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3 Title

Coupled, decoupled, and abrupt responses of vegetation to climate across timescales

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6263 Peer-review Statement

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65 This manuscript has been submitted to *Science* and is not peer-reviewed. This preprint has been

66 submitted to EarthArXiv. Subsequent versions of this manuscript may have slightly different

67 content. If accepted, the final version of this manuscript will be available via the 'Peer-reviewed

68 Publication DOI' link on the right-hand side of this webpage.

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- 70 71

93 Abstract

94

95 Climate and ecosystem dynamics vary across timescales, but research into climate-driven

96 vegetation dynamics usually focuses on singular timescales. We develop a spectral analysis-

97 based approach that provides detailed estimates of the timescales at which vegetation tracks

98 climate change, from 10^1 to 10^5 years. We report similarity of vegetation and climate even at

- 99 centennial frequencies (149⁻¹ to 18,012⁻¹ years⁻¹). A breakpoint in vegetation turnover (797⁻¹
- 100 years⁻¹) matches a breakpoint between stochastic and autocorrelated climate processes,
- 101 suggesting that ecological dynamics are governed by climate across these frequencies.
- Heightened vegetation turnover at millennial frequencies $(4,650^{-1} \text{ years}^{-1})$ highlights the risk of
- abrupt responses to climate change, while vegetation-climate decoupling at frequencies >149⁻¹
- 104 years⁻¹ may indicate long-lasting consequences of anthropogenic climate change for ecosystem
 105 function and biodiversity.
- 106

107 Keywords

108

109 Spectral power continuum, community turnover, climate variability, dynamic equilibrium, non-

110 linear ecological dynamics, temporal beta diversity, vegetation 111

112 Manuscript Text

113

114 Characterizing ecological dynamics across timescales is urgently required to understand how and

at what rates ecosystems are likely to respond to anthropogenic climate change. Species and

116 ecosystems differ in their responses to changing climates and these dynamics are timescale

dependent (1-4). The climate system exhibits two interconnected modes of variability: short-

118 term, stochastic, weather variations that scale to large, autoregressive, climate fluctuations at

timescales longer than 100 to 1,000 years (5, 6). Yet, most studies of climate-driven ecological

- 120 dynamics have focused on narrow ranges of timescales (7).
- 121

122 Global networks of ecological and paleontological data (8, 9) now enable us to characterize, in

- 123 ways not previously possible, ecological responses to climate forcing across timescales and
- 124 modes of climate variability. Former research has shown that fast ecological dynamics track
- 125 climate change (10, 11), while slow dynamics are lagged or decoupled from climate (12-15).
- 126 Ecosystems can also linearly or nonlinearly respond to forcing, with the potential to lead to
- 127 unexpected species' compositional changes (16).
- 128

129 Here, we focus on the relationships among temperature, precipitation, and vegetation

130 compositional turnover in paleoecological records spanning hundreds to hundreds of thousands

131 of years over the last 600,000 years. To quantify the coupling, decoupling, and scaling of climate

- drivers and ecological responses across timescales, we create and apply a conceptual and
- analytical framework rooted in spectral analysis (17). Whereas, many time series methods are
- 134 only capable of examining vegetation-climate coupling at discrete temporal lags, in the
- 135 frequency domain spectral analysis overcomes this limitation by comprehensively decomposing
- time series variability into specific timescales of observation. This decomposition is quantified in the neuron encourage and provides insists the relative specific timescale of the relative
- 137 the power spectrum and provides insights into the relative contributions of different timescales to
- 138 overall climate or vegetation variability.

- 139
- Through this approach, we generate global power spectra of vegetation variability by averaging 140
- 141 site-level power spectra for fossil pollen assemblages across a global compilation of 1,321 sites
- 142 (8, 9), with the densest coverage for the last 20,000 years (Fig. S1, Fig. S2). We compare these
- 143 global vegetation compositional changes to power spectra of temperature and precipitation from
- 144 a climate model simulation of the last 21,000 years (TraCE-21ka, Fig. S3, Fig. S4, Fig. S5, Fig.
- 145 S6) (18, 19). To capture lower-frequency climate variability, we include proxy temperature
- 146 reconstructions that approximate global climate over the last two million years (20, 21).
- 147

148 Paired Spectral Analysis of Climate and Vegetation: Analytical and Conceptual Framework

- 149 150
- 151 The exponential coefficient (β) of the power-law relationship (S(f) \propto f^{- β}) between spectral power
- 152 (S) and frequency (f) defines the spectral continuum, quantifies how variance is partitioned
- 153 across frequencies in power spectra of climate and ecological turnover, and identifies dynamic
- 154 similarity between these systems across timescales (Fig. S7) (22, 23). If vegetation composition
- 155 changes in parallel with climate variability, the β s for vegetation should be similar to climate
- 156 variability. For instance, a shift in low-frequency climate variability will induce a change in
- 157 vegetation turnover at the same frequencies. However, the drivers of vegetation compositional
- 158 change vary in relative importance across timescales (Fig. 1): disturbance, biotic interactions,
- 159 and demographic processes are thought to be more important at short timescales; migration lags 160
- and other dispersal limitation, population dynamics, restriction to refugia, and ecosystem
- 161 transformation dominate at intermediate timescales; and macroevolutionary processes such as 162 speciation and extinction prevail on longer timescales (Fig. 1) (1, 2). These processes modulate
- 163 vegetation responses to climate and may cause the continuum of vegetation variability to diverge
- 164 from climate ($\beta_{\text{veg}} \neq \beta_{\text{clim}}$).
 - 165
 - 166 We expect that matching β s for climate and vegetation are likely to emerge at intermediate
 - frequencies (~1,000⁻¹ to 100,000⁻¹ years⁻¹) given previous work (10, 11) (Fig. 1). At these 167
 - intermediate frequencies, the processes regulating assemblage composition can keep up with 168 169 climate change (10, 11) leading to $\beta_{\text{veg}} = \beta_{\text{clim}}$ (Fig. 1A). Across frequencies when $\beta_{\text{veg}} = \beta_{\text{clim}}$, we
 - 170 infer that vegetation is tracking climate and use the term 'fast tracking' (11), even though our
 - 171 methods do not test for causal links.
 - 172
 - 173 The relationship between climate and vegetation dynamics at lower ($< 100,000^{-1}$ years⁻¹) and
 - 174 higher frequencies (> $1,000^{-1}$ years⁻¹) remains an open question, as does the frequencies at which
 - 175 the assumption of fast tracking no longer holds (12). High frequencies are particularly crucial for
 - 176 predicting vegetation responses to rapid, anthropogenic climate warming, as they examine how
 - 177 ecological and life-history factors may override the influence of climate variability. The
 - 178 vegetation response at high frequencies may be slow, because trees tend to have lifespans of 10^2
 - 179 to 10³ years (24), producing larger β in vegetation turnover than in climate (Fig. 1B, $\beta_{veg} > \beta_{clim}$).
 - 180 Conversely, disturbance through herbivory, fire, human land use, and disease could increase
 - 181 vegetation turnover at high frequencies decreasing β relative to climate (Fig. 1B, $\beta_{veg} < \beta_{clim}$)
 - 182 (25).
 - 183

- 184 At low frequencies, vegetation dynamics distinct from intermediate and high frequencies may
- 185 emerge. Climate tracking could persist, as expected at intermediate frequencies (Fig. 1C, $\beta_{veg} =$
- 186 β_{clim}), or adaptive evolution could increase species' tolerances to new climate regimes (26),
- 187 potentially reducing compositional responses to climate forcing. Consequently, vegetation 188 turnover variability would increase minimally relative to climate variations (Fig. 1C, $\beta_{veg} < \beta_{clim}$).
- 189 Conversely, if vegetation responses to environmental forcings are characterized by strong non-
- 190 linearities (16, 27), variability in vegetation turnover would be high relative to climate (Fig. 1C,
- 191 $\beta_{\text{veg}} > \beta_{\text{clim}}$).
- 192

193 Spectral continuum of vegetation variability

194

195 To meaningfully compare climate and vegetation turnover we align their spatio-temporal

- 196 characteristics through downsampling and low-pass filtering the climate model simulations (28).
- 197 The proxy estimates of global climate variability cannot undergo this processing, resulting in
- spatiotemporal characteristics that differ from the fossil pollen records. We assess the effects of
- temporal uncertainty and uneven spatiotemporal coverage of the vegetation turnover data on the
- 200 averaged power spectra (Fig. 2) by resampling sites and their corresponding posterior age
- 201 estimates to produce an ensemble of power spectra, estimates of β , and estimates of the
- 202 breakpoints in β (28). Lastly, we assess the sensitivity of our results to sedimentary (Fig. 2),
- resolution (Fig. S8), dimensionality reduction (Fig. S9, Fig. S10, Fig. S11, Fig. S12), power
- 204 spectra and β estimation (Fig. S9, Fig. S10, Fig. S13, Fig. S14), and spatiotemporal sampling
- biases (Fig. S15, Fig. S16, Fig. S17) and find that our conclusions are insensitive to each (28).
- 206 207 We find that the spectral continuum of variability in vegetation turnover carries clear similarities
- 208 to that of the climate system (Fig. 2), yet the relationship to climate varies with frequency. The
- 209 power spectrum of vegetation turnover appears to follow the climate system across the scaling 210 breakpoint reported in previous studies (5, 6) and also found here, supporting the interpretation
- breakpoint reported in previous studies (5, 6) and also found here, supporting the interpretation that vegetation dynamically tracks the climate system at intermediate frequencies (Fig. 1, Fig. 2,
- Table S1, 693^{-1} — 649^{-1} years⁻¹ for temperature; 691^{-1} — 660^{-1} years⁻¹ for precipitation; 862^{-1} —
- 212 ratio 51,055 or years for temperature, 051 000 years for precipitation, 802 213 797^{-1} years⁻¹ for vegetation turnover) (10). However, unlike temperature and precipitation (5, 6),
- the vegetation turnover power spectrum has two additional breakpoints, at 149^{-1} years⁻¹ (95% CI:
- 215 154^{-1} , 145^{-1}) and $18,012^{-1}$ years⁻¹ (18,952⁻¹, 17,254⁻¹) (uncertainties for all parameters estimated
- are reported in Table S1). The vegetation turnover power spectra are therefore characterized by four scaling regimes: high frequencies ($< 149^{-1}$ years⁻¹); high-intermediate frequencies (149⁻¹ to
- 217 Four scaling regimes. Ingli requencies ($> 149^{-1}$ years $^{-1}$); ingli-intermediate frequencies (797^{-1} to $18,012^{-1}$ years $^{-1}$); and low frequencies (>
- $18,012^{-1}$ years ⁻¹). The additional breakpoints in the continuum of the vegetation turnover power
- spectrum found in the global average (Fig. 2) are also found in the spectra of individual time
- series (Fig. S18), indicating that the patterns are not an artifact of the ensemble approach.
- 222 Together, these features of the vegetation turnover power spectra provide evidence that the
- relationship between plant assemblages and climate is timescale-dependent and complex.
- Ecological communities and climate may co-vary on some timescales but differ in their dynamics on others, which we detail below.
- 225 226
- **Timescales of Ecological Dynamics**
- 228
- 229 Coupled Dynamics

- 230
- We show evidence of climate and vegetation coupling between 149⁻¹ to 18,012⁻¹ years⁻¹ (Fig. 2),
- which is a narrower range of frequencies than previously theorized (10). First, for both
- 233 vegetation and climate, β s are near zero at frequencies from 149⁻¹ to 797⁻¹ years⁻¹, and ~2 at
- frequencies from 797⁻¹ to 18,012⁻¹ years⁻¹. Second, scaling breakpoints are aligned for vegetation
- and climate between 672^{-1} and 797^{-1} years⁻¹ (Fig. 1). This period of vegetation and climate coupling spans the theorized (29) and observed scaling break (5, 6) that separates weather and
- climate variability and suggests a foundational shift in vegetation turnover from autocorrelated to
- 238 stochastic at frequencies of ca. 670 to 800⁻¹ years ⁻¹ is related to coupled atmosphere-ocean-
- 239 vegetation processes (29).
- 240
- 241 This finding sharpens our understanding of the frequencies at which plant communities rapidly
- and dynamically adjust composition and structure in response to climate forcing. Prior theory and the observations of orbital signals in pollen records have led to the widespread agreement of
- and the observations of orbital signals in pollen records have led to the widespread agreement of fast tracking of climate by vegetation composition at frequencies of $1,000^{-1}$ to $100,000^{-1}$ years⁻¹
- 1244 fast tracking of climate by vegetation composition at frequencies of 1,000 ⁻¹ to 100,000 ⁻¹ years ⁻¹ (10, 11). However, whether vegetation rapidly tracks climate at sub-millennial frequencies (10^{-2}
- (10, 11). However, whether vegetation rapidly tracks climate at sub-infinential frequencies (10) to 10^{-3} years⁻¹) was previously unclear, with evidence for and against climate disequilibrium at
- frequencies of 50^{-1} to 200^{-1} years $^{-1}$ (12, 30). Our work thus expands prior knowledge by
- suggesting climate tracking by vegetation for frequencies as short as 149⁻¹ years⁻¹.
- 249
- The small $\beta \sim 0$ for vegetation turnover between 149⁻¹ to 797⁻¹ years⁻¹ indicates that variance is
- equally partitioned across this frequency range and suggests stochastic processes, such as
- extreme weather events or disturbances, yield small changes in abundance without a wholesale
- 253 change in vegetation composition (Fig. 2). In contrast, a $\beta \sim 2$ from 797⁻¹ to 18,012⁻¹ years⁻¹
- 254 indicates more variance at lower frequencies and autocorrelated dynamics. These dynamics can
- 255 result from vegetation directly tracking autocorrelated processes in the climate system or from
- ecological processes that increase autocorrelation, such as density-dependent processes and
- 257 priority effects.
- 258
- Although the breakpoint for vegetation turnover at 797⁻¹ years⁻¹ is statistically distinguishable from temperature and precipitation (Table S2), these differences likely reflect the limitations of
- the approach. The non-random subset of communities recorded by these vegetation assemblage
- records, our choice of climate model, or biased local/regional spectral estimates from climate
- 263 models (*31*) all could affect the precise location of the breakpoint and lead to an apparent offset.
- However, if this offset between the vegetation and climate breakpoints is real, two hypotheses
 may explain the brief decoupling of climate and vegetation between frequencies of 676⁻¹—672⁻¹
- 266 years⁻¹ and 797⁻¹ years⁻¹: a lag in vegetation response to the transition from low β to higher β 267 weather-climate scaling regimes or the greater importance of non-climatic forcing (such as
- 268 disturbance regimes) at these frequencies.
- 269

