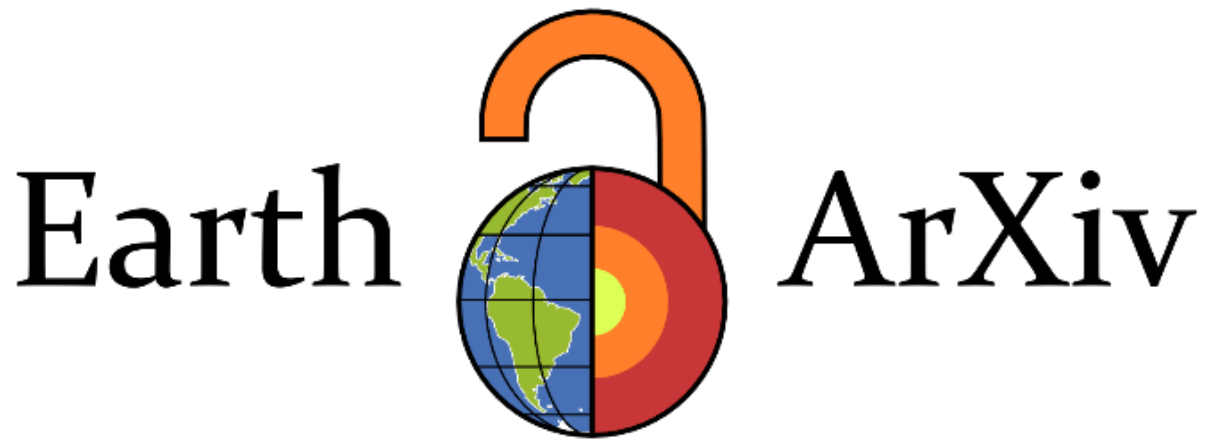




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State-Dependent Biophysical Processes Prevented a Late Paleozoic Snowball Earth

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Abstract

Terrestrial vegetation modulates Earth's climate through two distinct pathways—biogeochemically drawing down CO₂ through enhanced organic carbon burial [1, 2] and silicate weathering [3, 4], and biophysically altering surface energy and water balances through potentially competing albedo and evapotranspiration changes [5, 6]. Although the biogeochemical pathway is widely invoked to explain the Late Paleozoic Ice Age (LPIA, ~370–260 Ma) [7–10], the role of biophysical processes remains poorly constrained. Here we show that the net biophysical effect of vegetation over the last 380 million years has been a strongly state-dependent warming: modest under greenhouse conditions but dramatically amplified as temperature declines. During the LPIA, an absence of these biophysical processes would have caused up to 19 °C of additional cooling, pushing global mean temperature below 0 °C and driving sea ice equatorward of 30° latitude, crossing the critical threshold for initiation of a Snowball Earth episode.

Our findings reveal and resolve a stabilising paradox: while vegetation expansion biogeochemically drove Earth into an icehouse through CO₂ drawdown, its biophysical presence prevented a collapse into Snowball Earth, thereby regulating the climate system over long timescales and maintaining Earth’s habitability.

Keywords: Biophysical processes, State-dependence, Late Paleozoic Ice Age, Snowball Earth

Introduction

Terrestrial vegetation fundamentally influences Earth’s climate on multiple timescales through modulating energy, moisture, and biogeochemical fluxes [5, 6]. In particular, the evolution of land plants has impacted global temperatures over geological timescales [11–13] through two distinct pathways—biogeochemical and biophysical. Previous work has primarily focused on the biogeochemical pathway, whereby land plants enhance both silicate weathering [3, 4, 14, 15] and organic carbon burial [1, 2], thereby drawing down atmospheric CO₂ ($p\text{CO}_2$), and inducing long-term cooling. In contrast, the biophysical pathway operates on much shorter timescales, providing a direct feedback on surface radiation and hydrological budgets. As land plants evolved, these rapid biophysical responses substantially impacted temperature by modifying surface energy balance through altered albedo and cloud cover [16–19], and by modifying surface hydrological balance through altered aerodynamic roughness and evapotranspiration [20–22]. Biophysical effects can either warm or cool regional climates depending on the background climate state (related, for example, to latitude, altitude, and continentality) and ecosystem type; for example, boreal forests warm by masking highly reflective snow [5, 23, 24], while tropical forests cool through enhanced evapotranspiration [5, 25]. Recent work highlights that biophysical effects can be large enough to outweigh biogeochemical effects in specific contexts [19, 26]. Therefore, the net climatic impact of vegetation emerges from the balance between these two

pathways—a balance that is neither globally homogeneous nor constant over time,
and may itself vary with the background climate.

Despite decades of work quantifying vegetation–climate feedbacks in modern and
near-future contexts [e.g. 27, 28], a critical gap persists: we still lack a systematic
understanding of how the strength of vegetation processes, particularly the biophys-
ical component, varies across fundamentally different climate regimes over geological
time. Earth has oscillated between greenhouse and icehouse states throughout the
Phanerozoic [29, 30], and climate sensitivity itself is strongly state-dependent [31–35].
This implies the possibility that biophysical vegetation processes may exhibit similar
climate state dependence, a nonlinearity already observed in future climate mitigation
projections [36]. Yet paleoclimate studies of vegetation–climate interactions typically
target isolated time slices, limiting our ability to assess how biophysical processes
respond to changing climate state [e.g. 37–39]. If these biophysical feedbacks intensify
under cold conditions—driven, for instance, by the stark albedo contrast between dark
forest canopies and highly reflective snow cover— they could represent an unrecognised
stabilising—or destabilising—mechanism during icehouse intervals.

The Late Paleozoic Ice Age (LPIA; ~ 370 – 260 Ma) offers a stringent test of state-
dependent vegetation feedbacks. It was the most severe and prolonged icehouse of the
last half-billion years [7, 8], with expansive ice sheets across southern Gondwana and
possible low-latitude glaciation [40]. Although recent work has highlighted the role
of continental exposure [41], the conventional narrative attributes LPIA cooling pri-
marily to the biogeochemical effects of land plants: the Devonian–Carboniferous rise
of deeply rooted vegetation enhanced silicate weathering [3, 42, 43], while widespread
coal-forming forests promoted exceptional organic carbon burial [10, 44]—reaching
global rates of up to $\sim 6.5 \times 10^{18}$ mol Myr $^{-1}$, the highest of the Phanerozoic [45].
Together, these processes drove $p\text{CO}_2$ downward to among the lowest levels of the
Phanerozoic [7, 9], with proxy reconstructions indicating minima near $\sim 200 \pm 100$ ppm

139 during peak glaciation at ~ 298 Ma [46–48]. High-resolution boron isotope records fur-
 140 ther confirm that CO_2 was maintained at $\sim 330 \pm 210$ ppm throughout the LPIA,
 141 with a rapid fourfold increase at ~ 294 Ma marking its termination [46]. Model sim-
 142 ulations suggest that under late Carboniferous–Early Permian boundary conditions,
 143 such low CO_2 brought the climate system close to a runaway ice–albedo instability
 144 [1]. Yet no Snowball Earth occurred during the Phanerozoic [49]. Although changes
 145 in CO_2 degassing played a potential role [50], what prevented the LPIA from tipping
 146 into global glaciation remains an unresolved question.

152 Here we address this paradox using 77 continuous time-slice simulations spanning
 153 the past 382 Myr with the HadCM3L coupled atmosphere–ocean model. For each
 154 time slice, we perform a pair of simulations, one with dynamic vegetation enabled
 155 and one with vegetation removed, to isolate the net biophysical effect of terrestrial
 156 vegetation across the full range of background climate states (see Methods). This
 157 parallel ensemble approach allows us to quantify how the net biophysical effect of
 158 vegetation varies with background climate state, and to test the hypothesis that state-
 159 dependent biophysical feedbacks could have prevented a Snowball Earth during the
 160 LPIA.

