* **9**, 2562. (doi:10.1038/s41467-018-04971-6)
37. Schuur EAD *et al.* 2015 Climate change and the permafrost carbon feedback. *Nature* **520**, 171–179. (doi:10.1038/nature14338)
38. Sierra CA, Trumbore SE, Davidson EA, Vicca S, Janssens I. 2015 Sensitivity of decomposition rates of soil organic matter with respect to simultaneous changes in temperature and moisture. *J. Adv. Model. Earth Syst.* **7**, 335–356. (doi:10.1002/2014MS000358)
39. Sciumbata M *et al*. 2023 First estimates of fine root production in tropical peat swamp and terra firme forests of the central Congo Basin. *Nat. Sci. Rep.* **13**, 12315. (doi:10.1038/s41598-023-38409-x)
40. Erb MP, McKay NP, Steiger N, Dee S, Hancock C, Ivanovic RF, Gregoire LJ, Valdes P. 2022 Reconstructing Holocene temperatures in time and space using paleoclimate data assimilation. *Clim. Past* **18**, 2599–2629 (doi:10.5194/cp-18-2599-2022)
41. Hancock CL, McKay NP, Erb MP, Kaufman DS, Routson CR, Ivanovic RF, Gregoire LJ, Valdes P. 2023 Global synthesis of regional Holocene hydroclimate variability using proxy and model data. *Paleoceanogr. Paleoclimatol.* **38**, e2022PA004597. (doi:10.1029/2022PA004597)
42. Ivanovic RF, Gregoire LJ, Kageyama M, Roche DM, Valdes PJ, Burke A, Drummond R, Peltier WR, Tarasov L. 2016 Transient climate simulations of the deglaciation 21-9 thousand years before present (version 1)-PMIP4 core experiment design and boundary conditions. *Geosci. Model. Dev.* **9**, 2563–2587. (doi:10.5194/gmd-9-2563-2016)
43. Allen RG, Pereira LS, Raes D, Smith M. 1998 *Crop evapotranspiration—guidelines for computing crop water requirements*. Report no. 56. Rome, Italy: FAO.
44. Cook PA 2026 CongoPeat JULES Paleo [Dataset].Zenodo (doi:10.10.5281/zenodo.21378123)
45. Cook P *et al.* 2026 Supplementary material from: Improving the representation of tropical peatland processes in the JULES land surface model using data from the central Congo Basin. Figshare. (doi:10.6084/m9.figshare.c.8558051)

Downloaded from royalsocietypublishing.org/rstb/article-pdf/doi/10.1098/rstb.2024.0487/6159419/rstb.2024.0487.pdf
by guest
on 06 October 2026