270 Uncoupled Dynamics

- 271
- 272 Vegetation and climate appear decoupled at frequencies higher than 149⁻¹ years⁻¹ and lower than
- 273 18,012⁻¹ years⁻¹. β is 4.34 (3.64, 4.96) for vegetation turnover at the highest frequencies, while
- for temperature and precipitation, β is -0.24 (-0.29, -0.18) and -0.52 (-0.58, -0.49), respectively
- 275 (Fig. 2, Table S1). This finding supports prior observations of higher β s in vegetation turnover at

276 these high frequencies (32) but appears sensitive to the amount of weight given to abundant and 277 rare taxa when estimating vegetation turnover with dissimilarity metrics and the fossil pollen 278 record under consideration (Fig. S9). Some combination of taphonomy, sampling, and ecological 279 processes could explain higher β s in vegetation turnover at these high frequencies. Decadal-scale 280 mixing of lake sediments and scale gaps caused by discontinuous sampling of sediments may 281 enhance autocorrelation in vegetation turnover variability from these archives (33, 34). In 282 addition, the large β s at the highest frequencies may result from the long life spans of some 283 plants (e.g. trees, which are well-represented in fossil pollen assemblages), limiting the ability of 284 the full assemblage to track high frequency climate variability due to slow turnover times. 285 Indeed, the median tree lifespan from the International Tree Ring Data Bank (35, 36) is 246 286 years (n = 4,773) (Fig. S19). A long lifespan may impart a high β as vegetation turnover would 287 increase approaching the frequency of median tree longevity from increasing mortality. 288 Anthropogenic land use change may also contribute to climate decoupling at high frequencies 289 (37, 38), possibly interacting with tree longevity. Notably, a greater β for vegetation turnover at 290 the highest frequencies is consistent with observations of slow vegetation responses to climate 291 variability and evidence of climate debt (13–15, 39). These slow responses are expected to create 292 mismatches between species' climate preferences and climate and thus reduce organismal fitness 293 and ecosystem function.

294

295 For frequencies lower than 18,012⁻¹ years⁻¹ (18,952⁻¹, 17,254⁻¹), β =-0.08 (-0.23, -0.06) for the

- 296 vegetation turnover power spectrum (Fig. 2). This contrasts with the climate power spectra,
- which maintain the long-term climate system β s of ~2-3 due to the influence of astronomical forcing (Fig. 2) (40). There are two possible explanations for low β s in vegetation turnover at
- these low frequencies. First, the community dissimilarity metric we use to quantify vegetation
- 300 turnover within each time series may reach a maximum value (i.e. metric saturation, Fig. S20)
- 301 and fail to record turnover beyond a complete replacement of the vegetation assemblage (41).
- 302 For example, if climate change caused multiple assemblage turnovers (assemblage A replaced by
- 303 B replaced by C), community dissimilarity metrics will saturate and underestimate the true
- 304 ecological impact of past climate change, producing an apparent decrease in vegetation turnover
- 305 with decreasing frequency. Second, fast evolutionary adaptation would increase species tolerance
- to environmental variation and result in vegetation communities appearing relatively resistant to
- 307 climate forcing. Although local adaptation cannot be excluded as an explanation, the hypothesis
- 308 of metric saturation appears sufficient to explain the reduced vegetation turnover variability at 309 low frequencies (Fig. S9).
- 310

311 Non-Linearity in the Climate-Vegetation Relationship

312

High spectral power at 4,650⁻¹ years⁻¹ is unique to vegetation turnover and is absent in the power spectra of the climate proxies and climate simulations we evaluated (Fig. 2, Fig. S3). Climate in

- the North Atlantic has been argued to contain apparent modes of climate variability at $1,470^{-1}$
- and $4,670^{-1}$ years⁻¹ (42) and provides a plausible mechanism for forcing vegetation turnover (30,
- 317 43, 44). However, global compilations of Holocene climate records lack high spectral power at
- any of these frequencies (Fig. S3)(45), as do the spectra of simulated temperature and
- 319 precipitation (Fig. 2). This disconnect at the global scale (and in the subset of sites we
- 320 investigated) between climate and vegetation turnover leads us to hypothesize that relatively

321 subtle or regional millennial-scale climate variations are amplified in the vegetation response by

- 322 non-linear ecological dynamics (27, 46).
- 323

However, analytical artifacts may also contribute to high spectral power at 4,650⁻¹ years⁻¹. Most

of our records span 20,000 years, with fewer longer records (186 sites, Fig. S1, Data S1). The

- relatively low number of sites sampled could bias our spatial and environmental coverage at low
- 327 frequencies, producing a spurious peak in spectral power. Despite these potential artifacts,
- evidence for nonlinear responses in vegetation assemblages to small environmental changes is
 well-documented (27). Our observations suggest slow vegetation responses to climate variability
- at high frequencies alongside high turnover at $4,650^{-1}$ years⁻¹, demonstrating how gradual
- 331 vegetation changes can be accompanied by abrupt, nonlinear shifts in vegetation assemblages.

332 Hence, even without clear patterns of climate variability in the North Atlantic at this frequency,

the vegetation dynamics over the last 600,000 years underscore the potential for abrupt changes

in plant assemblages over the coming decades of warming (47).

335

336 Latitudinal Gradient in Assemblage Dynamics

337

We find that the relationship between vegetation turnover variability and climate variability differs across latitudes. Climatically, the high latitudes experience greater temperature variability than the tropics at all frequencies (5), while the tropics experience greater precipitation variability (Fig. 3). Even though accurately simulating precipitation remains challenging, vegetation turnover appears to resemble temperature, in that tropical sites (< 23.5°) have less

vegetation turnover appears to resemble temperature, in that tropical sites (< 23.5⁻) have less vegetation variability than extra-tropical sites (> 23.5^o) (Fig. 3A). In addition, at frequencies of

 712^{-1} (730⁻¹, 698⁻¹) to 13,885⁻¹ (14,495⁻¹, 13,160⁻¹) years⁻¹, extra-tropical sites have a β of 2.20

(2.16, 2.26) that is similar to those of temperature and precipitation, while tropical sites have a β

of 1.30 (1.21, 1.38) (Fig. 3). Thus, tropical vegetation assemblages may be less sensitive to

347 climate forcing across the frequencies investigated, are sensitive to climate forcings other than

temperature and precipitation, are affected more by non-climatic factors, or are more stable and

349 resistant to turnover. Along these lines, recent observations show that while net primary 350 production in low latitudes is constrained by solar radiation and precipitation, high northern

350 production in low latitudes is constrained by solar radiation and precipitation, high northern latitude productivity is limited by temperature (48), suggesting these latitudinal differences in β

351 failude productivity is limited by temperature (48), suggesting these failudinal difference352 could result from spatially variable climate controls on vegetation variability.

353

354 Conclusions

355

356 Our theoretical framework, based on spectral analyses, provides a new pathway forward to

357 disentangle a fundamental question in ecology: how closely are ecological dynamics coupled or

decoupled with environmental dynamics across timescales? The methods shown here are flexible

and adaptable to all ecological systems with observational data across a range of timescales.

360 Through this framework, we show that the relationship between vegetation turnover and climate

361 variability is non-linear and timescale-dependent over frequencies from 10⁻¹ to 100,000⁻¹ years⁻¹.

362 The many similarities between vegetation and climate power spectra suggest that vegetation

363 variation is governed by climate variability across intermediate frequencies. Modes of

364 heightened variability in vegetation relative to climate at millennial frequencies underscore the

risk of nonlinear and abrupt vegetation responses to current climate change. Conversely, the

366 decoupling of vegetation and climate variability at higher frequencies (>149⁻¹ years⁻¹) reinforces

concerns that biotic processes will be slow to respond to anthropogenic climate change and
 changing climate variability (*12*, *49*), leading to delayed and widespread ecological transitions
 that challenge predicting vegetation responses to current warming.

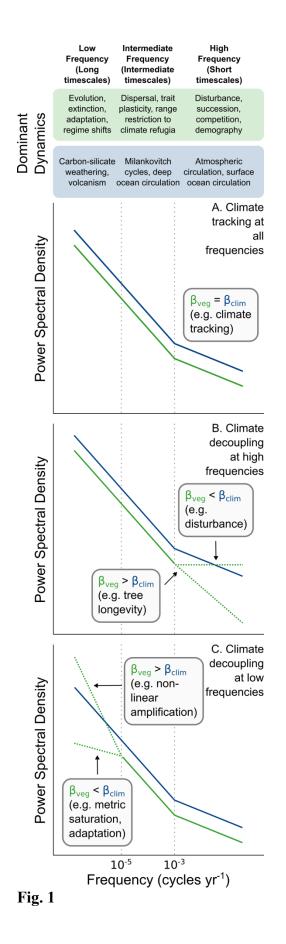
371 Acknowledgements

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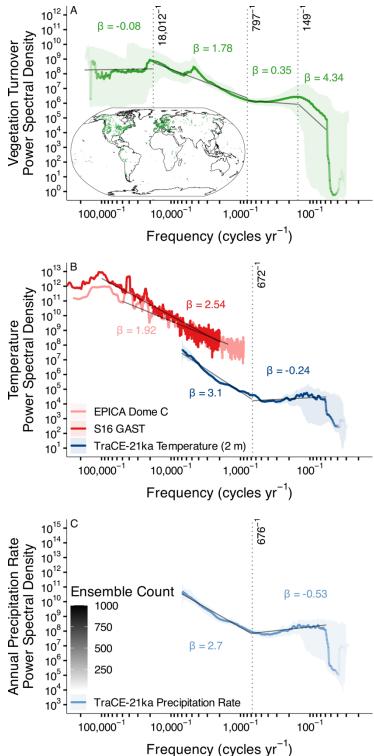
373 We are grateful to Yasuhiro Kubota for convening the P-SEEDS workshop where the idea for 374 this project began. Many thanks to the Syracuse University High Throughput Computing 375 Campus Grid (OrangeGrid) for providing computational resources and to Jon Cheney for 376 technical support. Fossil pollen data were obtained from the Neotoma Paleoecology Database 377 (http://www.neotomadb.org) and its constituent databases: the African Pollen Database, 378 European Pollen Database, Indo-Pacific Pollen Database, Latin American Pollen Database, and 379 North American Pollen Database. The work of data contributors, data stewards, and the Neotoma 380 community is gratefully acknowledged. We thank the anonymous reviewers for their feedback, 381 which greatly improved the manuscript. Funding: This project is a contribution to the 382 BioDeepTime project, supported by Paleosynthesis Project, which is funded by the Volkswagen 383 Foundation (Az 96 796). DF acknowledges postdoctoral support from NSF OCE-2103015, NSF 384 AGS-2402498, and the College of Arts and Sciences at Syracuse University. Funding for 385 OrangeGrid is provided by ACI-1341006. EES acknowledges support from a Leverhulme Prize 386 and NERC grant NE/V011405/1. LJ is supported through the German climate modeling initiative 387 PALMOD, funded by the German Ministry of Science and Education (BMBF, 01LP1922A). 388 MCR acknowledges support from the German Research Foundation (DFG) through the Cluster 389 of Excellence 'The Ocean Floor – Earth's Uncharted Interface' (EXC 2077, grant no. 390 390741603). PMH acknowledges sabbatical support from the Swiss Federal Institute for Forest, 391 Snow and Landscape Research. SRM acknowledges sabbatical support from UW-Madison and a 392 Guggenheim Fellowship. JWW acknowledges sabbatical support from UW-Madison and NSF 393 award 2410961. Author contributions: DF and PMH developed the research questions and 394 study design. DF, SRM, EES, JWW, and PMH co-developed the conceptual and analytical 395 framework. DF performed all analyses with help from SRM and EES. DF led writing with 396 support from SRM, EES, JWW, and PMH. The ideas for this paper originated from discussions 397 in the BioDeepTime working group. All authors reviewed and contributed to the article. Data 398 and materials availability: Data and code needed to reproduce all analyses are available on 399 Zenodo (74). 400

- 400
- 401
- 402 Figures



405 **Conceptual framework for eco-climate spectral analyses**

- 406 A conceptual framework for interpreting the relationship between vegetation and climate using
- 407 power spectra through the power-law scaling relationship between spectral power and frequency
- 408 $(S(f) \propto f^{\beta})$. The blue line corresponds to β for climate variability and the green line corresponds
- 409 to β for vegetation compositional turnover. The breakpoint in climate spectral power in all three
- 410 panels is based on prior work that indicates a breakpoint in climate variability at approximately
- 411 100^{-1} to 1,000⁻¹ years⁻¹ (5, 6). Key characteristics include the slope (β , i.e. continuum) of
- vegetation turnover relative to climate and the placement of breakpoints (dashed vertical lines).
 Three scenarios illustrate potential relationships between climate and vegetation. (A) Vegetation
- 415 Three scenarios inustrate potential relationships between climate and vegetation. (A) vegetation 414 composition exhibits linear responses to climate across all frequencies and so the slope of
- 415 vegetation spectral power parallels that of climate (10). (B) Vegetation linearly tracks climate at
- 416 intermediate frequencies and low frequencies (10) but is decoupled from climate at high
- 417 frequencies (50). At high frequencies, a higher β for vegetation than climate suggests that
- 418 processes such as tree longevity influence vegetation turnover while a lower β for vegetation
- 419 indicates that disturbance may be a primary control on turnover (25). (C) Vegetation tracks
- 420 climate across high and intermediate frequencies but is decoupled at low frequencies from
- 421 processes like evolutionary adaptation (lower β for vegetation) or non-linear amplification
- 422 through processes such as threshold responses (higher β for vegetation). Other scenarios and
- 423 biological processes are possible beyond those shown here.