168 Results and Discussion

171 Biophysical process-loss triggers near-Snowball

174 Our baseline simulations (Fig. 1, red dashed line; ensemble $ENS_{p\text{CO}_2\text{-tuned}}$; see Meth-
 175 ods) are consistent with proxy-inferred global mean surface temperature (GMST)
 176 evolution through the last 382 million years [29], including the standard LPIA cooling
 177 trajectory. However, removing the biophysical effects of vegetation (while maintaining
 178 the weathering impacts of vegetation through identical prescribed $p\text{CO}_2$) consistently
 179 causes substantial cooling (7.3 ± 3.1 °C, mean $\pm$ standard deviation; Fig. 1, black line).
 180 The simulations suggest that the late Paleozoic Earth system lies close to the threshold

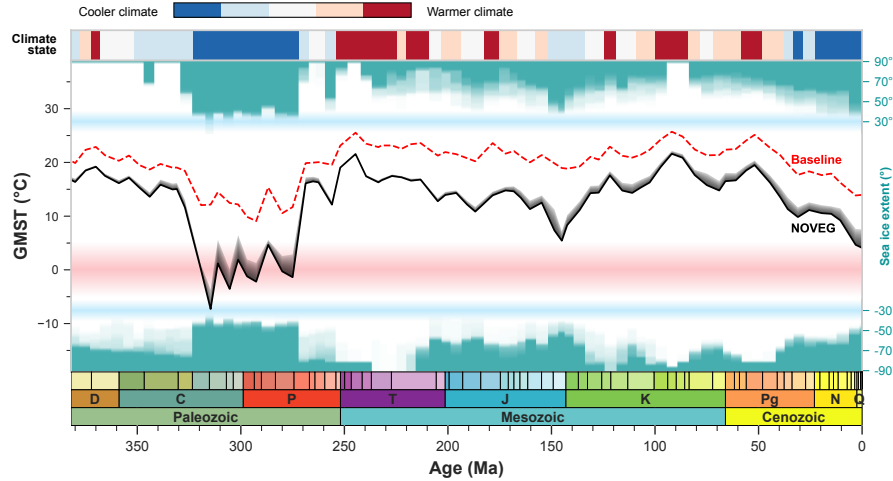


Fig. 1 Phanerozoic temperature evolution with and without terrestrial vegetation. Simulated global mean surface temperature (GMST) for the past 382 million years. Red dashed line shows baseline simulations (ensemble $ENS_{pCO_2\text{-tuned}}$) with dynamic vegetation enabled; black solid line shows corresponding NOVEG simulations with vegetation removed. Grey shading indicates estimated compensatory warming from terrestrial carbon release. Red horizontal shading marks the 0°C threshold. Teal bars show sea ice latitudinal extent for NOVEG simulations (right axis). Top bar indicates climate state from cooler (blue) to warmer (red). Geological periods: D, Devonian; C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; N, Neogene; Q, Quaternary.

for runaway ice-albedo feedback into a “near-Snowball” state (Fig. 1, red shading), and was maintained in a habitable state primarily by the biophysical presence of terrestrial vegetation. The most extreme response occurs in the Moscovian (314.6 Ma), where GMST drops from 12.1 °C to −7.3 °C—a cooling of 19.4 °C, and sea ice advances to 20° latitude in the Northern Hemisphere (Fig. 1; Supplementary Data 1). Energy balance models and coupled climate simulations indicate that low-latitude sea-ice advance can trigger runaway ice-albedo feedback or produce soft-Snowball/waterbelt states, depending on sea ice and ocean dynamics [51–54].

We further assess whether the release of terrestrial carbon associated with the absence of biophysical vegetation could counteract this cooling (see Methods). In the most extreme case, the results indicate that terrestrial carbon release would provide +3.7 °C of compensatory warming, but adjusted GMST remains below 0 °C (−3.6 °C; Fig. 1, black shading).

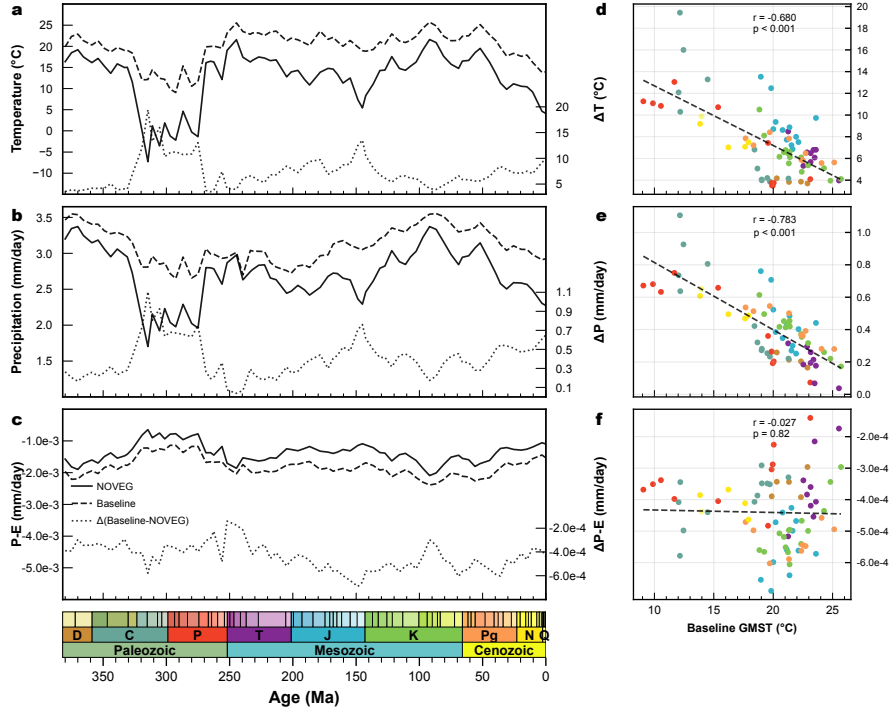


Fig. 2 State-dependence of vegetation biophysical effects on temperature and the hydrological cycle. Left column: time series of global mean temperature (a), precipitation (b), and precipitation minus evaporation (P–E; c) for the past 382 million years. Dashed lines show baseline simulations; solid lines show NOVEG simulations; dotted lines show the difference (baseline minus NOVEG; right axis). Right column: scatter plots of the vegetation effect (Δ) versus baseline GMST for the temperature (d), precipitation (e), and P–E (f). Points are coloured by geological period. Dashed lines show linear regression fits; r and p values indicate Pearson correlation coefficients and significance levels.

Because our model configuration uses prescribed ice sheets, the simulated biophysical cooling is driven solely by atmospheric and surface feedbacks (e.g., including the expansion of seasonal and perennial snow cover over land, the equatorward advance of sea ice, and associated changes in sea surface temperatures and ocean heat transport) without the additional amplification from dynamically expanding ice sheets. Thus the actual cooling would likely be even more severe. Nevertheless, the climate system reaches a “Slushball” state with extensive sea ice but equatorial open water [53–55]; coupling a dynamic ice-sheet model would likely transition this state into a

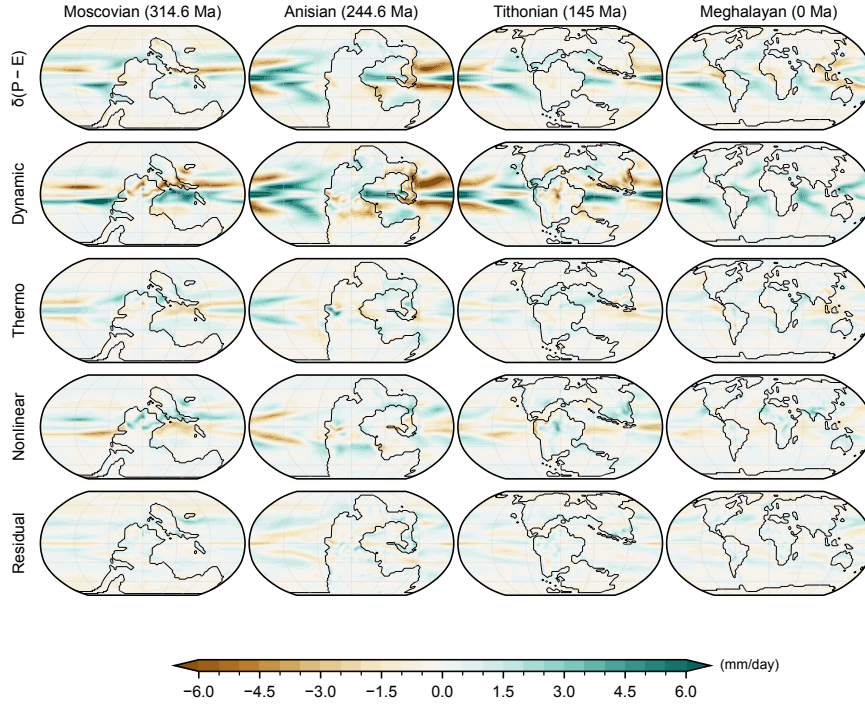


Fig. 3 Moisture budget decomposition for selected time periods. Spatial patterns of precipitation minus evaporation anomalies ($\delta(P - E)$; NOVEG minus baseline) and their decomposition into dynamic, thermodynamic, nonlinear, and residual components (rows) for four representative time slices (columns): Moscovian (314.6Ma), Anisian (244.6Ma), Tithonian (145Ma), and Meghalayan (0Ma). Brown shading indicates drying; teal shading indicates moistening. Black outlines show continental configurations for each time period.

“hard” Snowball Earth, implying that the biophysical presence of vegetation acted as a critical barrier against irreversible glaciation.