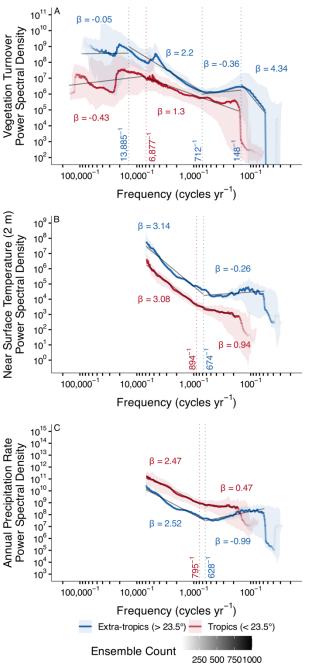
424 425 **Fig. 2**

426 The continuum of global vegetation turnover and climate variability

427 The spectral continuum of (A) vegetation turnover (green), (B) temperature (blue, red, pink), and

- 428 (C) precipitation (light blue) variability based on the median from an ensemble of spectral power
- 429 estimates. Power spectra line opacity indicates the number of ensemble members that resolve
- 430 each frequency with the corresponding legend for all plots in (C). β in the high frequency band

- 431 was fit to the maximum frequency that yielded an unbiased estimate (28). Solid gray lines
- 432 correspond to β from ordinary least squares regressions of log-spectral power and log-frequency.
- 433 Vertical dashed lines correspond to breakpoints identified in the spectral continuum. Climate
- 434 estimates from TraCE-21ka have been downsampled in space and time and low-pass filtered to
- 435 match the temporal characteristics of the fossil pollen abundances. Uncertainties for β and 426 here broken a superstation to the superstation of the superstat
- 436 breakpoints and permutation tests comparing these parameters are reported in Table S1, Table S3 437 Table S2 Fig. S21
- 437 Table S2, Fig. S21.
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441 Fig. 3

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442 The continuum of tropical and extra-tropical vegetation turnover and climate variability

- 443 The continuum of (A) vegetation turnover, (B) near-surface temperature, and (C) annual
- 444 precipitation rate variability, averaged for the extra-tropics (blue, $> 23.5^{\circ}$) and tropics (red, <
- 445 23.5°) based on the median from an ensemble of spectral power estimates. Power spectra line
- 446 opacity indicates the number of ensemble members that resolve each frequency. β in the high
- 447 frequency band was fit to the maximum frequency that yielded an unbiased estimate (28).
- 448 Vertical dashed lines correspond to breakpoints identified in the spectral continuum and are
- 449 colored by the corresponding spatial average. All climate estimates are from TraCE-21ka and
- 450 have been downsampled as in Fig. 2. Uncertainties for β and breakpoints, and permutation tests
- 451 comparing these parameters, are reported in Table S1, Table S4 Table S7, Fig. S22.
- 452

453 **References**

- J. Overpeck, C. Whitlock, B. Huntley, "Terrestrial Biosphere Dynamics in the Climate System: Past and Future" in *Paleoclimate, Global Change and the Future*, K. D. Alverson, T. F. Pedersen, R. S. Bradley, Eds. (Springer, Berlin, Heidelberg, 2003; https://doi.org/10.1007/978-3-642-55828-3_5)*Global Change — The IGBP Series*, pp. 81–103.
- 458
 458
 459
 2. E. M. Wolkovich, B. I. Cook, K. K. McLauchlan, T. J. Davies, Temporal ecology in the Anthropocene. *Ecology Letters* 17, 1365–1379 (2014).
- 460 3. D. Jablonski, Biotic interactions and macroevolution: extensions and mismatches across scales and
 461 levels. *Evolution* 62, 715–739 (2008).
- 462 4. R. E. Ricklefs, Community Diversity: Relative Roles of Local and Regional Processes. *Science* 235, 167–171 (1987).
- 464 5. P. Huybers, W. Curry, Links between annual, Milankovitch and continuum temperature variability.
 465 *Nature* 441, 329–332 (2006).
- 466
 6. F. Zhu, J. Emile-Geay, N. P. McKay, G. J. Hakim, D. Khider, T. R. Ault, E. J. Steig, S. Dee, J. W.
 467
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 468
 468
 468
 468
 468
 468
 46
- 469 7. M. Yasuhara, R. Danovaro, Temperature impacts on deep-sea biodiversity. *Biological Reviews* 91, 275–287 (2016).
- J. W. Williams, E. C. Grimm, J. L. Blois, D. F. Charles, E. B. Davis, S. J. Goring, R. W. Graham,
 A. J. Smith, M. Anderson, J. Arroyo-Cabrales, A. C. Ashworth, J. L. Betancourt, B. W. Bills, R. K.
 Booth, P. I. Buckland, B. B. Curry, T. Giesecke, S. T. Jackson, C. Latorre, J. Nichols, T. Purdum, R.
 E. Roth, M. Stryker, H. Takahara, The Neotoma Paleoecology Database, a multiproxy,
 international, community-curated data resource. *Quaternary Research* 89, 156–177 (2018).
- J. Smith, M. C. Rillo, Á. T. Kocsis, M. Dornelas, D. Fastovich, H.-H. M. Huang, L. Jonkers, W.
 Kiessling, Q. Li, L. H. Liow, M. Margulis-Ohnuma, S. Meyers, L. Na, A. M. Penny, K. Pippenger,
 J. Renaudie, E. E. Saupe, M. J. Steinbauer, M. Sugawara, A. Tomašových, J. W. Williams, M.
 Yasuhara, S. Finnegan, P. M. Hull, BioDeepTime: A database of biodiversity time series for
 modern and fossil assemblages. *Global Ecology and Biogeography* n/a (2023).
- 481 10. T. Webb, Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data.
 482 *Vegetatio* 67, 75–91 (1986).

- 483 11. J. W. Williams, A. Ordonez, J.-C. Svenning, A unifying framework for studying and managing
 484 climate-driven rates of ecological change. *Nat Ecol Evol* 5, 17–26 (2021).
- 485 12. J.-C. Svenning, B. Sandel, Disequilibrium vegetation dynamics under future climate change.
 486 *American Journal of Botany* 100, 1266–1286 (2013).
- 487 13. M. V. Talluto, I. Boulangeat, S. Vissault, W. Thuiller, D. Gravel, Extinction debt and colonization
 488 credit delay range shifts of eastern North American trees. *Nat Ecol Evol* 1, 1–6 (2017).
- 489 14. R. Bertrand, J. Lenoir, C. Piedallu, G. Riofrío-Dillon, P. de Ruffray, C. Vidal, J.-C. Pierrat, J.-C.
 490 Gégout, Changes in plant community composition lag behind climate warming in lowland forests.
 491 *Nature* 479, 517–520 (2011).
- 492 15. B. J. Butterfield, R. S. Anderson, C. A. Holmgren, J. L. Betancourt, Extinction debt and delayed
 493 colonization have had comparable but unique effects on plant community–climate lags since the
 494 Last Glacial Maximum. *Global Ecology and Biogeography* 28, 1067–1077 (2019).
- 495 16. M. Scheffer, S. Carpenter, J. A. Foley, C. Folke, B. Walker, Catastrophic shifts in ecosystems.
 496 *Nature* 413, 591–596 (2001).
- 497 17. D. J. Thomson, Spectrum estimation and harmonic analysis. *Proceedings of the IEEE* 70, 1055–
 498 1096 (1982).
- 499 18. F. He, Simulating Transient Climate Evolution of the Last Deglaciation with CCSM 3 (2011)vol. 72.
- 500 19. Z. Liu, B. L. Otto-Bliesner, F. He, E. C. Brady, R. Tomas, P. U. Clark, A. E. Carlson, J. Lynch501 Stieglitz, W. Curry, E. Brook, D. Erickson, R. Jacob, J. Kutzbach, J. Cheng, Transient Simulation of
 502 Last Deglaciation with a New Mechanism for Bølling-Allerød Warming. *Science* 325, 310–314
 503 (2009).
- 504 20. C. W. Snyder, Evolution of global temperature over the past two million years. *Nature* 538, 226–
 505 228 (2016).
- J. Jouzel, V. Masson-Delmotte, O. Cattani, G. Dreyfus, S. Falourd, G. Hoffmann, B. Minster, J.
 Nouet, J. M. Barnola, J. Chappellaz, H. Fischer, J. C. Gallet, S. Johnsen, M. Leuenberger, L.
 Loulergue, D. Luethi, H. Oerter, F. Parrenin, G. Raisbeck, D. Raynaud, A. Schilt, J. Schwander, E.
 Selmo, R. Souchez, R. Spahni, B. Stauffer, J. P. Steffensen, B. Stenni, T. F. Stocker, J. L. Tison, M.
 Werner, E. W. Wolff, Orbital and Millennial Antarctic Climate Variability over the Past 800,000
 Years. *Science* 317, 793–796 (2007).
- 512 22. T. Platt, K. L. Denman, Spectral Analysis in Ecology. Annu. Rev. Ecol. Syst. 6, 189–210 (1975).
- 513 23. M. E. Dillon, H. A. Woods, G. Wang, S. B. Fey, D. A. Vasseur, R. S. Telemeco, K. Marshall, S.
 514 Pincebourde, Life in the Frequency Domain: the Biological Impacts of Changes in Climate
 515 Variability at Multiple Time Scales. *Integrative and Comparative Biology* 56, 14–30 (2016).
- 516 24. G. M. Locosselli, R. J. W. Brienen, M. de S. Leite, M. Gloor, S. Krottenthaler, A. A. de Oliveira, J.
 517 Barichivich, D. Anhuf, G. Ceccantini, J. Schöngart, M. Buckeridge, Global tree-ring analysis
 518 reveals rapid decrease in tropical tree longevity with temperature. *Proceedings of the National*519 Academy of Sciences 117, 33358–33364 (2020).

- 520 25. L. B. Brubaker, Responses of tree populations to climatic change. Vegetatio 67, 119–130 (1986).
- Scheepens, Evolution of plant drought strategies and herbivore tolerance after two decades of climate change. *New Phytologist* 235, 773–785 (2022).
- 524 27. J. W. Williams, J. L. Blois, B. N. Shuman, Extrinsic and intrinsic forcing of abrupt ecological 525 change: case studies from the late Quaternary. *Journal of Ecology* **99**, 664–677 (2011).
- 526 28. Materials and methods are available as supplementary materials.
- 527 29. K. Hasselmann, Stochastic climate models Part I. Theory. *Tellus* 28, 473–485 (1976).
- J. W. Williams, D. M. Post, L. C. Cwynar, A. F. Lotter, A. J. Levesque, Rapid and widespread
 vegetation responses to past climate change in the North Atlantic region. *Geology* 30, 971–974
 (2002).
- 531 31. T. Laepple, E. Ziegler, N. Weitzel, R. Hébert, B. Ellerhoff, P. Schoch, B. Martrat, O. Bothe, E.
 532 Moreno-Chamarro, M. Chevalier, A. Herbert, K. Rehfeld, Regional but not global temperature
 533 variability underestimated by climate models at supradecadal timescales. *Nat. Geosci.* 16, 958–966
 534 (2023).
- 8. Hébert, L. Schild, T. Laepple, U. Herzschuh, Biome- and timescale-dependence of Holocene
 vegetation variability in the Northern Hemisphere. *Ecology and Evolution* 13, e10585 (2023).
- 33. R. Hébert, K. Rehfeld, T. Laepple, Comparing estimation techniques for temporal scaling in palaeoclimate time series. *Nonlinear Processes in Geophysics* 28, 311–328 (2021).
- Statistic and Statistic and Statistical S
- 541 35. H. D. Grissino-Mayer, H. C. Fritts, The International Tree-Ring Data Bank: an enhanced global database serving the global scientific community. *The Holocene* 7, 235–238 (1997).
- 543 36. S. Zhao, N. Pederson, L. D'Orangeville, J. HilleRisLambers, E. Boose, C. Penone, B. Bauer, Y.
 544 Jiang, R. D. Manzanedo, The International Tree-Ring Data Bank (ITRDB) revisited: Data
 545 availability and global ecological representativity. *Journal of Biogeography* 46, 355–368 (2019).
- 546 37. O. Mottl, S. G. A. Flantua, K. P. Bhatta, V. A. Felde, T. Giesecke, S. Goring, E. C. Grimm, S.
 547 Haberle, H. Hooghiemstra, S. Ivory, P. Kuneš, S. Wolters, A. W. R. Seddon, J. W. Williams, Global acceleration in rates of vegetation change over the past 18,000 years. *Science* 372, 860–864 (2021).
- 549 38. L. Stephens, D. Fuller, N. Boivin, T. Rick, N. Gauthier, A. Kay, B. Marwick, C. G. Armstrong, C. 550 M. Barton, T. Denham, K. Douglass, J. Driver, L. Janz, P. Roberts, J. D. Rogers, H. Thakar, M. 551 Altaweel, A. L. Johnson, M. M. Sampietro Vattuone, M. Aldenderfer, S. Archila, G. Artioli, M. T. 552 Bale, T. Beach, F. Borrell, T. Braje, P. I. Buckland, N. G. Jiménez Cano, J. M. Capriles, A. Diez 553 Castillo, C. Cilingiroğlu, M. Negus Cleary, J. Conolly, P. R. Coutros, R. A. Covey, M. Cremaschi, 554 A. Crowther, L. Der, S. di Lernia, J. F. Doershuk, W. E. Doolittle, K. J. Edwards, J. M. Erlandson, 555 D. Evans, A. Fairbairn, P. Faulkner, G. Feinman, R. Fernandes, S. M. Fitzpatrick, R. Fyfe, E. 556 Garcea, S. Goldstein, R. C. Goodman, J. Dalpoim Guedes, J. Herrmann, P. Hiscock, P. Hommel, K. 557 A. Horsburgh, C. Hritz, J. W. Ives, A. Junno, J. G. Kahn, B. Kaufman, C. Kearns, T. R. Kidder, F.