These collapses fall within the main phase of the LPIA ($\sim 335\text{--}260$ Ma) [8, 56]. We identify seven such near-Snowball events ($\text{GMST} \leq 0^\circ\text{C}$) in our NOVEG simulations between the Bashkirian (319.2 Ma) and Kungurian (275.0 Ma), five of which also place sea ice at or equatorward of 30° latitude (Supplementary Data 1). This systemic vulnerability is robust to $p\text{CO}_2$ uncertainties: an alternative $ENS_{p\text{CO}_2\text{-proxy}}$ ensemble—in which atmospheric CO_2 was prescribed to match proxy-derived estimates rather than the temperature reconstructions of Scotese et al.[29]—yields 10 comparable events from the Visean to Capitanian (338.8–262.5 Ma; Extended Data

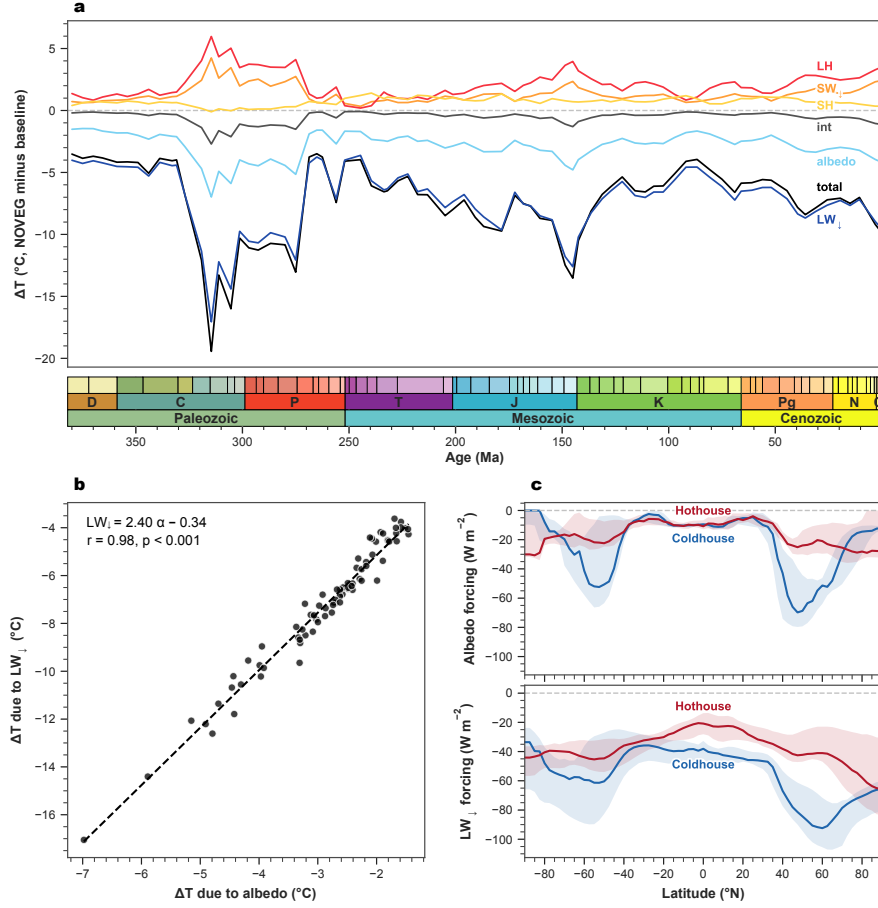


Fig. 4 Radiative decomposition of vegetation biophysical effects. **a**, Time series of temperature change contribution (NOVEG minus baseline) from surface energy budget components: downward shortwave ($SW_{\downarrow}$), surface albedo, interaction term (int), downward longwave ($LW_{\downarrow}$), latent heat (LH), sensible heat (SH), and total. **b**, Relationship between temperature changes due to albedo versus $LW_{\downarrow}$; dashed line shows linear regression with equation and correlation coefficient. **c**, Zonal mean radiative flux due albedo (top) and $LW_{\downarrow}$ (bottom) for hothouse (red) and coldhouse (blue) periods. Solid lines show medians; shading indicates 16th-84th percentile ranges.

Fig. 1; Supplementary Data 2), including four low-latitude ice-edge cases. In both ensembles, collapses are confined to the window of the lowest Phanerozoic pCO_2 (230–375 ppm). Notably, the late Cenozoic experienced similarly low pCO_2 conditions (< 300 ppm), yet our vegetation-free simulations maintained GMST above 4.1 °C in $ENS_{pCO_2\text{-tuned}}$ and 6.2 °C in $ENS_{pCO_2\text{-proxy}}$. This divergence highlights the specific susceptibility of the late Paleozoic Earth system, where lower solar luminosity ($\sim 3\%$

lower than present) combined with the Gondwanan continental configuration—placing extensive land masses at high southern latitudes where snow-albedo masking by vegetation is most effective—maximised the planet’s reliance on the biophysical buffering of terrestrial vegetation to avoid a Snowball state.

Cold states amplify biophysical cooling

The net biophysical effect of vegetation on the Earth system is strongly state-dependent. Across the 382 Myr simulations, the magnitude of vegetation-loss cooling (ΔT) is inversely correlated with baseline GMST ($r = -0.680, P < 0.001$; Fig. 2a,d). Spatial temperature anomalies across the full primary ensemble show that this cooling is geographically widespread and largest during cold late Paleozoic intervals (Extended Data Fig. 4). The cooling is moderate ($\sim 3.5^\circ\text{C}$) in warm greenhouse states, but amplifies non-linearly as the baseline climate cools. This state-dependence is mechanistically linked to the response of the hydrological cycle to surface modification. While the global precipitation deficit scales linearly with baseline warming ($r = -0.783, P < 0.001$; Fig. 2b,e), spatial precipitation anomalies across the primary ensemble show that this hydrological response is widespread but geographically heterogeneous (Extended Data Fig. 5). The partitioned land moisture balance (see Methods) reveals a critical divergence. The land precipitation-minus-evaporation anomaly ($\Delta(P - E)$) shows a weaker but significant relationship with baseline GMST ($r = 0.460, P < 0.001$; Extended Data Fig. 2f), consistent with substantial modulation by paleogeography and atmospheric circulation state. In warmer baselines, the atmospheric circulation maintains moisture convergence over land. However, in the colder LPIA baseline, vegetation removal triggers continental aridification (lower $P - E$), facilitating the dynamical export of moisture from land to oceans (Fig. 2, 3). This depletion of continental water vapour and the associated greenhouse cooling creates a positive feedback loop that is most active during cold states.

Decomposition of the surface energy budget (see Methods; Fig. 4a) confirms that the near-Snowball collapse is driven primarily by a reduced greenhouse effect from decreased water vapour [57], with a smaller contribution from increased surface albedo. Expressed as effective temperature contributions, the longwave and albedo terms covary tightly across the ensemble, with $\Delta T_{s,LW} = 2.4 \Delta T_{s,\alpha} - 0.34^\circ\text{C}$ ($r = 0.98$; Fig. 4b). Because both terms are defined as NOVEG minus baseline, negative values denote cooling; thus, the magnitude of the $LW_\downarrow$ contribution is typically about 2.4 times that of the albedo contribution. The $LW_\downarrow$ term includes changes in water vapour and clouds, but the moisture-budget analysis below links the dominant reduction to vegetation-driven drying. The remaining components of the surface energy budget—changes in downwelling shortwave radiation at the surface (F_{SW}), reflecting adjustments in cloud cover, and turbulent heat fluxes (F_{LH} , F_{SH})—contribute comparatively less to the global temperature response (Fig. 4a). The zonal distribution of the radiative fluxes reveals the spatial fingerprint of this state-dependent amplification (Fig. 4c). During coldhouse intervals, the albedo-induced radiative flux peaks sharply at mid-latitudes ($40 - 60^\circ$ N/S), reaching median values of approximately -65 W m^{-2} in the Northern Hemisphere, more than three times larger than during hothouse intervals at the same latitudes. This amplification reflects the expansion of snow and sea ice when vegetation is removed under already-cold baseline conditions, triggering ice-albedo feedback. The longwave radiative flux similarly intensifies at high latitudes during coldhouse intervals, with median values exceeding -60 W m^{-2} compared to -40 to -45 W m^{-2} during hothouse intervals. Both fluxes show substantially greater variability during coldhouse states (wider 16th–84th percentile ranges), consistent with the system’s proximity to a critical threshold where small perturbations could yield disproportionately large responses. Moisture budget analysis (see Methods) further attributes this $LW_\downarrow$ reduction to atmospheric restructuring. The dominant contribution is the dynamic moisture-flux convergence term (Fig. 3; see Methods),

indicating that vegetation removal reorganizes atmospheric circulation in a way that exports moisture from land to ocean. Reduced surface roughness and transpiration sources accelerate the advection of dry air and the export of moisture to the oceans. This “dynamical drying” feedback loop is particularly strong in the cold LPIA baseline, where the background atmosphere already holds minimal water vapour following the Clausius-Clapeyron relation. Under these conditions, the biophysical loss of vegetation greatly reduces the greenhouse effect associated with water vapour, exposing the Earth to full radiative cooling and pushing the system towards a Cryogenian-style Snowball state.

Our simulations carry uncertainties from three main sources: the use of prescribed ice sheets, bare-soil albedo assumptions in the vegetation-removal experiments, and the representation of Paleozoic vegetation with modern Plant Functional Types (see Supplementary Note 4 for detailed assessment). These factors affect absolute magnitudes but do not change our principal conclusions. The likely underestimate arising from the use of prescribed ice sheets—which exclude the positive feedback of dynamic ice-sheet expansion—and the potential overestimate from using a relatively high-albedo mineral-soil end member in the NOVEG experiments operate in opposing directions. Furthermore, the state-dependent amplification pattern identified here is driven by snow-albedo feedback and moisture-dependent longwave fluxes, rather than by the exact taxonomic identity of the simulated vegetation, and is therefore robust to reasonable uncertainty in Paleozoic vegetation properties.

Vegetation drives and prevents Snowball states

A critical paradox arises when reconciling our results with the long-term carbon cycle. The colonization of continents by vascular plants is widely recognised as a primary driver of enhanced silicate weathering [14, 58], which drew down atmospheric $p\text{CO}_2$

507 and initiated the LPIA [4, 42]. However, our findings reveal that the biophysical pres-
 508 ence of vegetation prevented global glaciation. This raises a fundamental question:
 509 how can the same vegetation be both the driver and preventer of a Snowball Earth
 510 episode? Our results resolve this paradox by demonstrating that the evolution of com-
 511 plex vegetation introduced two inextricably linked mechanisms to the Earth system:
 512 biogeochemical cooling (enhanced weathering) and biophysical warming through sur-
 513 face darkening, snow masking, aerodynamic roughness and moisture recycling. The
 514 cooling associated with the low $p\text{CO}_2$ levels of the LPIA was only mitigated because
 515 the $p\text{CO}_2$ drawdown was biologically induced. If an equivalent $p\text{CO}_2$ drawdown had
 516 been driven by abiotic processes—such as the tectonic fragmentation invoked for the
 517 Neoproterozoic—without the concomitant surface darkening and moisture recycling
 518 by vegetation, the Earth would likely have cooled further, crossing the Snowball initi-
 519 ation threshold point into global glaciation. The terrestrial biosphere thus engineered
 520 a new climate state: a “deep icehouse” that was maintained at habitable temperatures
 521 through a combination of biogeochemical cooling and biophysical warming, a state
 522 unattainable on a barren planet.

533 Our findings also refine the “tectonic safety net” hypothesis ([50]), which attributes
 534 the absence of Phanerozoic Snowball Earth events to elevated volcanic CO_2 degassing.
 535 Recent Earth system modelling further demonstrates that Phanerozoic icehouses
 536 resulted from multiple solid-Earth cooling mechanisms acting in concert [59]. Whereas
 537 tectonic forcing can set the baseline boundary conditions for habitability, our results
 538 highlight the limitations of this control during critical intervals. Crucially, the biogeo-
 539 chemical models underpinning this hypothesis (e.g., COPSE/GEOCARB [14, 60, 61])
 540 are zero-dimensional and typically parameterize surface temperature solely as a
 541 function of $p\text{CO}_2$ and solar luminosity, neglecting the state-dependent biophysical
 542 feedbacks identified here. Our data indicate that during the Carboniferous-Permian
 543 transition, a window of relatively low tectonic degassing and maximised weathering
 544

potential, the CO₂-degassing buffer against runaway glaciation was small. In this near-threshold state, the biophysical presence of vegetation became the dominant control preventing climate collapse. While tectonic degassing may have prevented Snowball Earth on multi-hundred-million-year timescales, it was the biophysical effect of vegetation that prevented global glaciation through the coldest Paleozoic intervals. Vegetation thus acted as a self-regulating thermostat that prevented the late Paleozoic from collapsing into a runaway Snowball Earth. These results suggest a hierarchy of controls on Earth's habitability, in which biological innovation can provide the essential control mechanism when tectonic regulation weakens.

Supplementary information. This paper is accompanied by Extended Data Figures 1-5, and Supplementary Information (Supplementary Notes 1 and Supplementary Tables 1-2).

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Data and code availability. All the climate outputs are available from <https://www.paleo.bristol.ac.uk/ummodel/scripts/papers/>.

Competing interests. The authors declare no competing interests.

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Methods

Model configuration and physics

We employed the HadCM3L coupled atmosphere-ocean general circulation model (AOGCM), a version of the UK Met Office Unified Model optimized for paleoclimate simulations on geological timescales. The model features a spatial resolution of $3.75^\circ \times 2.5^\circ$ longitude $\times$ latitude in the atmosphere and rigid-lid ocean, with 19

atmospheric and 20 oceanic vertical levels. The specific configuration of the model is HadCM3BL-M2.1aD, in the nomenclature of Valdes et al.[61]. To address the high-latitude cold bias common in deep-time simulations, relative to the standard configuration[62] we incorporated specific improvements to the cloud microphysics parameterization[63]. In particular, following the protocols of Kiehl and Shields[64], we modified the Cloud Condensation Nuclei (CCN) density and effective cloud droplet radius. This parameterization reduces the optical depth of polar clouds, thereby decreasing the equator-to-pole temperature gradient and improving agreement with high-latitude proxy records across diverse climate states. Internal model parameters were further optimized following the perturbed physics ensemble methodology of Irvine et al.[65] to ensure stability under extreme boundary conditions. A key improvement in our configuration involves the land-surface scheme (MOSES 2.1). Unlike previous Phanerozoic ensembles that utilized a uniform bare-soil albedo[62], our model implements a dynamic albedo scheme where surface reflectivity is functionally dependent on soil carbon content. This allows for a more realistic representation of the biophysical feedbacks associated with soil evolution.

Baseline experiment and boundary conditions

We analyzed two parallel ensembles of simulations ($ENS_{pCO_2\text{-proxy}}$ and $ENS_{pCO_2\text{-tuned}}$) spanning the Phanerozoic (540 Ma to present), totaling 109 time slices. Both ensembles utilize the stage-level paleogeographic reconstructions of Scotese [29], but differ in their atmospheric CO_2 forcing strategies to bracket the uncertainty in paleo- pCO_2 records:

- **$ENS_{pCO_2\text{-proxy}}$:** Atmospheric CO_2 concentrations were prescribed primarily based on the multi-proxy compilation of Foster et al.[66]. For the Late Cretaceous and Cenozoic intervals, CO_2 forcing was refined to maintain consistency with the boron

1059 isotope-derived record of Rae et al.[67]. This ensemble is identical to the ‘Scotese_07’
1060 simulations described in Judd et al.[30].

1062 • **$ENS_{pCO_2\text{-tuned}}$** : In this ensemble, atmospheric CO_2 was prescribed for each time
1063 slice such that the model-simulated GMST approached the Phanerozoic temperature
1064 reconstruction of Scotese et al.[29]. This ensemble is identical to the ‘Scotese_08’
1065 simulations of Judd et al.[30].

1066
1067 In all baseline simulations, the vegetation distribution was dynamically simulated
1068 by TRIFFID (Top-down Representation of Interactive Foliage and Flora Including
1069 Dynamics) [68, 69], the dynamical vegetation model internal to HadCM3BL, using
1070 modern Plant Functional Types (PFTs). The baseline simulations serve as the control
1071 state against which vegetation-removal sensitivity experiments were compared.
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1073 Experiment design for removing vegetation

1074 The vegetation removal process was executed in two distinct phases to ensure both
1075 thermodynamic equilibrium and the complete elimination of biophysical memory.

1076 **Phase I: Physiologically-forced vegetation die-back.** In the initial phase, we
1077 induced global vegetation mortality by imposing an unphysical constraint on the phys-
1078 iological parameters of all five PFTs within the TRIFFID dynamic global vegetation
1079 model. Specifically, the optimal temperature range for photosynthesis was shifted to
1080 an extreme window of 99°C to 99.5°C for all PFTs. Under Phanerozoic climate con-
1081 ditions, this constraint forces the gross primary productivity (GPP) to zero globally,
1082 preventing carbon assimilation. Consequently, vegetation biomass declined continu-
1083 ously through natural mortality and disturbance turnover terms until PFT fractions
1084 reached zero across all land grid cells. The model was integrated for 3,000 years for
1085 each time slice to allow the deep ocean circulation and thermal structure to equilibrate
1086 to the “no vegetation” state.

Phase II: Elimination of soil carbon artifacts. Upon reaching equilibrium in Phase I, analysis revealed that while vegetation biomass was successfully eliminated, trace amounts of residual soil carbon persisted in high-latitude and high-elevation grid cells. This persistence is physically attributable to the temperature dependency of soil organic matter decomposition in the MOSES2.1-TRIFFID scheme. The decay rates of the four soil carbon pools (decomposable/resistant plant material, microbial biomass, and humus) are a function of temperature. In cold regions where soil temperatures remain near or below freezing, the decay rate approaches zero, thereby effectively inhibiting heterotrophic respiration and locking residual carbon in the soil matrix indefinitely, despite the cessation of litterfall input. Although the magnitude of this residual carbon was small, its presence introduces potential biases in surface albedo calculations, which are functionally dependent on soil carbon content in our model configuration. To eliminate this artifact and ensure a pristine bare-soil boundary condition, we performed a secondary perturbation: manual removal of all remaining soil carbon stocks from the Phase I restart files. The model was then integrated for an additional 200 years. This second phase ensured that land-surface properties—particularly soil albedo and hydrology—fully equilibrated to the carbon-free state, allowing a robust quantification of the pure biophysical impact of terrestrial vegetation.