- 558 Lanoë, D. Lawrence, G.-A. Lee, M. J. Levin, H. B. Lindskoug, J. A. López-Sáez, S. Macrae, R. 559 Marchant, J. M. Marston, S. McClure, M. D. McCoy, A. V. Miller, M. Morrison, G. Motuzaite Matuzeviciute, J. Müller, A. Nayak, S. Noerwidi, T. M. Peres, C. E. Peterson, L. Proctor, A. R. 560 561 Randall, S. Renette, G. Robbins Schug, K. Ryzewski, R. Saini, V. Scheinsohn, P. Schmidt, P. 562 Sebillaud, O. Seitsonen, I. A. Simpson, A. Sołtysiak, R. J. Speakman, R. N. Spengler, M. L. Steffen, 563 M. J. Storozum, K. M. Strickland, J. Thompson, T. L. Thurston, S. Ulm, M. C. Ustunkaya, M. H. 564 Welker, C. West, P. R. Williams, D. K. Wright, N. Wright, M. Zahir, A. Zerboni, E. Beaudoin, S. 565 Munevar Garcia, J. Powell, A. Thornton, J. O. Kaplan, M.-J. Gaillard, K. Klein Goldewijk, E. Ellis, 566 Archaeological assessment reveals Earth's early transformation through land use. Science 365, 897-567 902 (2019).
- 568 39. K. Zhu, C. W. Woodall, J. S. Clark, Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology* 18, 1042–1052 (2012).
- 570 40. S. R. Meyers, L. A. Hinnov, Northern Hemisphere glaciation and the evolution of Plio-Pleistocene
 571 climate noise. *Paleoceanography* 25 (2010).
- 572 41. S. Ferrier, G. Manion, J. Elith, K. Richardson, Using generalized dissimilarity modelling to analyse
 573 and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and*574 *Distributions* 13, 252–264 (2007).
- 42. G. Bond, W. Showers, M. Cheseby, R. Lotti, P. Almasi, P. deMenocal, P. Priore, H. Cullen, I.
 Hajdas, G. Bonani, A pervasive millennial-scale cycle in North Atlantic Holocene and glacial
 climates. *Science* 278, 1257–1266 (1997).
- 578 43. D. Fastovich, J. M. Russell, S. T. Jackson, T. R. Krause, S. A. Marcott, J. W. Williams, Spatial
 579 fingerprint of Younger Dryas cooling and warming in eastern North America. *Geophysical*580 *Research Letters* 47, e2020GL090031 (2020).
- 44. B. Huntley, J. R. M. Allen, Y. C. Collingham, T. Hickler, A. M. Lister, J. Singarayer, A. J. Stuart,
 M. T. Sykes, P. J. Valdes, Millennial climatic fluctuations are key to the structure of last glacial
 ecosystems. *PloS one* 8 (2013).
- 45. H. Wanner, J. Beer, J. Butikofer, T. J. Crowley, U. Cubasch, J. Fluckiger, H. Goosse, M. Grosjean,
 F. Joos, J. O. Kaplan, M. Kuttel, S. A. Muller, I. C. Prentice, O. Solomina, T. F. Stocker, P.
 Tarasov, M. Wagner, M. Widmann, Mid- to Late Holocene climate change: an overview. *Quaternary Science Reviews* 27, 1791–1828 (2008).
- 588 46. D. Magri, Patterns of post-glacial spread and the extent of glacial refugia of European beech (Fagus sylvatica). *Journal of Biogeography* 35, 450–463 (2008).
- 47. M. G. Turner, W. J. Calder, G. S. Cumming, T. P. Hughes, A. Jentsch, S. L. LaDeau, T. M. Lenton,
 B. N. Shuman, M. R. Turetsky, Z. Ratajczak, J. W. Williams, A. P. Williams, S. R. Carpenter,
 Climate change, ecosystems and abrupt change: science priorities. *Philosophical Transactions of the Royal Society B: Biological Sciences* 375, 20190105 (2020).
- 48. R. R. Nemani, C. D. Keeling, H. Hashimoto, W. M. Jolly, S. C. Piper, C. J. Tucker, R. B. Myneni,
 S. W. Running, Climate-Driven Increases in Global Terrestrial Net Primary Production from 1982
 to 1999. *Science* 300, 1560–1563 (2003).

- 597 49. J. Aguirre-Gutiérrez, S. Díaz, S. W. Rifai, J. J. Corral-Rivas, M. G. Nava-Miranda, R. González-M. 598 A. B. Hurtado-M, N. S. Revilla, E. Vilanova, E. Almeida, E. A. de Oliveira, E. Alvarez-Davila, L. 599 F. Alves, A. C. S. de Andrade, A. C. Lola da Costa, S. A. Vieira, L. Aragão, E. Arets, G. A. Aymard 600 C., F. Baccaro, Y. V. Bakker, T. R. Baker, O. Bánki, C. Baraloto, P. B. de Camargo, E. Berenguer, 601 L. Blanc, D. Bonal, F. Bongers, K. M. Bordin, R. Brienen, F. Brown, N. C. C. S. Prestes, C. V. 602 Castilho, S. C. Ribeiro, F. C. de Souza, J. A. Comiskey, F. C. Valverde, S. C. Müller, R. da Costa 603 Silva, J. D. do Vale, V. de Andrade Kamimura, R. de Oliveira Perdiz, J. del Aguila Pasquel, G. 604 Derroire, A. Di Fiore, M. Disney, W. Farfan-Rios, S. Fauset, T. R. Feldpausch, R. F. Ramos, G. F. 605 Llampazo, V. F. Martins, C. Fortunel, K. G. Cabrera, J. G. Barroso, B. Hérault, R. Herrera, E. N. 606 Honorio Coronado, I. Huamantupa-Chuquimaco, J. J. Pipoly, K. J. Zanini, E. Jiménez, C. A. Joly, 607 M. Kalamandeen, J. Klipel, A. Levesley, W. L. Oviedo, W. E. Magnusson, R. M. dos Santos, B. S. 608 Marimon, B. H. Marimon-Junior, S. M. de Almeida Reis, O. A. Melo Cruz, A. M. Mendoza, P. 609 Morandi, R. Muscarella, H. Nascimento, D. A. Neill, I. O. Menor, W. A. Palacios, S. Palacios-Ramos, N. C. Pallqui Camacho, G. Pardo, R. T. Pennington, L. de Oliveira Pereira, G. Pickavance, 610 611 R. C. Picolotto, N. C. A. Pitman, A. Prieto, C. Ouesada, H. Ramírez-Angulo, M. Réjou-Méchain, Z. 612 R. Correa, J. M. Reyna Huaymacari, C. R. Rodriguez, G. Rivas-Torres, A. Roopsind, A. Rudas, B. 613 Salgado Negret, M. T. van der Sande, F. D. Santana, F. A. Maës Santos, R. S. Bergamin, M. R. 614 Silman, C. Silva, J. S. Espejo, M. Silveira, F. C. Souza, M. J. P. Sullivan, V. Swamy, J. Talbot, J. J. 615 Terborgh, P. J. van der Meer, G. van der Heijden, B. van Ulft, R. V. Martinez, L. Vedovato, J. 616 Vleminckx, V. A. Vos, V. Wortel, P. A. Zuidema, J. A. Zwerts, S. G. W. Laurance, W. F. Laurance, 617 J. Chave, J. W. Dalling, J. Barlow, L. Poorter, B. J. Enquist, H. ter Steege, O. L. Phillips, D. 618 Galbraith, Y. Malhi, Tropical forests in the Americas are changing too slowly to track climate 619 change. Science 387, ead15414 (2025).
- M. B. Davis, "Quaternary history and the stability of forest communities" in *Forest Succession: Concepts and Application*, D. C. West, H. H. Shugart, D. B. Botkin, Eds. (Springer New York, New York, NY, 1981; https://doi.org/10.1007/978-1-4612-5950-3 10), pp. 132–153.
- 51. M. Chevalier, B. A. S. Davis, O. Heiri, H. Seppa, B. M. Chase, K. Gajewski, T. Lacourse, R. J.
 Telford, W. Finsinger, J. Guiot, N. Kuhl, S. Y. Maezumi, J. R. Tipton, V. A. Carter, T. Brussel, L.
 N. Phelps, A. Dawson, M. Zanon, F. Valle, C. Nolan, A. Mauri, A. de Vernal, K. Izumi, L.
 Holmstrom, J. Marsicek, S. Goring, P. S. Sommer, M. Chaput, D. Kupriyanov, Pollen-based climate
 reconstruction techniques for late Quaternary studies. *Earth-Sci. Rev.* 210, 33 (2020).
- 52. T. Webb, S. E. Howe, R. H. W. Bradshaw, K. M. Heide, Estimating plant abundances from pollen
 percentages: The use of regression analysis. *Review of Palaeobotany and Palynology* 34, 269–300 (1981).
- 631 53. A. Parnell, Bchron: Radiocarbon dating, age-depth modelling, relative sea level rate estimation, and
 632 non-parametric phase modelling. *R package version* 4 (2014).
- 633 54. A. C. Parnell, J. Sweeney, T. K. Doan, M. Salter-Townshend, J. R. M. Allen, B. Huntley, J. Haslett,
 634 Bayesian inference for palaeoclimate with time uncertainty and stochastic volatility, *Journal of the*635 *Royal Statistical Society: Series C (Applied Statistics)*. 64 (2014)pp. 115–138.
- 55. P. J. Reimer, W. E. N. Austin, E. Bard, A. Bayliss, P. G. Blackwell, C. B. Ramsey, M. Butzin, H.
 Cheng, R. L. Edwards, M. Friedrich, P. M. Grootes, T. P. Guilderson, I. Hajdas, T. J. Heaton, A. G.
 Hogg, K. A. Hughen, B. Kromer, S. W. Manning, R. Muscheler, J. G. Palmer, C. Pearson, J. van der
 Plicht, R. W. Reimer, D. A. Richards, E. M. Scott, J. R. Southon, C. S. M. Turney, L. Wacker, F.
 Adolphi, U. Büntgen, M. Capano, S. M. Fahrni, A. Fogtmann-Schulz, R. Friedrich, P. Köhler, S.
 Kudsk, F. Miyake, J. Olsen, F. Reinig, M. Sakamoto, A. Sookdeo, S. Talamo, The IntCal20

- Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). *Radiocarbon* 62, 725–
 757 (2020).
- A. G. Hogg, T. J. Heaton, Q. Hua, J. G. Palmer, C. S. Turney, J. Southon, A. Bayliss, P. G.
 Blackwell, G. Boswijk, C. B. Ramsey, C. Pearson, F. Petchey, P. Reimer, R. Reimer, L. Wacker,
 SHCal20 Southern Hemisphere Calibration, 0–55,000 Years cal BP. *Radiocarbon* 62, 797–778
 (2020).
- 57. S. G. A. Flantua, O. Mottl, K. P. Bhatta, V. A. Felde, T. Giesecke, S. J. Goring, E. C. Grimm, S. G.
 Haberle, H. Hooghiemstra, S. J. Ivory, P. Kuneš, S. Wolters, A. W. R. Seddon, J. W. Williams,
 Mottl et al. (2021, Science) Taxonomic harmonization tables for North America, Latin America,
 Europe, Asia, Africa, figshare (2021); https://doi.org/10.6084/m9.figshare.13049735.v2.
- 58. D. Fastovich, J. M. Russell, S. T. Jackson, J. W. Williams, Deglacial temperature controls on noanalog community establishment in the Great Lakes Region. *Quaternary Science Reviews* 234, 106245 (2020).
- 55. F. Biondi, D. M. Meko, G. Piovesan, Maximum tree lifespans derived from public-domain dendrochronological data. *iScience* 26, 106138 (2023).
- 657 60. S. R. Meyers, "Astrochron: An R package for astrochronology" (manual, 2014); https://cran.r 658 project.org/package=astrochron.
- 659 61. R Core Team, "R: A language and environment for statistical computing" (manual, Vienna, Austria, 2021); https://www.R-project.org/.
- 661 62. J. C. Gower, Some distance properties of latent root and vector methods used in multivariate
 analysis. *Biometrika* 53, 325–338 (1966).
- 663 63. J. T. Overpeck, T. Webb, I. C. Prentice, Quantitative interpretation of fossil pollen spectra 664 dissimilarity coefficients and the method of modern analogs. *Quaternary Research* 23, 87–108
 665 (1985).
- 666 64. D. G. Gavin, W. W. Oswald, E. R. Wahl, J. W. Williams, A statistical approach to evaluating distance metrics and analog assignments for pollen records. *Quaternary Research* 60, 356–367 (2003).
- 669 65. T. Laepple, P. Huybers, Reconciling discrepancies between Uk37 and Mg/Ca reconstructions of
 670 Holocene marine temperature variability. *Earth and Planetary Science Letters* 375, 418–429 (2013).
- 671 66. D. Fastovich, Code and Data for Timescale-dependent response of vegetation to climate change,
 672 version 1.0, Zenodo (2024); https://doi.org/10.5281/ZENODO.12726798.
- 673 67. J. W. Kirchner, Aliasing in \$1/{f}^{\ensuremath{\alpha}}\$ noise spectra: Origins, consequences, and remedies. *Phys. Rev. E* 71, 066110 (2005).
- 675 68. R. Hébert, U. Herzschuh, T. Laepple, Millennial-scale climate variability over land overprinted by ocean temperature fluctuations. *Nat. Geosci.*, 1–7 (2022).
- 677 69. V. M. R. Muggeo, Estimating regression models with unknown break-points. *Statistics in Medicine*678 22, 3055–3071 (2003).