We evaluated equilibration using Gregory plots [70] spanning the full 3,200-year NOVEG integrations, including the subsequent 200-year soil-carbon-removal phase (Extended Data Fig. 3), ensuring that the drift in global mean surface temperature and top-of-atmosphere (TOA) net radiation flux was small.

Estimation of carbon-pool biogeochemical feedbacks

Since the HadCM3L simulations uses prescribed atmospheric CO₂, the vegetation-removal experiments (NOVEG) capture only the biophysical effects. To quantify the potential compensating warming from the release of terrestrial carbon, we performed

an offline calculation using carbon pools from the baseline experiments and state-dependent climate sensitivities diagnosed from the parallel ensemble design.

Terrestrial carbon inventory and atmospheric perturbation. For each time slice t , the total potential carbon loss (C_{loss}) was calculated as the sum of global vegetation biomass (C_{veg}) and soil carbon (C_{soil}) from the corresponding baseline simulation:

$$C_{\text{loss}}(t) = \sum_{i,j} [C_{\text{veg}}(i, j, t) + C_{\text{soil}}(i, j, t)] \quad (1)$$

where the summation encompasses all land grid points (i, j) , with C_{veg} , C_{soil} and C_{loss} in gigatonnes of carbon (GtC). We assumed the complete oxidation of these stocks and converted this mass to an atmospheric concentration anomaly ($\Delta p\text{CO}_2$, in ppm) using a conversion factor of $2.12 \text{ GtC ppm}^{-1}$ [71, 72]:

$$\Delta p\text{CO}_2(t) = \mu \cdot \frac{C_{\text{loss}}(t)}{2.12} \quad (2)$$

To account for ocean-atmosphere equilibration on the millennial timescales relevant to the collapse events, we applied a pulse-size-dependent airborne fraction (μ , dimensionless). Following the principle that larger carbon perturbations are less efficiently buffered by the ocean carbonate system [73], we assigned μ based on the magnitude of the release:

$$\mu = \begin{cases} 0.25 & \text{if } C_{\text{loss}} < 1800 \text{ GtC} \\ 0.35 & \text{if } C_{\text{loss}} \geq 1800 \text{ GtC} \end{cases} \quad (3)$$

These values are consistent with multi-model intercomparisons of carbon lifetime for pulses of $1,000 - 5,000 \text{ GtC}$ on $1 - 3 \text{ kyr}$ timescales [73].

Diagnosis of state-dependent climate sensitivity. To convert the retained atmospheric $\Delta p\text{CO}_2$ into a temperature response, we diagnosed the specific climate sensitivity for each time slice using the parallel $ENS_{p\text{CO}_2\text{-proxy}}$ and $ENS_{p\text{CO}_2\text{-tuned}}$ ensembles. The state-dependent sensitivity parameter ($\mathcal{S}(t)$, in $^{\circ}\text{C}$ per CO_2 doubling)

was derived as:

$$\mathcal{S}(t) = \frac{T_a(t) - T_b(t)}{\log_2(p\text{CO}_{2,a}(t)/p\text{CO}_{2,b}(t))} \quad (4)$$

where T (in °C) and $p\text{CO}_2$ (in ppm) are the GMST and atmospheric CO_2 concentrations for the respective ensembles. By deriving $\mathcal{S}(t)$ individually for each time slice, our calculation explicitly accounts for the non-linear dependence of climate feedbacks on the background climate state [31, 74].

Biogeochemical temperature adjustment. The warming effect (ΔT_{BGC} , in °C) was estimated by applying the diagnosed sensitivity $\mathcal{S}(t)$ to the change in radiative fluxes calculated from the adjusted CO_2 concentration:

$$\Delta T_{\text{BGC}}(t) = \mathcal{S}(t) \cdot \log_2 \left(\frac{p\text{CO}_{2,\text{base}}(t) + \Delta p\text{CO}_2(t)}{p\text{CO}_{2,\text{base}}(t)} \right) \quad (5)$$

This calculated offset was added to the biophysical cooling simulated in the vegetation-removal experiments to determine the net surface temperature change.

Surface energy balance decomposition

To attribute the simulated surface temperature anomalies (ΔT_s) to specific biophysical drivers, we employed a Surface Energy Balance (SEB) decomposition analysis[74, 75]. As the climate model does not have an input of energy into the surface layers from the subsurface, in equilibrium the surface energy budget relates the surface temperature (T_s) to radiative and non-radiative fluxes via the Stefan-Boltzmann law:

$$\sigma T_s^4 = (1 - \alpha)SW_{\downarrow} + LW_{\downarrow} - (LH + SH) \quad (6)$$

where σ is the Stefan-Boltzmann constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$), T_s is the surface temperature (in K), α is the surface albedo (dimensionless), $SW_{\downarrow}$ and $LW_{\downarrow}$ are the downwelling shortwave and longwave radiation (in W m^{-2}), respectively, and LH and

1243 SH represent the turbulent latent and sensible heat fluxes (in W m^{-2}) directed away
 1244 from the surface.

1246 We define the climate anomaly as the difference between the NOVEG and baseline
 1247 experiments ($\Delta X = X_{\text{NOVEG}} - X_{\text{baseline}}$). By differencing Eq. 6 and decomposing the
 1248 change in absorbed shortwave radiation into contributions from insolation, albedo, and
 1249 their non-linear interaction, the total change in emitted surface radiation ($\Delta LW_{\uparrow} \approx$
 1250 $4\sigma T_s^3 \Delta T_s$) can be expressed as the sum of components of the radiative flux changes
 1251 F_x):

$$1256 \quad 4\sigma T_s^3 \Delta T_s \approx \sum F_x = F_{SW} + F_{\alpha} + F_{\text{int}} + F_{LW} + F_{LH} + F_{SH} \quad (7)$$

1258 The individual radiative flux components (in W m^{-2}) are quantified as:

$$1261 \quad F_{SW} = (1 - \alpha) \Delta SW_{\downarrow} \quad (8a)$$

$$1263 \quad F_{\alpha} = -SW_{\downarrow} \Delta \alpha \quad (8b)$$

$$1265 \quad F_{\text{int}} = -\Delta \alpha \Delta SW_{\downarrow} \quad (8c)$$

$$1267 \quad F_{LW} = \Delta LW_{\downarrow} \quad (8d)$$

$$1269 \quad F_{LH} = -\Delta LH \quad (8e)$$

$$1271 \quad F_{SH} = -\Delta SH \quad (8f)$$

1274 Here, F_{SW} represents the change in radiative flux due to changes in incoming solar
 1275 radiation (e.g., due to cloud cover changes), while F_{α} isolates the impact of surface
 1276 albedo changes (e.g., from vegetation removal or snow cover adjustment). F_{int} captures
 1277 the second-order interaction term. F_{LW} represents the change in downwelling longwave
 1278 radiation (the greenhouse effect of water vapour and clouds). For the non-radiative
 1279 turbulent fluxes (F_{LH} and F_{SH}), the negative sign indicates that a reduction in surface
 1280 heat loss (e.g., reduced evapotranspiration in the NOVEG case) acts as a positive
 1281 warming mechanism. To facilitate comparison with global temperature anomalies, the
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energetic contributions were converted to effective temperature changes ($\Delta T_{s,x}$, in $^{\circ}\text{C}$)

using a first-order linearization of the Planck feedback response:

$$\Delta T_{s,x} \approx \frac{F_x}{4\sigma \bar{T}_s^3} \quad (9)$$

where $\bar{T}_s$ is the global mean surface temperature of the baseline simulation (in K).

While this linearization introduces a small residual error given the large magnitude of cooling in the LPIA simulations, it provides a robust metric for attributing the relative importance of radiative versus non-radiative drivers.

Moisture budget decomposition

To attribute the simulated hydrological anomalies ($\delta(P - E)$) to specific atmospheric drivers, we performed a moisture budget decomposition following the Eulerian approach[76, 77]. The atmospheric water balance relates the net surface freshwater flux ($P - E$) to the atmospheric moisture storage tendency and the vertically integrated moisture flux convergence:

$$P - E = -\frac{1}{g\rho_w} \frac{\partial}{\partial t} \int_0^{p_s} q, dp - \frac{1}{g\rho_w} \nabla \cdot \int_0^{p_s} \mathbf{u}q, dp \quad (10)$$

where g is gravitational acceleration (9.81 m s^{-2}), ρ_w is the density of water ($1,000 \text{ kg m}^{-3}$), p_s is surface pressure(in Pa), $\mathbf{u}$ is the horizontal wind vector (in m s^{-1}), and q is the specific humidity (in kg kg^{-1}). The resulting $P - E$ and its decomposed components are expressed as a water-equivalent flux (in mm day^{-1}).