- 679 70. C. Wunsch, The spectral description of climate change including the 100 ky energy. *Climate Dynamics* 20, 353–363 (2003).
- M. E. Mann, J. M. Lees, Robust estimation of background noise and signal detection in climatic time series. *Climatic Change* 33, 409–445 (1996).
- 5. Coats, J. E. Smerdon, S. Stevenson, J. T. Fasullo, B. Otto-Bliesner, T. R. Ault, Paleoclimate
 Constraints on the Spatiotemporal Character of Past and Future Droughts. *Journal of Climate* 33, 9883–9903 (2020).
- 686 73. S. Minobe, A 50–70 year climatic oscillation over the North Pacific and North America.
 687 *Geophysical Research Letters* 24, 683–686 (1997).
- 688 74. D. I. Vyushin, P. J. Kushner, Power-Law and Long-Memory Characteristics of the Atmospheric
 689 General Circulation. *Journal of Climate* 22, 2890–2904 (2009).
- 690 75. J. M. Lora, D. E. Ibarra, The North American hydrologic cycle through the last deglaciation.
 691 *Quaternary Science Reviews* 226, 25 (2019).
- 692 76. S. A. Marcott, P. U. Clark, L. Padman, G. P. Klinkhammer, S. R. Springer, Z. Y. Liu, B. L. Otto693 Bliesner, A. E. Carlson, A. Ungerer, J. Padman, F. He, J. Cheng, A. Schmittner, Ice-shelf collapse
 694 from subsurface warming as a trigger for Heinrich events. *Proceedings of the National Academy of*695 *Sciences of the United States of America* 108, 13415–13419 (2011).
- F. He, J. D. Shakun, P. U. Clark, A. E. Carlson, Z. Y. Liu, B. L. Otto-Bliesner, J. E. Kutzbach,
 Northern Hemisphere forcing of Southern Hemisphere climate during the last deglaciation. *Nature* **494**, 81–85 (2013).
- 699 78. C. Buizert, V. Gkinis, J. P. Severinghaus, F. He, B. S. Lecavalier, P. Kindler, M. Leuenberger, A. E.
 700 Carlson, B. Vinther, V. Masson-Delmotte, J. W. C. White, Z. Liu, B. Otto-Bliesner, E. J. Brook,
 701 Greenland temperature response to climate forcing during the last deglaciation. *Science* 345, 1177–
 702 1180 (2014).
- 703 79. R. F. Ivanovic, L. J. Gregoire, A. Burke, A. D. Wickert, P. J. Valdes, H. C. Ng, L. F. Robinson, J. F.
 704 McManus, J. X. Mitrovica, L. Lee, J. E. Dentith, Acceleration of Northern Ice Sheet Melt Induces
 705 AMOC Slowdown and Northern Cooling in Simulations of the Early Last Deglaciation.
 706 Paleoceanogr. Paleoclimatology 33, 807–824 (2018).
- 80. S. A. Marcott, T. K. Bauska, C. Buizert, E. J. Steig, J. L. Rosen, K. M. Cuffey, T. J. Fudge, J. P.
 Severinghaus, J. Ahn, M. L. Kalk, J. R. McConnell, T. Sowers, K. C. Taylor, J. W. C. White, E. J.
 Brook, Centennial-scale changes in the global carbon cycle during the last deglaciation. *Nature* 514, 616 (2014).
- 81. E. Monnin, A. Indermühle, A. Dällenbach, J. Flückiger, B. Stauffer, T. F. Stocker, D. Raynaud, J.M. Barnola, Atmospheric CO2 Concentrations over the Last Glacial Termination. *Science* 291, 112–114 (2001).
- 82. S. C. Brown, T. M. L. Wigley, B. L. Otto-Bliesner, C. Rahbek, D. A. Fordham, Persistent
 Quaternary climate refugia are hospices for biodiversity in the Anthropocene. *Nat Clim Change* 10, 244-+ (2020).

- 83. S. C. Brown, C. Mellin, J. García Molinos, E. D. Lorenzen, D. A. Fordham, Faster ocean warming
 threatens richest areas of marine biodiversity. *Global Change Biology* 28, 5849–5858 (2022).
- 84. D. A. Fordham, F. Saltré, S. Haythorne, T. M. L. Wigley, B. L. Otto-Bliesner, K. C. Chan, B. W.
 Brook, PaleoView: a tool for generating continuous climate projections spanning the last 21 000
 years at regional and global scales. *Ecography* 40, 1348–1358 (2017).
- 85. J. R. Petit, J. Jouzel, D. Raynaud, N. I. Barkov, J.-M. Barnola, I. Basile, M. Bender, J. Chappellaz,
 M. Davis, G. Delaygue, M. Delmotte, V. M. Kotlyakov, M. Legrand, V. Y. Lipenkov, C. Lorius, L.
 PÉpin, C. Ritz, E. Saltzman, M. Stievenard, Climate and atmospheric history of the past 420,000
 years from the Vostok ice core, Antarctica. *Nature* 399, 429–436 (1999).
- 726 86. C. Barbante, J.-M. Barnola, S. Becagli, J. Beer, M. Bigler, C. Boutron, T. Blunier, E. Castellano, O. 727 Cattani, J. Chappellaz, D. Dahl-Jensen, M. Debret, B. Delmonte, D. Dick, S. Falourd, S. Faria, U. 728 Federer, H. Fischer, J. Freitag, A. Frenzel, D. Fritzsche, F. Fundel, P. Gabrielli, V. Gaspari, R. 729 Gersonde, W. Graf, D. Grigoriev, I. Hamann, M. Hansson, G. Hoffmann, M. A. Hutterli, P. 730 Huybrechts, E. Isaksson, S. Johnsen, J. Jouzel, M. Kaczmarska, T. Karlin, P. Kaufmann, S. 731 Kipfstuhl, M. Kohno, F. Lambert, A. Lambrecht, A. Lambrecht, A. Landais, G. Lawer, M. 732 Leuenberger, G. Littot, L. Loulergue, D. Lüthi, V. Maggi, F. Marino, V. Masson-Delmotte, H. 733 Meyer, H. Miller, R. Mulvanev, B. Narcisi, J. Oerlemans, H. Oerter, F. Parrenin, J.-R. Petit, G. 734 Raisbeck, D. Raynaud, R. Röthlisberger, U. Ruth, O. Rybak, M. Severi, J. Schmitt, J. Schwander, 735 U. Siegenthaler, M.-L. Siggaard-Andersen, R. Spahni, J. P. Steffensen, B. Stenni, T. F. Stocker, J.-736 L. Tison, R. Traversi, R. Udisti, F. Valero-Delgado, M. R. van den Broeke, R. S. W. van de Wal, D. 737 Wagenbach, A. Wegner, K. Weiler, F. Wilhelms, J.-G. Winther, E. Wolff, EPICA Community 738 Members, One-to-one coupling of glacial climate variability in Greenland and Antarctica. Nature 739 444, 195–198 (2006).
- 740 87. D. Kaufman, N. McKay, C. Routson, M. Erb, C. Datwyler, P. S. Sommer, O. Heiri, B. Davis,
 741 Holocene global mean surface temperature, a multi-method reconstruction approach. *Scientific Data*742 7, 13 (2020).
- 88. S. T. Jackson, "Pollen and spores in Quaternary lake sediments as sensors of vegetation
 composition: theoretical models and empirical evidence" in *Sedimentation of Organic Particles*, A.
 Traverse, Ed. (Cambridge University Press, Cambridge, 1994;
- https://www.cambridge.org/core/books/sedimentation-of-organic-particles/pollen-and-spores-inquaternary-lake-sediments-as-sensors-of-vegetation-composition-theoretical-models-and-empiricalevidence/DCC368064032C32E792D2BBB291EFA36), pp. 253–286.
- 749 89. J. D. Hays, J. Imbrie, N. J. Shackleton, Variations in the Earth's Orbit: Pacemaker of the Ice Ages.
 750 Science 194, 1121–1132 (1976).
- 751 90. A. Berger, Milankovitch Theory and climate. *Reviews of Geophysics* 26, 624–657 (1988).
- W. Zhao, P. E. Tarasov, A. V. Lozhkin, P. M. Anderson, A. A. Andreev, J. A. Korzun, M. Melles,
 E. Y. Nedorubova, V. Wennrich, High-latitude vegetation and climate changes during the MidPleistocene Transition inferred from a palynological record from Lake El'gygytgyn, NE Russian
 Arctic. *Boreas* 47, 137–149 (2018).
- Y. Zhao, P. C. Tzedakis, Q. Li, F. Qin, Q. Cui, C. Liang, H. J. B. Birks, Y. Liu, Z. Zhang, J. Ge, H.
 Zhao, V. A. Felde, C. Deng, M. Cai, H. Li, W. Ren, H. Wei, H. Yang, J. Zhang, Z. Yu, Z. Guo,

- Evolution of vegetation and climate variability on the Tibetan Plateau over the past 1.74 million
 years. *Science Advances* 6, eaay6193 (2020).
- P. C. Tzedakis, Long-term tree populations in northwest Greece through multiple Quaternary climatic cycles. *Nature* 364, 437–440 (1993).
- A. L. Berger, Long-Term Variations of Caloric Insolation Resulting from the Earth's Orbital
 Elements1. *Quaternary Research* 9, 139–167 (1978).
- J. Imbrie, A. Berger, E. A. Boyle, S. C. Clemens, A. Duffy, W. R. Howard, G. Kukla, J. Kutzbach,
 D. G. Martinson, A. McIntyre, A. C. Mix, B. Molfino, J. J. Morley, L. C. Peterson, N. G. Pisias, W.
 L. Prell, M. E. Raymo, N. J. Shackleton, J. R. Toggweiler, On the structure and origin of major
 glaciation cycles 2. The 100,000-year cycle. *Paleoceanography* 8, 699–735 (1993).
- 768 96. C. J. F. ter Braak, Canonical Correspondence Analysis: A New Eigenvector Technique for
 769 Multivariate Direct Gradient Analysis. *Ecology* 67, 1167–1179 (1986).
- Press, ed. 1, 1993; https://www.cambridge.org/core/product/identifier/9780511622762/type/book).
- P8. E. C. Ellis, J. O. Kaplan, D. Q. Fuller, S. Vavrus, K. Klein Goldewijk, P. H. Verburg, Used planet:
 A global history. *Proceedings of the National Academy of Sciences* 110, 7978–7985 (2013).
- 774 99. E. Dinerstein, D. Olson, A. Joshi, C. Vynne, N. D. Burgess, E. Wikramanayake, N. Hahn, S. 775 Palminteri, P. Hedao, R. Noss, M. Hansen, H. Locke, E. C. Ellis, B. Jones, C. V. Barber, R. Hayes, 776 C. Kormos, V. Martin, E. Crist, W. Sechrest, L. Price, J. E. M. Baillie, D. Weeden, K. Suckling, C. 777 Davis, N. Sizer, R. Moore, D. Thau, T. Birch, P. Potapov, S. Turubanova, A. Tyukavina, N. De 778 Souza, L. Pintea, J. C. Brito, O. A. Llewellyn, A. G. Miller, A. Patzelt, S. A. Ghazanfar, J. 779 Timberlake, H. Klöser, Y. Shennan-Farpón, R. Kindt, J.-P. B. Lillesø, P. Van Breugel, L. Graudal, 780 M. Voge, K. F. Al-Shammari, M. Saleem, An Ecoregion-Based Approach to Protecting Half the 781 Terrestrial Realm. BioScience 67, 534-545 (2017).
- W. R. Peltier, Global glacial isostasy and the surface of the ice-age Earth: the ICE-5G (VM2) model
 and GRACE. *Annual Review of Earth and Planetary Sciences* 32, 111–149 (2004).

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788	Supplementary Materials for
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790	Coupled, decoupled, and abrupt responses of vegetation to climate across timescales
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800	The PDF file includes:
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802	Materials and Methods
803	Figs. S1 to S22
804	Tables S1 to S8
805	Data S1
806	References
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809 Materials and Methods

810 Fossil Pollen Abundances and Age Depth Modeling

811

812 We estimate vegetation turnover from fossil pollen abundances stored in geologic archives, such 813 as lacustrine sediments (51). Fossil pollen tracks plant assemblage composition through time, 814 albeit with some biases and limitations. Taxonomic resolution is often to the genus level (e.g. 815 Picea), though species-level identification is possible (e.g. Alnus rugosa) for some fossil pollen 816 morphotypes, and only family-level identification is possible for others (e.g. Poaceae). 817 Additionally, some taxa overproduce pollen and others underproduce pollen relative to the 818 source vegetation assemblage. For instance, pine (Pinus) is often overrepresented in pollen 819 assemblages while fir (Abies) tends to be underrepresented (52). Our analyses account for these 820 production biases by including metrics that downweigh abundant fossil pollen taxa and increase 821 the weight of rarer taxa (e.g. squared chord dissimilarity metric incorporates a square root 822 transform and we square root transform the fossil pollen assemblages before correspondence 823 analysis). When these biases are considered and accounted for in analyses, as we do here, fossil 824 pollen is an effective representation of the source plant assemblage. We refer the reader to 825 Chevalier et al. (51) for a comprehensive review of fossil pollen as a proxy for plant assemblage 826 composition.

827

828 We gathered fossil pollen abundance data from the Neotoma Paleoecology Database (8) in May

829 2022, which was included as a part of the BioDeepTime database (9). For this fossil pollen data

aggregation, we searched all fossil pollen records in Neotoma with at least 10 fossil pollen

assemblages through time. Our initial search was based on the site list from Mottl et al. (37),

which compiled 1,181 high-quality fossil pollen records from Neotoma that met our

requirements. However, we did not temporally limit our search to 18,000 years as in Mottl et al.
(37), which produced an additional 181 fossil pollen records, hereafter referred to as "sites".

(37), which produced an additional 181 fossil pollen records, hereafter referred to as "sites".
Note, however, that in Neotoma, one site-level sedimentary archive may have multiple fossil

pollen records (e.g. if there are multiple cores from a lake or mire). In total, we compiled 1,362

sites with at least 10 observations of a fossil pollen assemblage through time (e.g. at least 10

- 838 points in each assemblage time series).
- 839

840 We created age-depth models using Bchron (53, 54) to improve upon existing Neotoma age

841 estimates, which sometimes rely on age-depth models that can underestimate error. Bchron uses

842 information from sparse but specific ages for depths in sedimentary archives for the sites to

843 develop a continuous model of sedimentation from which ages at every depth can be estimated

844 (54). An ensemble of possible sedimentation rates is estimated from the chronological controls to

generate a posterior distribution of age-depth relationships that allows uncertainty about the age-

846 depth relationship in a sedimentary archive to be propagated to all analyses. Age controls

847 included radiocarbon years, varve years, biostratigraphic markers, and core-top age.

848

849 Behron models were run with default parameters (54), except for the radiocarbon calibration

850 curve, which requires hemisphere-specificity to convert radiocarbon years to calendar years due

to interhemispheric differences in $^{14}CO_2$ production, uptake, and reservoir effects. Sites in the

852 Northern Hemisphere were calibrated using IntCal20 (55) and sites in the Southern Hemisphere

853 were calibrated using SHCal20 (56). Non-radiocarbon ages were incorporated into Bchron as

calendar years before 1950, with Gaussian errors. Chronological controls with no given age

- 855 uncertainties, often the case with biostratigraphic ages, were assigned a Gaussian, one standard
- deviation, age error that was 10% of the age estimate (e.g. for an age estimate of 1,000 years
- 857 with no assigned error, the ages followed a $N(1000, 100^2)$ distribution in Bchron). From our
- 858 compilation, 19 sites had only one chronological control and were excluded from further
- 859 analyses. Additionally, the Bchron algorithm failed to initialize for five sites that were also 860 excluded.
- 861

862 After creating new age-depth models, we harmonized the taxonomy across these sites using taxa 863 lists from Flantua et al. (57). We were not able to match taxa in Flantua et al. (57) for 21 sites, so 864 these sites were removed from further analyses. Of these removed sites, 16 were in Oceania and 865 Australia because the taxonomy harmonization lists from Flantua et al. (57) do not include these 866 regions. Lastly, one site (Foy Lake, Data S1) contained negative abundances for some fossil 867 pollen counts and was removed from further analyses. Five sites had issues with both 868 chronological controls and taxonomy harmonization, therefore the final compilation of fossil 869 pollen abundances included 1,321 datasets with good spatiotemporal coverage (Data S1). 870 Sites span the Southern Hemisphere midlatitudes to the Northern Hemisphere Arctic, with the 871 densest sampling between 40° N and 50° N, and the least dense sampling between 20° S and 50° 872 S (Fig. S1). Although we perform analyses on tropical/extra-tropical averages, the abundance of 873 temperate midlatitude sites may make globally averaged results more sensitive to temperature, 874 especially considering that these sites demonstrate strong responses to past temperature changes 875 (e.g. Bonnett Lake in 58). The Northern Hemisphere is better represented across sites than the 876 Southern Hemisphere.

877

878 Temporally, these records span the last 600,000 years, with one site spanning an interval from 879 1.4 to 1.5 Ma, and they are heavily concentrated in the last 20,000 years (Fig. S1). Based on the 880 median age-depth model for each site, 389 sites have a temporal span less than 10,000 years, 746 881 sites have a temporal span between 10,000 to 20,000 years, 72 have a temporal span between 882 20,000 to 30,000 years, 43 have a temporal span between 30,000 to 40,000 years, 17 have a 883 temporal span between 40,000 to 50,000 years, 19 have a temporal span between 50,000 to 884 60,000 years, seven have a temporal span between 60,000 to 70,000 years, six have a temporal 885 span between 70,000 to 80,000 years, three have a temporal span between 80,000 to 90,000 years, one has a temporal span between 90,000 to 100,000 years, and 18 have a temporal span 886 887 greater than 100,000 years. Of this final compilation, seven sites had different fossil pollen 888 assemblages at identical depths (Dataset IDs: 22,636, 22,797, 3,973, 4,196, 4,197, 4,7975, 525 in 889 Data S1). For each duplicate depth, we retained the first entry.

- 890
- 891 <u>Tree Longevity Estimates</u>
- 892

893 We estimated tree longevity with observations from all taxa available in the International Tree

Ring Data Bank (ITRDB) (35, 36). We gathered all tree ring width records and retained tree ring collections where at least one tree ring record spanned 90% of the tree-ring collection

collections where at least one tree ring record spanned 90% of the tree-ring collection chronology, to minimize underestimation and overestimation of longevity (24). We used the

longest tree ring record in a collection to estimate longevity for that collection and report the

- median across all collections in the main text (*59*). The spatial distribution of the ITRDB is
- comparable to the fossil pollen sites, which have the greatest density of tree ring width records in
- 900 North America and Europe and comparatively fewer records in the Southern Hemisphere (Fig.

901 S1) (36). The ITRDB lacks records in the tropics, but our median estimate of tree longevity (246 902 years) agrees with a compilation of tree ring width records from the tropics (24).

903

904 Spectral Analysis

905

906 We used Thomson's multitaper method (MTM) (17) to estimate the power spectra of fossil 907 pollen turnover using the astrochron R-package (R version 4.4.2, astrochron version 1.4) (60, 908 61). MTM is a Fourier-based method that reduces spectral bias (e.g., spectral leakage) through 909 the application of multiple orthogonal data "tapers" that weigh a time series according to Slepian 910 functions (17), of which we used five 3π prolate tapers. The application of Slepian data tapers 911 imparts several positive attributes to MTM when compared to the standard discrete Fourier 912 transform: a reduction in spectral leakage and optimal bias protection for a specified bandwidth 913 resolution, and leveraging of the multiple tapers to provide a statistical sample for estimation of 914 spectral power and its uncertainty (17). We scale spectral estimates from MTM by energy per 915 unit frequency to return power spectral density, hereafter referred to as the power spectrum (5). 916 An underlying assumption in these analyses, and all spectral analyses, is that a single power

917 spectrum is a good representation of the entire time series.

918

919 We further processed the fossil pollen abundances to meet the MTM requirements of a

920 univariate, regularly sampled time series. We addressed the requirement of a single time series

921 by using principal coordinate analysis (PCO) (62) on fossil pollen dissimilarity matrices to

reduce the dimensionality of the fossil pollen abundances. Pollen dissimilarity matrices were 922 923 calculated for each individual time series using the squared chord distance metric (63), which

924 consistently outperforms other distance metrics in distinguishing between two distinct fossil

925 pollen assemblages (63, 64). We retained the primary (PCO1) and secondary (PCO2) dimensions

926 of variability for further analysis via MTM and presented the results from the primary dimension

- 927 of variability in the main manuscript (Fig. S2).

928 929 We sought to identify latitudinal differences in fossil pollen dissimilarity, for comparison with 930 climate variables which are known to have a variance structure that varies by latitude (5). To that 931 end, we multiplied PCO1 by the square root of its corresponding eigenvalue. This procedure

932 scales PCO1 for each fossil pollen assemblage by the variance explained by that dimension. That

933 is, a fossil pollen assemblage where PCO1 explains a substantial amount of compositional

934 variance will have a large eigenvalue corresponding to PCO1 and PCO1 will be up-weighted,

935 producing high spectral energy across all frequencies. In contrast, a fossil pollen assemblage

936 where PCO1 explains little variance will have a small eigenvalue corresponding to PCO1 and

937 PCO1 will be down-weighted. Total spectral energy (i.e. area under a power spectral density

938 spectrum) is equal to the variance of the time series (Parseval's theorem). Therefore, any spatial

939 patterns in the variance explained by PCO1 are imprinted onto the time series and will produce

940 high spectral power when PCO1 is up-weighted and low spectral power when PCO1 is down-941 weighted. This effect carries forward to spatially averaged power spectra (i.e. tropical and extra-

942 tropical averaged power spectra) thereby enabling an assessment of whether there are spatial

943 patterns in fossil pollen turnover.

944

Temporal sampling that is evenly spaced (i.e. identical temporal distance between all consecutive 945 946 samples) is required by MTM, but this condition is rarely met by proxy data extracted from

- 947 geologic archives. Therefore, we interpolated PCO1 of all fossil pollen assemblages using a
- 948 linear interpolation approach adapted from (65). This approach aims to determine an optimal
- 949 interpolation resolution and minimize energy loss at high frequencies by comparing the PCO1
- 950 power spectra to the power spectra of a power law process where $\beta = 1$. The optimal
- 951 interpolation resolution is identified when the ratio between the theoretical and empirical power 0.52
- 952 spectra crosses 0.7 (65). This approach objectively determines an optimal interpolation 953 resolution and includes filtering to minimize the aliasing of high frequency variance that
- resolution and includes filtering to minimize the aliasing of high frequency variance that is often present in sedimentary archives (implemented in the new *astrochron* function 'linterpLH13') and
- 955 present in the Zenodo data repository (66)).
- 956

957 We estimated the power spectra of global ecological turnover by performing MTM on PCO1 for 958 individual sites after subtracting the mean from each site-level PCO1 time series, then bin 959 spectral power by log10(frequency), and average spectral power across sites within each 960 frequency bin. This choice was made to avoid convoluting temporal and spatial variance in the 961 eigenvector decomposition of the community dissimilarity matrix, as would have occurred if we 962 considered all sites and samples together. By averaging power spectra across sites, we leverage 963 both short, highly-sampled records to resolve high frequencies and long, sparsely-sampled 964 records to resolve low frequencies - characteristics that would be difficult to achieve using any 965 single site's power spectrum alone. For averaging site-level power spectra, we used a bin size of 0.01 in log10(frequency) coordinates, which equates to 22,000⁻¹ years⁻¹ near the smallest 966 frequencies (e.g. $10^{-6} - 10^{-5.99}$ years⁻¹) and <1 year near the largest frequencies (e.g. $10^{0.99} - 10^{10}$ 967

968 969 years⁻¹).

970 After estimating the power spectra of global vegetation turnover we evaluated the continuum of 971 global vegetation turnover for specific frequency bands using an ordinary least squares linear 972 regression in log-log space for frequencies resolved by at least two sites (5, 6). Prior to the 973 regression, we smoothed the spatially averaged power spectra using a Gaussian kernel in log10 974 frequency coordinates with a width of 0.03 (67, 68). Using the smoothed global estimate of 975 spectral power for global vegetation turnover, frequency is a predictor of spectral power and the 976 resulting slope is the β exponent in the S(f) \propto f^{- β} power law relationship (5, 6). To determine the 977 frequency bands of distinct temporal scaling regimes in spectral power for global vegetation 978 turnover we identified breakpoint locations in the log-log relationship between spectral power 979 and frequency through piecewise linear regressions in the segmented R package (version 2.1.3) 980 (69). We constrained segmented regressions to identify three breakpoints (low, intermediate, and 981 high frequencies) for fossil pollen turnover and one breakpoint for simulated temperature and 982 precipitation. The number of breakpoints was based on prior expectations for climate (5, 6) and 983 visual inspection for fossil pollen. Although the number of breakpoints is constrained in the 984 segmented regressions, the location of these breakpoints depends on the power spectrum. For 985 vegetation turnover, β was then fit across the four frequency ranges between the three identified 986 breakpoints: (1) the lowest frequency resolved and the low frequency breakpoint, (2) the low 987 frequency breakpoint and the intermediate frequency breakpoint, (3) the intermediate frequency 988 breakpoint and high frequency breakpoint, and (4) the high frequency breakpoint to the highest 989 frequency that produces unbiased estimates of β (see *Estimating the Highest Resolvable* 990 Frequency for Spectral Analyses). For example, if a breakpoint in the log-log relationship between spectral power and frequency was identified at 115⁻¹ years⁻¹, 600⁻¹ years⁻¹, and 4,000⁻¹ 991 992 years⁻¹, β was fit between (1) the lowest frequency resolved and 4,000⁻¹ years⁻¹, (2) from 4,000⁻¹

- 993 years⁻¹ and 600⁻¹ years⁻¹, (3) from 600⁻¹ years⁻¹ to 115 years⁻¹, and (4) from 115 years⁻¹ to the
- 994 highest frequency that produces unbiased estimates of β . For temperature and precipitation, we
- 995 fit β between the lowest frequency resolved and the one breakpoint identified and again from the 996 one breakpoint identified to the highest frequency that produces unbiased estimates of β .
- 997
- 998 Within a time series, β characterizes memory (i.e. temporal autocorrelation) and how variance is
- 999 partitioned across frequencies (70). If the exponential coefficient (β) of the power-law
- 1000 relationship between frequency and spectral power is small ($\beta \sim 0$), variance is equally
- 1001 partitioned among all frequencies (i.e., white noise; Fig. S7) (70). In contrast, $\beta > 0$ indicates
- 1002 more variance at lower frequencies (longer periods), with $\beta = 2$ defining a random walk (i.e., red 1003
- noise; Fig. S7) (70). The climate system contains two scaling regimes: small, uncorrelated 1004 variability with a low β and large, autocorrelated variability with a high β . The small, stochastic,
- 1005 uncorrelated variability of the climate system is present in frequencies as low as 100⁻¹ to 1,000⁻¹
- years⁻¹ (5, 6) and encompasses "weather" components of the climate system (29). At lower 1006
- 1007 frequencies, β increases as slowly responding, coupled components of the "climate" system
- 1008 increase the magnitude of climate fluctuations while also imparting high autocorrelation (29).
- 1009 Here, the terms "climate" and "weather" delineate these two scaling regimes (29).
- 1010
- 1011 Recently, methods for estimation of temporal scaling in time series were compared for their
- 1012 ability to reproduce β in synthetic paleoclimate time series with known β and performed
- 1013 reasonably well (33). In these analyses, MTM emerged biased towards larger β values when
- 1014 evaluating the full frequency range, compared to other spectral transformation methods (33).
- However, MTM showed little bias at long timescales (greater than nine times the mean 1015
- 1016 resolution), moderate bias at intermediate timescales (greater than 4 times the mean resolution),
- 1017 and generally outperformed competing methods such as spectral transformation from the Lomb-1018 Scargle periodogram when β is high and the input data is irregularly sampled (33). Only Haar
- 1019 structure functions more accurately estimated β from the synthetic dataset, but the approach is
- 1020 limited to $-1 < \beta < 3$ (33) and does not allow for the identification/influence of
- 1021 quasiperiodic/periodic signals that may bias estimates of the spectral continuum (71).
- 1022 Additionally, MTM has seen broad use in paleoclimatology (5, 68, 72) and atmospheric sciences (73, 74) for estimating β , providing baseline estimates for comparison with our study.
- 1023
- 1024
- 1025 TraCE-21ka and Proxy Paleoclimate Estimates
- 1026