We analyzed the difference between the NOVEG and baseline experiments ($\delta(\cdot) = (\cdot)_{\text{NOVEG}} - (\cdot)_{\text{Baseline}}$). Following Feng et al.[77], the perturbation to the moisture budget can be expanded using Reynolds decomposition on monthly climatologies. We denote baseline monthly climatologies with the subscript B and anomalies relative

to the baseline with δ . Unlike comparisons between distinct geological eras where topographic changes drive significant surface pressure anomalies (δp_s), our pairs of simulations utilize identical orography. Consequently, the contributions from surface pressure variations (quantified as the ‘RES 1’ term in Feng et al.[77]) are negligible. Neglecting these minor pressure deviations and the long-term moisture storage tendency, the hydrological anomaly is partitioned into thermodynamic, dynamic, and non-linear components:

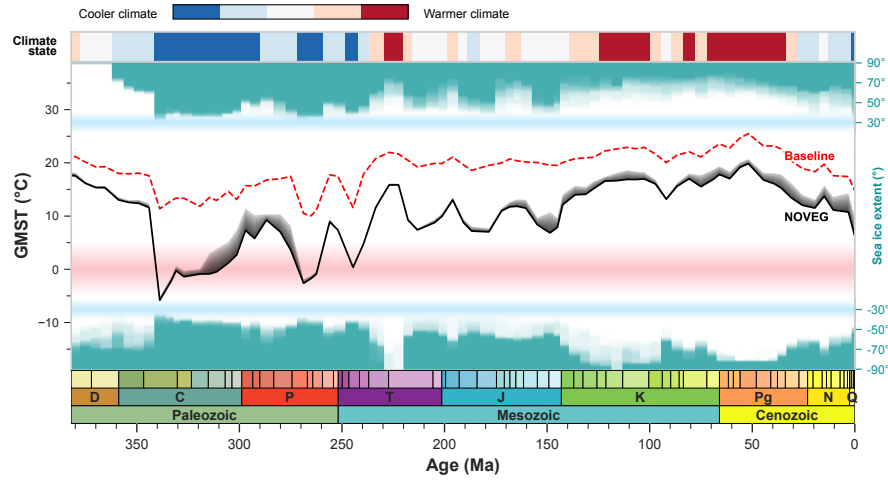
$$\delta(P - E) \approx -\frac{1}{g\rho_w} \nabla \cdot \int_0^{\bar{p}_{s,B}} \left(\underbrace{\bar{\mathbf{u}}_B \delta \bar{q}}_{\text{Thermo}} + \underbrace{\delta \bar{\mathbf{u}} \bar{q}_B}_{\text{Dynamic}} + \underbrace{\delta \bar{\mathbf{u}} \delta \bar{q}}_{\text{Nonlinear}} \right) dp + \mathcal{R} \quad (11)$$

Here, the overbar ($\bar{\cdot}$) denotes the monthly climatological mean. Variables carrying the subscript B (i.e., $\bar{\mathbf{u}}_B, \bar{q}_B$) represent the baseline state, while δ terms denote the anomalies in the NOVEG experiment. The integration is performed from the top of the atmosphere ($p = 0$) to the baseline surface pressure ($\bar{p}_{s,B}$). The physical components are defined as:

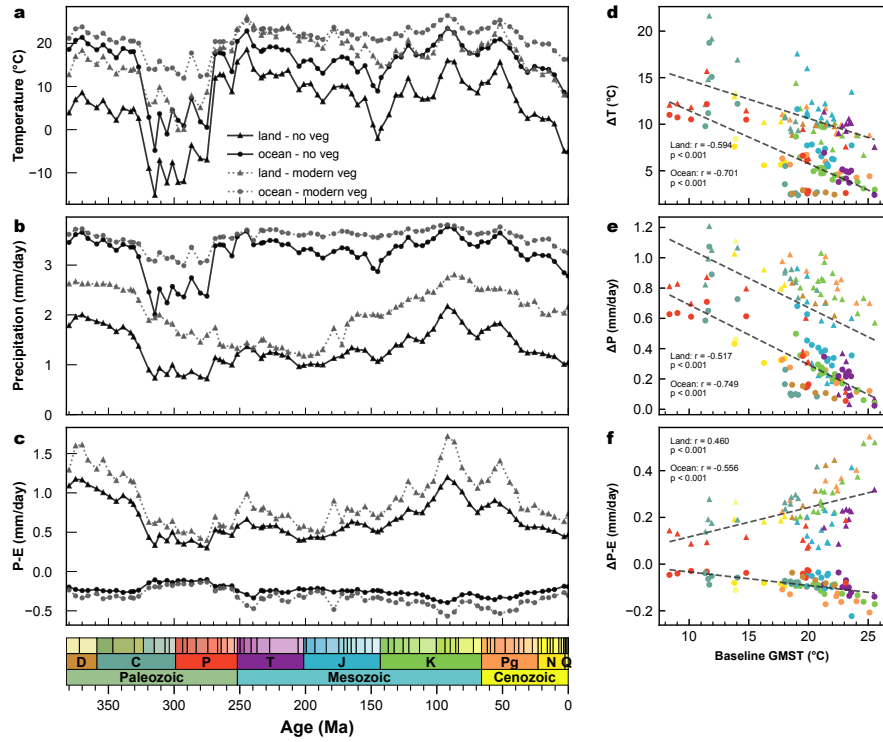
- **Thermodynamic contribution** ($-\nabla \cdot (\bar{\mathbf{u}}_B \delta \bar{q})$): Represents changes in moisture convergence driven solely by specific humidity anomalies ($\delta \bar{q}$) transported by the background circulation. Since $\delta \bar{q}$ scales with temperature via the Clausius-Clapeyron relation, this term isolates the “holding capacity” effect of the atmosphere.
- **Dynamic contribution** ($-\nabla \cdot (\delta \bar{\mathbf{u}} \bar{q}_B)$): Quantifies the impact of circulation anomalies ($\delta \bar{\mathbf{u}}$) acting on the background moisture field. This term captures hydrological shifts caused by the reorganization of wind fields (e.g., due to surface roughness changes).
- **Non-linear interaction** ($-\nabla \cdot (\delta \bar{\mathbf{u}} \delta \bar{q})$): Accounts for the covariance between wind and moisture anomalies.

The residual term ($\mathcal{R}$) encompasses contributions from sub-monthly transient eddies	1381
(which cannot be explicitly resolved with monthly mean output) and minor errors	1382
arising from vertical integration and discretization.	1383
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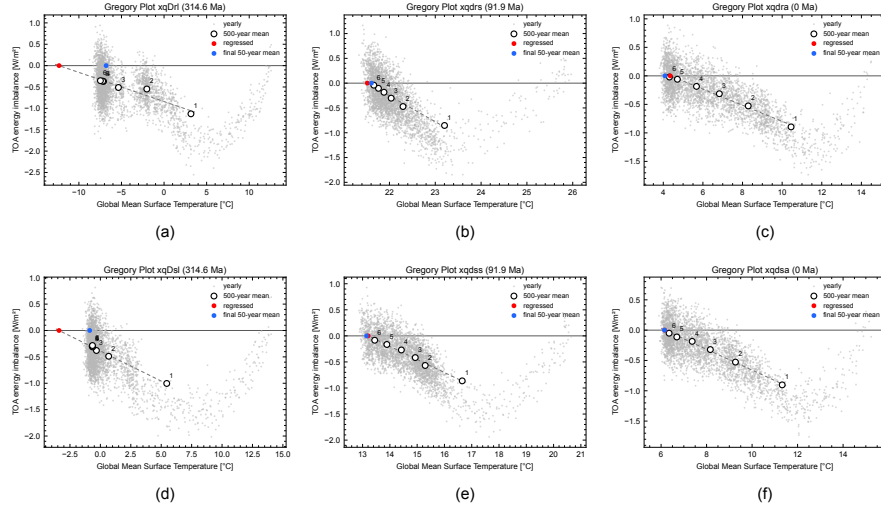
Extended Data



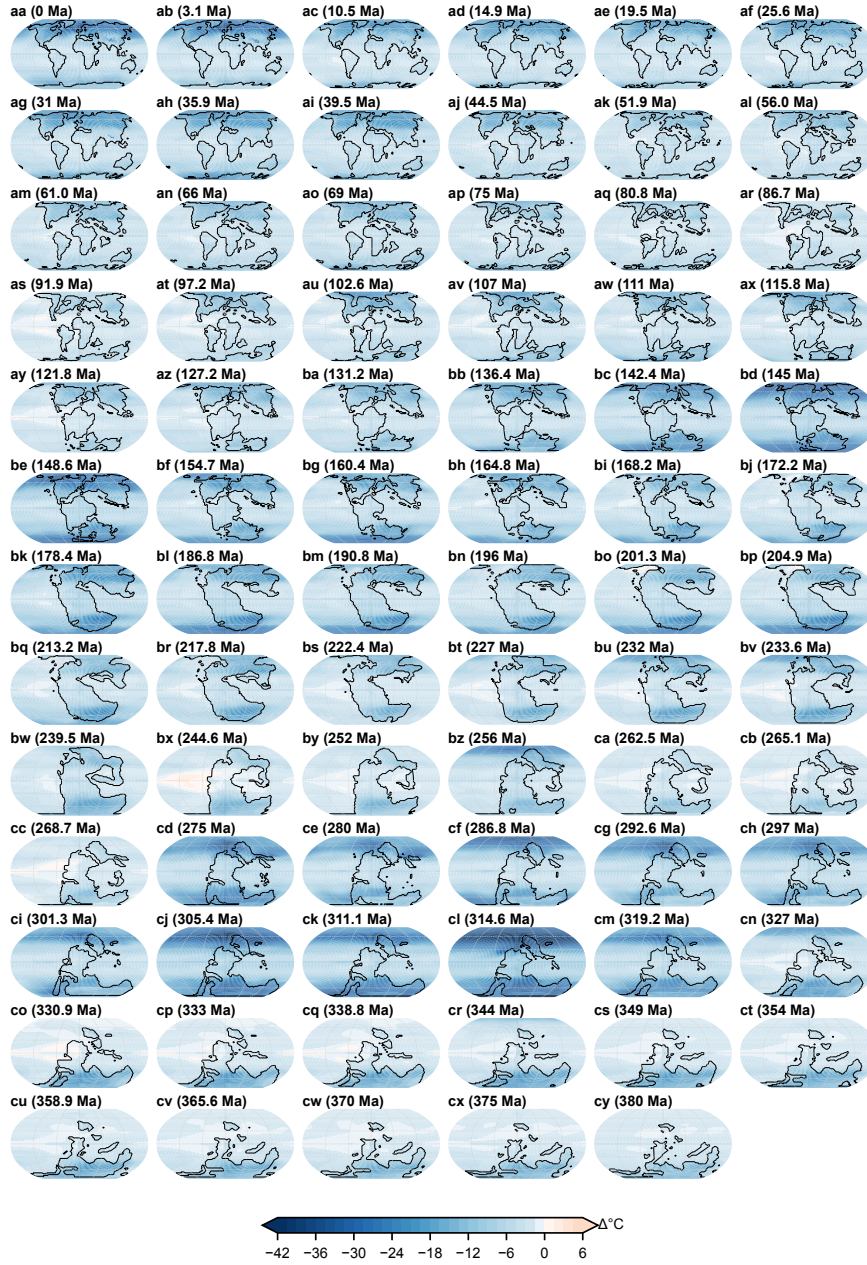
Extended Data Fig. 1 Phanerozoic temperature evolution with and without terrestrial vegetation: $ENS_{pCO_2\text{-proxy}}$ ensemble. As Fig. 1, but for the $ENS_{pCO_2\text{-proxy}}$ ensemble (see Methods for ensemble definition). Red dashed line, baseline simulations with vegetation; black solid line, simulations with vegetation removed (NOVEG). Grey shading, estimated compensatory warming from terrestrial carbon release. Red horizontal shading, 0°C threshold. Teal bars, sea ice latitudinal extent for NOVEG simulations (right axis). Top bar, climate state from cooler (blue) to warmer (red). Geological periods: D, Devonian; C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; N, Neogene; Q, Quaternary.



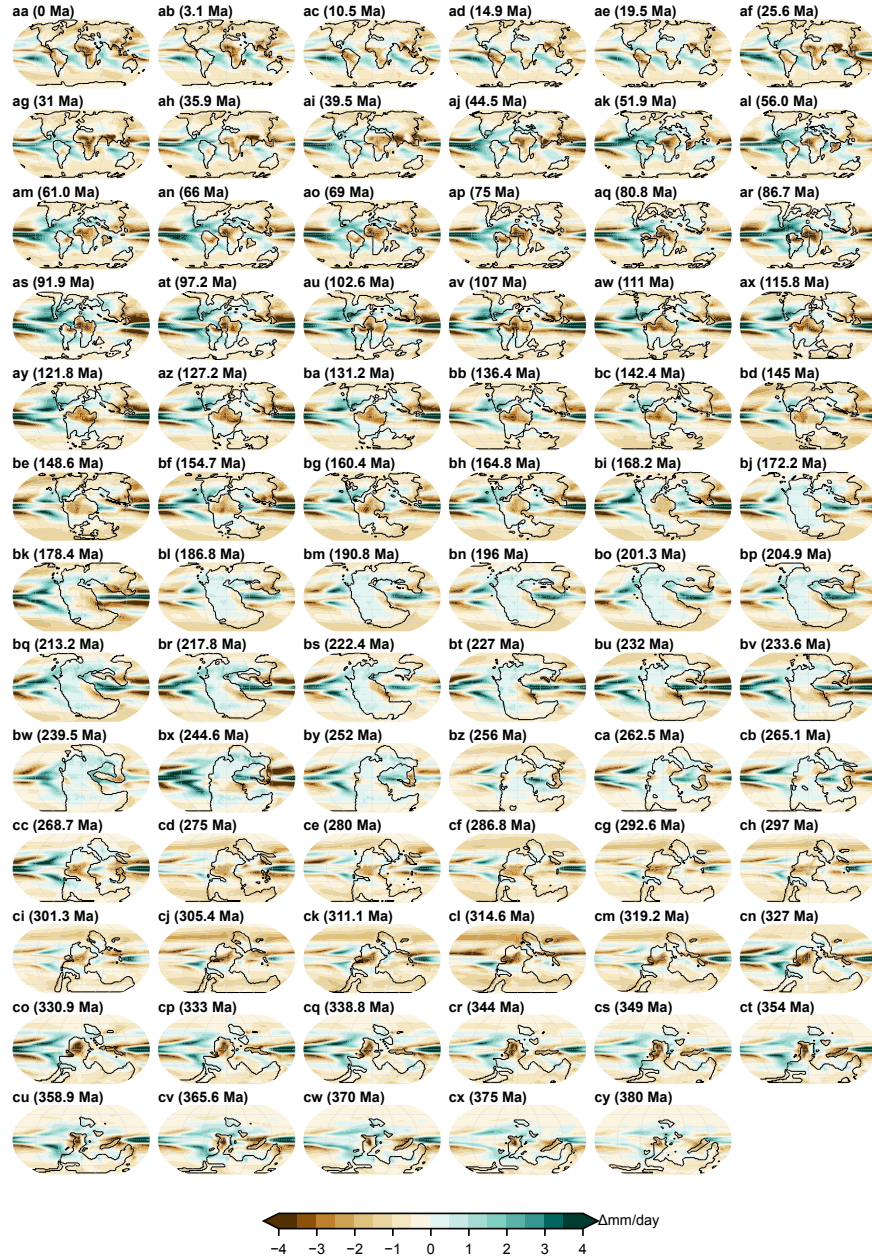
Extended Data Fig. 2 Land versus ocean partitioning of the vegetation biophysical effect. **a–c,** Time series of area-weighted mean temperature (**a**), precipitation (**b**), and precipitation minus evaporation (P–E; **c**) for the past 382 million years, partitioned into land and ocean components for baseline and NOVEG simulations (line styles as indicated in the legend). **d–f,** Scatter plots of the vegetation biophysical effect (Δ = baseline minus NOVEG) versus baseline GMST for temperature (**d**), precipitation (**e**), and P–E (**f**), with land and ocean shown separately. Dashed lines show linear regression fits. Pearson correlation coefficients (r) and significance levels are annotated; $n = 77$ time slices for each correlation. Geological periods as in Fig. 1.



Extended Data Fig. 3 Gregory-plot assessment of NOVEG simulation equilibration. Gregory plots for selected NOVEG simulations from the ENS_{pCO_2} -tuned (xqdr; **a–c**) and ENS_{pCO_2} -proxy (xqds; **d–f**) ensembles at 314.6 Ma (**a, d**), 91.9 Ma (**b, e**), and 0 Ma (**c, f**). Light-grey points show annual global mean surface temperature and top-of-atmosphere (TOA) energy imbalance for the full 3,200-year integrations, reflecting the 3,000-year vegetation-removal phase followed by the 200-year soil-carbon-removal phase described in Methods. Large black circles show 500-year means, labelled 1–6 from the first to the final 500-year interval. Red circles mark the zero-TOA-imbalance intercept of the regression through the 500-year means, representing the inferred equilibrium GMST. Blue circles show the mean of the final 50 simulation years.



Extended Data Fig. 4 Surface temperature response to vegetation removal through the past 382 Myr. aa–cy, Annual-mean surface temperature anomalies (shading; unit, °C) for the 77 paired simulations in the primary $ENS_{pCO_2\text{-tuned}}$ ensemble, calculated as NOVEG minus baseline from final 100-year means. Panels are ordered from youngest to oldest, with the age of each time slice given above each map. Blue shading denotes cooling after vegetation removal and red shading denotes warming. Black lines show the continental configuration for each time slice.



Extended Data Fig. 5 Precipitation response to vegetation removal through the past 382 Myr. aa–cy, Annual-mean precipitation anomalies (shading; unit, mm day^{-1}) for the 77 paired simulations in the primary $ENS_{p\text{CO}_2\text{-tuned}}$ ensemble, calculated as NOVEG minus baseline from final 100-year means. Panels are ordered from youngest to oldest, with the age of each time slice given above each map. Brown shading denotes reduced precipitation after vegetation removal and teal shading denotes increased precipitation. Black lines show the continental configuration for each time slice.