1027 TraCE-21ka is a series of fully coupled climate model experiments that simulate the effect of 1028 transient climate forcings of the most recent deglaciation with the Community Climate System 1029 Model, version 3 (18, 19). Components of the Community Climate System Model, version 3 1030 include the Portable Ocean Model, Community Land Model, and Community Sea Ice Model 1031 (18). The climate simulations have a nominal horizontal resolution of 3.75° with 26 vertical 1032 levels (18). Surface elevation was averaged within each grid cell resulting in an imperfect 1033 representation of mountain ranges that only span several grid cells, such as the Andes (Fig. S4). 1034 TraCE-21ka includes transient changes in ice sheet topography, meltwater forcing, orbital 1035 configuration, and greenhouse gas concentration that matched then-current proxy reconstructions 1036 (18, 19). These climate simulations have been pillars of paleoclimatological research and have 1037 undergone substantial comparisons against proxy reconstructions and generally perform well 1038 (18, 19, 75–78). Unlike proxy-based climate reconstructions, TraCE-21ka offers full fields that

- are annually resolved and well-suited for comparison against spectral estimates from fossil
- 1040 pollen. For climate parameters such as precipitation, while proxy-based reconstructions remain
- 1041 challenging to develop, physically plausible simulations provide valuable and insightful tools for
- 1042 understanding historical patterns. Temperature and precipitation anomalies for the TraCE-21ka
- simulation relative to 1850 to 1900 CE baseline are presented in Fig. S5 and Fig. S6.
- 1044

1045 TraCE-21ka has known deficiencies such as seasonal precipitation biases in North America (75)

- and imperfect greenhouse gas and meltwater forcings (79–81). Precipitation is particularly
 challenging to simulate for all climate models because processes like raindrop formation and
- 1048 convection occur at a sub-grid scale. What's more, all climate models overestimate high
- 1049 frequency climate variability and underestimate low frequency climate variability at local and
- 1050 regional scales (31), but our low-pass filtering procedure (summarized below) partially mitigates
- this climate model limitation by reducing high frequency variability. Nonetheless, TraCE-21ka
- remains the most comprehensive set of paleoclimatic simulations for the last deglaciation, which
- 1053 are widely used to assess ecological relationships to paleoclimate (82-84). Recently, the TraCE-
- 1054 21ka experiments were the first climate simulations to show a scaling break in the continuum of
- mean global temperature that is expected to exist given physical principles (6). For climateparameters like precipitation, simulations
- 1057

1058 We averaged monthly near-surface temperature (2 m) and total precipitation rate into annual

- averages. We sought to make direct comparisons between power spectra of simulated
- 1060 temperature, simulated precipitation, and vegetation turnover and therefore degraded the TraCE-
- 1061 21ka climate simulation to match the spatial and temporal characteristics of the fossil pollen
- 1062 sites. Specifically, we subsampled TraCE-21ka spatially to get the nearest grid cell for every
- 1063 fossil pollen site and applied a low-pass filter with a characteristic timescale of twice the mean 1064 resolution of the corresponding fossil pollen record to guard against aliasing of high-frequency
- 1065 variance (33, 68). We then downsampled these low-pass filtered climate time series temporally,
- 1066 retaining only the years with fossil pollen data. This process produced a dataset of simulated
- 1067 temperature and precipitation that matched fossil pollen abundances in space and time with
- 1068 similar temporal characteristics (i.e. low-pass smoothing induced by sedimentation). Finally, we
- 1069 interpolated the simulated temperature and precipitation to a regular temporal grid using the
- same methodology applied to the fossil pollen data (65). All spectral analyses for TraCE-21ka
- 1071 were performed on these spatiotemporally subsampled and interpolated temperature and 1072 precipitation time series.
- 1072 1073

1074 For subsampling of the TraCE-21ka simulations, we excluded those fossil pollen samples that 1075 were outside of the temporal coverage of TraCE-21ka. Fossil pollen sites that did not contain any

- 1076 fossil pollen assemblage observations within the last 21,000 years were excluded and are not
- 1077 represented in the spectral estimates of the TraCE-21ka simulations.
- 1078

1079 To capture climate variability outside of the last 21,000 years we supplement our analysis of

- 1080 TraCE-21ka with two empirical proxy records that approximate global temperature variability
- 1081 for the last two million years. We use temperature reconstructions from the EPICA Dome C ice
- 1082 core in Antarctica (28). Temperature reconstructions from Antarctic ice cores primarily track
- 1083 global greenhouse gas concentrations and therefore global temperature changes (85). We also
- 1084 use global average surface temperature (GAST) reconstructions from Snyder (20). This estimate

1085 of GAST is based on proxy-based sea surface temperature reconstructions (SST) that are scaled

- 1086 to surface air temperatures with a value determined by examining SST-surface air temperature
- 1087 differences from the Paleoclimate Modelling Intercomparison Project (PMIP) model simulations.
- 1088 Comparisons between GAST reconstructions, EPICA Dome C, and greenhouse gasses 1089
- demonstrate that both sets of proxy records used here well approximate global climate evolution
- 1090 (20). Variations in ocean circulation emerge in EPICA Dome C oxygen isotopes (86) but as a 1091 second-order feature imposed on greenhouse gas-controlled temperature changes. The spectral
- 1092 continuum of temperature variability at EPICA Dome C and global surface air reconstructions
- 1093 were fit between $100^{-1}-15,000^{-1}$ years⁻¹ (5) and $2,000^{-1}-100,000^{-1}$ years⁻¹ (6), respectively.
- 1094
- 1095 Benchmarking TraCE-21ka Simulated Climate Variability Against Temperature12k
- 1096

1097 We compared TraCE-21ka to the Temperature 12k database (87), a global compilation of proxy

- 1098 temperature reconstructions that span the last 12,000 years. Note that several proxy
- 1099 reconstructions within Temperature12k extend well beyond the last 12,000 years. We first
- 1100 filtered the Temperature12k database to remove all pollen-based temperature estimates and then
- 1101 estimated the continuum of global temperature variability using the same framework defined in
- 1102 the TraCE-21ka and Proxy Paleoclimate Estimates and Spectral Analyses section. That is, we
- 1103 estimated power spectra for Temperature12k at a site level, and then averaged across sites to
- 1104 produce a globally averaged power spectrum. For TraCE-21ka, we performed the same
- 1105 procedure after spatiotemporally subsampling and low-pass filtering the temperature simulations.
- 1106 Six of the non-pollen temperature estimates in Temperature12k failed spectral analyses for
- various reasons (Table S8). No similar comparisons are made for precipitation due to the lack of 1107 1108 an analogous database to Temperature12k. However, low-frequency precipitation variability in
- 1109
- TraCE-21ka likely results from thermodynamic effects of temperature changes (Clausius-1110
- Clapeyron relationship) given the nearly identical power spectra presented in Fig. 2.
- 1111
- 1112 We find that TraCE-21ka can accurately simulate the three key features of the temperature
- 1113 continuum: 1) a high β at low frequencies (climate regime), 2) a low β at high frequencies 1114 (weather regime), and 3) a breakpoint in the scaling relationship between spectral power and
- 1115 frequency (Fig. S3). In the low frequency, climate, regime, β for Temperature 12k is 1.83 and
- TraCE-21ka simulates a β of 1.87. In the high frequency, weather, regime Temperature 12k has a 1116
- β of 0.54 while TraCE-21ka has a β of -0.25. The location of the break in the scaling relationship 1117
- for Temperature12k is 376⁻¹ years⁻¹ and 498⁻¹ years⁻¹ for TraCE-21ka. These results demonstrate 1118
- 1119 that TraCE-21ka performs well, despite the general struggle of climate models to accurately
- 1120 simulate temporal persistence in the high frequency, weather, regime. Much like other
- 1121 comparisons between empirical climate observations against climate models, TraCE-21ka poorly
- 1122 simulates temporal persistence in temperature variability (i.e. lower β in TraCE-21ka) in the high
- 1123 frequency regime (31). Despite this deficiency, TraCE-21ka captures the key features of the
- 1124 temperature continuum and is well-suited as a climate benchmark against which we can compare
- 1125 our globally averaged power spectra of vegetation turnover.
- 1126

1127 Estimating the Highest Frequency for Unbiased Estimates of β

- 1128
- 1129 In light of the limitations and biases of MTM for estimating β (33), we sought to estimate the
- 1130 highest frequency that produces unbiased estimates of β for each of our spatially averaged power

- 1131 spectra. We used the undegraded, annually resolved TraCE-21ka near-surface temperature time
- 1132 series, from the closest grid cell corresponding to each fossil pollen site, as a target signal with a
- 1133 known power spectrum. We then temporally degraded the TraCE-21ka near-surface temperature
- 1134 as outlined in the TraCE-21ka and Proxy Paleoclimate Estimates section and compared these
- degraded power spectra to the undegraded target (annually resolved) signal to estimate the 1135
- 1136 highest frequency where estimates of β are unbiased by sedimentary processes.
- 1137
- 1138 In our analyses and prior work (6), annually resolved near-surface temperature estimates from 1139 TraCE-21ka produce a power spectrum where spectral power is evenly distributed in a high 1140 frequency band (> 672^{-1} year⁻¹ from Fig. 2). At frequencies lower than this breakpoint, temperature variability increases with frequency (6) (Fig. S8). This pattern holds when averaged 1141 1142 across all fossil pollen sites (global estimate in Fig. S8), the extra-tropics (extra-tropical estimate 1143 in Fig. S8), and the tropics (tropical estimate in Fig. S8). Built upon the expectation that 1144 sedimentary processes such as sediment mixing (88), and sampling resolution, can decrease 1145 spectral power at the highest frequencies and increase β (33), we use the even distribution of 1146 spectral power in the high frequency band of the undegraded TraCE-21ka temperature power 1147 spectrum as the metric to identify when estimates of β become biased by sedimentary processes. We find that high frequency spectral power decreases in the degraded TraCE-21ka power spectra 1148 1149 and β increases in all spatial averages (Fig. S8). However, the temporal sampling characteristics 1150 of fossil pollen sites in each spatial average vary, leading to a spurious decrease in spectral 1151 power and an increase in β at the highest frequencies that varies across the spatial averages. The 1152 high latitudes are well represented in our fossil pollen compilation with several short, fossil 1153 pollen records with very high resolution (Fig. S1). Therefore, in the degraded global and extra-1154 tropical average power spectra of temperature, β in the high frequency regime is unbiased up to a frequency of 58⁻¹ and 57⁻¹ years⁻¹, respectively (Fig. S8). Above this frequency, there is a 1155 spurious decrease in spectral power and an increase in β (Fig. S8). In contrast, tropical fossil 1156 1157 pollen sites in our compilation are less well temporally resolved than the extra-tropics, which decreases the frequency where a spurious decrease in spectral power and increase in β begins to 1158 1159 160⁻¹ years⁻¹ (Fig. S8). Therefore, we fit β to frequencies lower than 58⁻¹, 57⁻¹, and 160⁻¹ years⁻¹, 1160 in all analyses for global, extra-tropical, and tropical power spectra, respectively. 1161
- 1162
 - Statistical Comparisons between Estimated Parameters from Spectral Analyses

1163

1164 We compared all estimated parameters (β , break location) from our ensembles of averaged 1165 power spectra for temperature, precipitation, and vegetation turnover using two-sided Fisher-Pitman permutation tests. A permutation test is used to determine whether the difference between 1166 two groups is statistically significant, without making assumptions about the underlying 1167 1168 distribution of the data. In our analysis, we use permutation tests to compare the medians of the estimated parameters between different variables (e.g., temperature vs. vegetation turnover). The 1169 process works as follows:

- 1170 1171
- 1172 1. We calculated the observed difference in medians between the two groups.
- 2. We then randomly reassigned the data points to the two groups and recalculated the 1173 1174 difference in medians.
- 1175 3. This process is repeated 10,000 times to create a distribution of possible differences 1176 under the null hypothesis of no true difference between groups.

- 4. We compare our observed difference to this distribution. If the observed difference falls in the 2.5% tails on either side, we consider the difference statistically significant at the 0.05 level.
- 1180

1181 This approach allows us to assess whether the observed differences in our spectral parameters are 1182 likely to have occurred by chance. We report the results of all these comparisons in Table S3 to 1183 Table S7.

1184

1185 We also test when estimated parameters are significantly different from 0 (and 2 for β) based on 1186 the confidence interval for the median parameter estimate across the ensemble for each 1187 parameter (Table S1). We calculated confidence intervals by bootstrapping the median. That is, 1188 each ensemble of parameter estimates was randomly resampled with replacement and the median 1189 was calculated for this random resample. This procedure was repeated 10,000 times to return a 1190 distribution of median estimates for each parameter. From this distribution of bootstrapped 1191 median estimates we report the 2.5% and 97.5% percentiles as the 95% CI

median estimates, we report the 2.5% and 97.5% percentiles as the 95% CI.

1192

1193 <u>Methodological Constraints on Milankovitch Signal Detection</u>

1194

1195 Milankovitch cycles are a primary control of global climate (89, 90) and have been identified in

1196 fossil pollen records that span the last 2,000,000 years (91, 92). Our analyses demonstrate

1197 increased spectral power associated with precession cycles at 21,000⁻¹ years⁻¹ in all spatially 1198 averaged power spectra but high spectral power in the obliquity band (41,000⁻¹ years⁻¹) is

missing and high spectral power in the eccentricity band (100,000⁻¹ years⁻¹) is only present in the

1200 vegetation turnover power spectrum for tropical sites (Fig. 3). We find that these missing

1201 periodicities result from 1) our dimensionality reduction procedure (i.e. PCO), 2) the spatial scale

1202 of our compilation, 3) few sites that span enough time to resolve variability in the Milankovitch

bands, and 4) variable temporal resolution of the data at each of these few sites.