Supplementary Note 1: Assessment of model

limitations

Prescribed ice sheets. Our simulations use fixed ice sheets based on geological reconstructions [62], meaning that the simulated cooling excludes the positive feedback from dynamically expanding ice sheets. Given that our vegetation-free simulations produce sea-ice advance equatorward of $\sim 30^\circ$ latitude—within the critical threshold range for runaway ice-albedo feedback [51–54]—coupling a dynamic ice-sheet model would likely amplify the cooling beyond what is reported here. The biophysical presence of vegetation therefore acted as a barrier against irreversible glaciation, a role that our fixed-ice-sheet simulations are likely to underestimate.

Bare-soil albedo representativeness. A related consideration is whether the bare-soil albedo in the vegetation removal experiments overestimates the reflectivity of unvegetated land surfaces, thereby amplifying the simulated cooling. In our NOVEG simulations, the complete removal of vegetation and soil organic carbon (see Methods) yields the bright mineral-soil end member permitted by the model’s carbon-dependent albedo scheme, i.e. the imposed maximum bare-soil albedo of 0.355. This should be interpreted as an end-member sensitivity experiment rather than a literal reconstruction of every pre-vascular land surface. Modern “bare” soils are products of a biologically active world: they are darkened by accumulated organic matter and humic compounds from litterfall and root turnover, by biological soil crusts, and by soil moisture sustained through root-mediated water retention and canopy shading [78, 79]. Biological soil crusts and cryptogamic ground covers can substantially reduce albedo relative to mineral substrates. For example, moss-biocrusts in a dryland ecosystem reduced mean surface albedo from 0.20 for bare soil to 0.11, while cyanobacterial crusts can warm soil surfaces by up to 10°C through scytonemin-mediated absorption, and experimental loss of dark moss- and lichen-dominated crusts increased dryland

1703 albedo by more than 30% [80–82]. Cryptogamic covers therefore would have provided
1704 some surface darkening before, and alongside, vascular vegetation.

1706 This caveat does not overturn the interpretation of the NOVEG experiments for
1707 three reasons. First, cryptogamic covers lack the canopy height, leaf area, snow-
1708 masking capacity, root-mediated soil-water storage, and deep soil organic carbon
1709 accumulation associated with vascular vegetation; thus they are not functionally equiv-
1710 alent to forests in the biophysical mechanisms identified here. Second, the true albedo
1711 of a vascular-vegetation-free but cryptogam-covered landscape would likely lie between
1712 our bright mineral-soil end member and the fully vegetated baseline, so this uncer-
1713 tainty affects the absolute magnitude of the baseline–NOVEG contrast rather than its
1714 sign. Third, our surface-energy decomposition shows that the LPIA cooling is domi-
1715 nated by moisture-dependent reductions in downward longwave radiation, with direct
1716 albedo changes providing a smaller but non-negligible contribution (Fig. 4); lowering
1717 the NOVEG soil albedo within plausible cryptogamic-cover bounds would therefore
1718 weaken, but not remove, the state-dependent amplification. To the extent that the
1719 NOVEG albedo is too reflective, this bias also operates opposite to the conservative
1720 bias introduced by prescribed ice sheets.

1731 **Representativeness of modern Plant Functional Types.** A further limi-
1732 tation is the use of modern Plant Functional Types (PFTs) to represent Paleozoic
1733 vegetation in the TRIFFID dynamic vegetation model. TRIFFID simulates five PFTs:
1734 broadleaf trees, needleleaf trees, C₃ grasses, C₄ grasses, and shrubs. These PFTs
1735 should be interpreted as functional surface classes rather than taxonomic assignments.
1736 No crown-angiosperms existed during the Paleozoic, and Carboniferous–Permian
1737 forests—dominated by arborescent lycopsids, tree ferns, seed ferns, sphenopsids, and
1738 coniferophytes, including cordaitaleans and early walchian conifers—differed from
1739 modern vegetation in canopy architecture, rooting systems, leaf traits, and stomatal
1740 physiology [10, 44, 83]. Moreover, grasses are a Cretaceous angiosperm lineage: the
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oldest reported Poaceae fossils are Early to Late Cretaceous, and the ecological expansion of C_4 grasslands occurred much later, during the late Miocene–Pliocene [84–86]. Thus, C_3 and C_4 grass PFTs have no Paleozoic taxonomic analogue.

The relevant question is therefore not whether each TRIFFID PFT has a Paleozoic taxonomic counterpart, but whether the simulated vegetation captures the first-order surface properties that control the diagnosed feedbacks: albedo, snow masking, aerodynamic roughness, evapotranspiration, and soil-water storage. This is a reasonable approximation for forested grid cells. We deliberately restrict our analysis to the interval from 382 Ma onward, by which time forests of arborescent tracheophytes—including cladoxylopsid trees, archaeopteridalean progymnosperms, and arborescent lycopsids—had established key ecosystem attributes such as substantial above-ground biomass, perennial rooting systems, and canopy structure [87–89]. By the LPIA, tropical wetland forests included arborescent lycopsids, marattialean tree ferns, seed ferns, and sphenopsids, while seasonally dry and extratropical settings included cordaitalean and walchian coniferophyte forests [44, 83]. These lineages differed substantially from one another, but a forest canopy from any of them would have been darker, rougher, and capable of greater transpiration than a vegetation-free mineral surface. The statement is therefore functional, not taxonomic: the model represents the presence of forest-like surface structure, not the detailed physiology of any extinct clade.

In the critical LPIA time slices, the dynamically simulated vegetation is dominated in colder mid-to-high latitude and high-elevation regions by needleleaf tree and shrub PFTs, with broadleaf tree PFTs concentrated mainly in warmer, lower-latitude humid regions. We do not interpret this distribution literally as modern conifers, modern shrubs, or angiosperm forests. Instead, it provides a functional mapping: needleleaf and shrub PFTs approximate lower-albedo, rough, woody vegetation in colder or drier environments, broadly comparable to cordaitalean and walchian coniferophyte dryland

1795 forests and low-woody floras; broadleaf tree PFTs approximate humid high-biomass
 1796 forests, broadly comparable to wetland lycopsid, tree-fern, and seed-fern assemblages.
 1797
 1798 This framing also addresses a potential issue around upland–lowland environments.
 1799
 1800 The fossil record preferentially preserves lowland coal-swamp vegetation, whereas sea-
 1801 sonally dry and upland floras are under-represented because their substrates were less
 1802 favourable for plant preservation [90, 91]. Nevertheless, direct evidence indicates that
 1803 Pennsylvanian uplands supported giant cordaitalean forests, and broader syntheses
 1804 argue that drought-tolerant floras were not restricted to uplands but occupied exten-
 1805 sive dryland habitats that are strongly under-sampled in the fossil record [91, 92].
 1806
 1807 Our model does not explicitly assign different Paleozoic taxa to upland and lowland
 1808 habitats. This is a limitation for reconstructing detailed vegetation ecology, but it
 1809 is less consequential for the climate experiment because both lowland/wetland and
 1810 upland/dryland settings could support forest or low-woody cover during the LPIA.
 1811 Lineage-specific differences in rooting depth, canopy density, and transpiration would
 1812 affect the magnitude of regional fluxes, but they do not remove the first-order contrast
 1813 between forested and unvegetated surfaces.
 1814
 1815 The grass PFTs require a separate caveat. Where TRIFFID allocates C_3 or C_4
 1816 grasses in Paleozoic simulations, these should not be read as literal grasses. Open
 1817 and low-stature Paleozoic habitats would instead have contained mixtures of herba-
 1818 ceous lycopsids, small ferns, sphenopsids, bryophytes, cryptogamic ground covers, and
 1819 bare substrate [83, 93, 94]. Relative to such assemblages, modern grass PFTs likely
 1820 overestimate leaf area, stomatal transpiration, and aerodynamic roughness, although
 1821 cryptogamic covers could locally produce lower albedo than grasses. This introduces
 1822 a possible non-conservative bias in grass-dominated grid cells: the simulated baseline–
 1823 NOVEG contrast may be too large where the Paleozoic landscape would have been
 1824 open, low-stature, or cryptogam-covered rather than grassland. This caveat would
 1825 affect the local and absolute energy fluxes, but it does not modify the main conclusion
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because the strongest LPIA amplification is associated with cold-region snow mask-
ing and moisture recycling by tree and shrub PFTs, not with a uniquely grass-driven
mechanism.

Thus, the modern PFT representation introduces parametric uncertainty, espe-
cially for open landscapes, but the core result is robust. The simulations test the
climatic importance of vascular vegetation as a set of surface properties—dark
canopies, snow masking, roughness, evapotranspiration, and soil-water storage—rather
than the climate effect of any particular modern clade. Taxonomic mismatch therefore
affects quantitative magnitudes but not the inferred state-dependent amplification of
the biophysical processes of vegetation.

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