1204

1205 Individual taxa or groups of taxa often demonstrate periodicity (as seen with arboreal pollen in 1206 (91) and (92)), but when all taxa are included in the dissimilarity matrix for PCO, as we do here, 1207 periodicity becomes less pronounced. The Ioannina dataset demonstrates this well (Dataset ID: 1208 4112) (93). Pinus pollen at Ioannina has a strong cyclical pattern (93), but this is weakened when 1209 additional taxa are considered when calculating the dissimilarity matrix for PCO (Fig. S13). 1210 Evidence of this is visible in Taner-filtered relative abundances for the three most abundant taxa 1211 at Ioannina. Pinus, Quercus, and Poaceae all show variability in the precession, obliquity, and 1212 eccentricity bands but all are out of phase (Fig. S13). When MTM is performed on Pinus relative 1213 abundance a periodic signal between the obliquity and precession bands is present. However, performing MTM on the primary dimension of variability for a dissimilarity matrix created using 1214 1215 Pinus and Quercus relative abundances demonstrates a decrease in this periodic signal because 1216 of the antiphase changes in Pinus and Quercus abundances (Fig. S13). The loss of spectral power in Pinus between the obliquity and precession bands is further diminished when Poaceae and 1217 1218 Quercus are included in the dissimilarity matrix calculation (Fig. S13). When averaging across a 1219 global compilation of sites with variable temporal data resolution, 41,000 and 100,000 year 1220 periodicities decrease in amplitude, even though individual sites demonstrate periodicity in these 1221 bands (e.g. ODP Site 658 (41194) and Páramo de Agua Blanca (21978) in Fig. S14A). As site-1222 level power spectra are averaged to form an estimate of the global power spectrum, high spectral

- 1223 power in the Milankovitch bands decreases even though it is present at individual sites (Fig.
- 1224 S14B). We hypothesize that high spectral power at 21,000⁻¹ years⁻¹ remains because we have
- more sites with a temporal span and sufficient data resolution that can resolve the 21,000 year
- 1226 periodicity, as compared to the 41,000 and 100,000 year periodicities (Data S1). The limited 1227 number of observations from high latitudes (> $65 \circ$ N), where obliquity effects are expected to be
- 1227 number of observations from high faitudes ($> 05^{\circ}$ N), where obliquity effects are expected to be 1228 the dominant mode of variability (94), may also explain why we detect precession but not
- 1229 obliquity signals in our spatial distribution of sites. In addition, precession has had a large
- influence on summer insolation over the last 400,000 years (95), which may also partly explain a
- 1231 clear precession signal and the absence of obliquity and eccentricity signals.
- 1232
- 1233 <u>Uncertainty Estimation</u>
- 1234

1235 We quantified uncertainty in our estimates of spectral power and the spectral continuum through 1236 Monte Carlo resampling of sites and Bchron posterior age estimates. Specifically, we drew 1,000 sites from our global compilation of 1,321 sites at random, and for each site, we drew a single 1237 1238 posterior age estimate for MTM. We then downsampled TraCE-21ka accordingly, as described 1239 in the TraCE-21ka and Proxy Paleoclimate Estimates section, and then performed MTM as 1240 described in the Spectral Analysis section. We repeated this procedure 1,000 times, which 1241 produced an ensemble of 1,000 estimates of global spectral power, β , and breakpoint locations, 1242 for climate and fossil pollen turnover, from which we reported the median and 95% confidence 1243 interval (Fig. S21, Fig. S22, Table S1). All sampling was performed using a uniform distribution 1244 without replacement. This uncertainty estimation procedure assesses the influence of age model uncertainty and site selection on the global and latitudinally averaged power spectra. 1245

1246

1247 <u>Sensitivity Tests</u>

1248

1249 We assessed the sensitivity of our results to our choice of fossil pollen dimensionality reduction, 1250 power spectra estimation methods, spatial averaging, and anthropogenic land use change (Fig. 1251 S9, Fig. S10, Fig. S11, Fig. S12, Fig. S15, Fig. S16). For dimensionality reduction, we tested 1252 alternative methods to reduce fossil pollen dimensionality and various community dissimilarity 1253 metrics. In these sensitivity tests, we calculated community dissimilarity using the Bray Curtis 1254 and Jaccard dissimilarity metrics. We also performed correspondence analysis after square root 1255 transforming the fossil pollen assemblages, which, unlike PCO, does not assume linearity (96). 1256 Lastly, to test the sensitivity of our analyses to fossil pollen analytical accuracy, we degraded the percent abundance fossil pollen observations to presence/absence, though the Jaccard distance 1257 1258 metric is presence/absence based as well.

1259

1260 Changing the dissimilarity metric and the dimension of variability analyzed had limited impacts
1261 on our conclusions, however, correspondence analyses produced results with the least total
1262 spectral power (Fig. S9, Fig. S10). We hypothesize that this occurs because PCO assumes
1263 linearity in the species-matrix decomposition while correspondence analysis does not assume
1264 linearity (96). Correspondence analysis also produced slightly different results for latitudinally
1265 averaged power spectra because of the scaling procedure we implemented (Fig. S11, Fig. S12).
1266 The eigenvalues in correspondence analyses do not indicate variance explained as they do in

- 1267 PCO. Rather, eigenvalues correspond to correlation coefficients between the coordinates for
- 1268 species in the fossil pollen assemblage (i.e. species score) and coordinates for time intervals (i.e.

site score) in the ordination coordinate system. However, our scaling procedure, which assumes

1270 that the eigenvalues correspond to the variance explained, is incompatible with correspondence

1271 analysis. Nevertheless, we include sensitivity tests for correspondence analysis to assess the

- assumption of linearity in PCO and the influence of metric saturation on our results. We chose to present the first dimension from PCO using the squared chord distance metric because of strong
- 1273 present the first dimension from PCO using the squared chord distance metric because of strong 1274 support for the efficacy of the squared chord distance metric to discriminate fossil pollen
- 1275 assemblages that source from distinct ecosystems (63, 64).
- 1276

1277 We also tested different methods for estimating the global spectral continuum of vegetation 1278 turnover by taking the mean of MTM adaptive spectral power (as shown in the main text), taking 1279 the median of MTM adaptive spectral power, averaging MTM spectral eigencoefficients, and 1280 averaging β for each site. The methodology for median estimates of MTM adaptive spectral 1281 power was identical to the main manuscript except we took the median, not the mean as in the 1282 main text. The procedure for returning a global average of spectral power by averaging 1283 eigencoefficients was nearly identical to averaging by spectral power. We first performed MTM 1284 on a single site and retained the five spectral eigencoefficients for each site that correspond to the 1285 five data tapers. We then averaged the five eigencoefficients across all sites by binning by frequency, as described in the Spectral Analysis section. We then calculated spectral power at 1286 each frequency using the averaged eigencoefficients and Equation 1, where $\hat{S}_k(f)$ is spectral 1287 power and $y_k(f)$ is the eigencoefficient for the kth data taper. Since we use five data tapers, this 1288 produces five estimates of $\hat{S}_{k}(f)$ which we average to estimate total spectral power (17). 1289

- 1290
- 1291 1292

 $\hat{S}_k(f) = |y_k(f)|^2$ (Equation 1)

1293 These estimates of total spectral power were used to estimate β . The eigencoefficient averaging 1294 provides an important complementary view to the MTM adaptive spectral power approaches 1295 noted above, as it explicitly considers the signal phase at each site. That is, strong signals that are 1296 antiphased at different locations will cancel, instead of being amplified as the case for the MTM 1297 adaptive spectral power approaches. Eigencoefficient averaging is expected to reduce the overall 1298 power at a given frequency in the reconstructed spectrum and to diminish periodic signals that 1299 are not in phase globally since it allows for destructive interference across sites.

1301 Lastly, we estimated the global continuum of vegetation turnover by directly averaging β at each 1302 site. Here, we performed MTM at each site as described in the *Spectral Analysis* section and then 1303 estimated β using an ordinary least squares regression in log-log space, retaining β at each site, 1304 not spectral power. Estimates of β were then averaged across sites resulting in a global estimate 1305 of the spectral continuum of fossil pollen turnover. These sensitivity tests were performed within 1306 the same Monte Carlo framework that we use to quantify uncertainty for the fossil pollen 1307 assemblages and TraCE-21ka climate parameters.

1308

1309 Our conclusions are robust to the method used to aggregate individual site-level power spectra of

1310 vegetation turnover into a global estimate. All four approaches reveal four characteristic

1311 timescales in global vegetation turnover each with distinct β s: high β at the highest frequencies,

1312 low β in the high-intermediate frequency band, high β in the low-intermediate frequency band,

1313 and low β in the low frequency band (Fig. S9). Across much of the frequency space,

1314 uncertainties for these approaches overlap, particularly at high and low frequencies where

- 1315 spectral power estimates diverge.
- 1316

1317 This divergence is most prominent in two areas: the high and low frequencies. At low

frequencies, global estimates that use the mean of site-level power spectra have greater spectral 1318

1319 power than estimates that use the median of site-level power spectra and the mean of site-level

1320 eigencoefficient estimates (Fig. S9). At high frequencies, global estimates that use the median of

1321 site-level power spectra and the mean of site-level eigencoefficient estimates have a band-limited

- 1322 increase in the globally estimated spectral power, not present in the global estimate that uses the 1323 mean of site-level power spectra (Fig. S9). These discrepancies may stem from the different
- 1324 underlying distributions of site-level spectral power and eigencoefficient estimates, and the phase
- 1325 relationships that are preserved in the eigencoefficient estimates.
- 1326

1327 The spectral power estimates from MTM of a Gaussian process follow a chi-square distribution 1328 with two degrees of freedom, while the distribution of eigencoefficients approximately follows a 1329 normal distribution (17, 97). This suggests that the estimated global power spectra of vegetation 1330 turnover using the mean of site-level spectral power should be systematically higher than median 1331 estimates and mean of eigencoefficient estimates, while the latter two should be similar. Our 1332 sensitivity tests capture this systematic offset (Fig. S9) and explain higher spectral power at low 1333 frequencies when using the mean of site-level spectral power. At low frequencies, individual

1334 sites with high spectral power pull the global estimate to higher values. While this offset should 1335 also exist at high frequencies, we observe a counterintuitive result: individual sites with low

1336 spectral power pull the global estimate that uses the mean of site-level spectral power to values

1337 comparable to the median and eigencoefficient global estimates (Fig. S9). In light of this

1338 unexpected observation, and considering that each approach produces identical conclusions, we

1339 present results using the mean of spectral power to maintain consistency with prior studies (5, 6, 6)1340 68).

1341

1342 In contrast to the robust conclusions when estimating the globally averaged power spectra of 1343 vegetation turnover using the mean, median, and mean of eigencoefficients we find that results

1344 were highly sensitive to averaging by β . This is a product of our piecewise regression procedure 1345 to determine the location of breaks in the log-log fit between spectral power and frequency in the

1346 high and intermediate frequency bands. Accurately identifying the location of breaks in β

- 1347 between the high and high-intermediate frequency bands requires high-resolution sampling
- 1348 which is present in a subset of fossil pollen assemblages (Fig. S9, Fig. S10). Performing
- 1349 breakpoint identification on spectral power at a site level increases the weight of the more

1350 abundant lower-resolution sites and reduces the weight of the less abundant high-resolution sites,

- 1351 reducing frequency resolution and biasing estimates of globally averaged β .
- 1352

We assessed the sensitivity of our conclusions to the influence of anthropogenic land-use change. 1353 1354 We performed all analyses after first removing all samples from the last 2,000 years (32), the 1355 interval during which anthropogenic influences in fossil pollen records are strongly expressed

1356 (37). Removing any samples within the last 2,000 years produces nearly identical power spectra

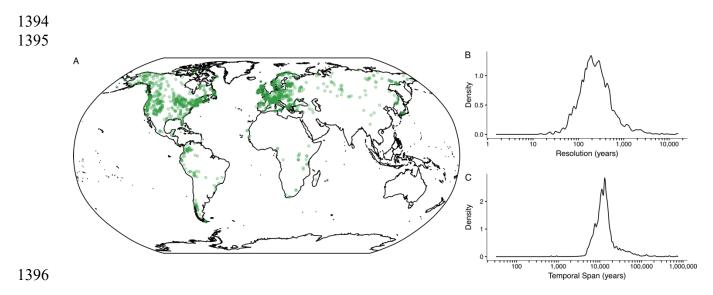
- 1357 at frequencies lower than 100⁻¹ years⁻¹ and suggests that climate tracking at millennial to multi-
- 1358 centennial scales persists (Fig. 2, Fig. S15). However, the detected breakpoints and β change if
- samples from the last 2,000 years are removed. The high frequency breakpoint (Fig. 2, 149⁻¹ 1359

years⁻¹) decreases to 527⁻¹ years⁻¹ and β decreases from 4.34 to 0.53; the breakpoint at 797⁻¹ 1360 years⁻¹ decreases to 3,602⁻¹ years⁻¹ and β increases from -0.1 to 1.96; the breakpoint at 18,012⁻¹ 1361 years⁻¹ decreases to 19,946⁻¹ years⁻¹ and β decreases from 1.84 to 1.09; and β for the lowest 1362 1363 frequencies increases from -0.08 to -0.008. Our sampling density increases as age decreases (Fig. S1) and sites with the highest temporal resolution span the last 2,000 years (Data S1), therefore 1364 1365 these changes in breakpoints and β may be a result of reduced sampling density. Despite 1366 statistically different β s at the highest frequencies, globally averaged power spectra still 1367 demonstrate a decrease in spectral power in the high frequency band which is particularly well 1368 demonstrated in the confidence intervals, matching results from the main manuscript (Fig. 2, Fig. 1369 S15) and results from similar analyses at a continental scale that also remove fossil pollen observations from the last 2,000 years (32). This suggests that climate decoupling at the highest 1370 1371 frequencies may contain some influence of anthropogenic land use change (38, 98) but this is not 1372 the only control on high frequency vegetation turnover.

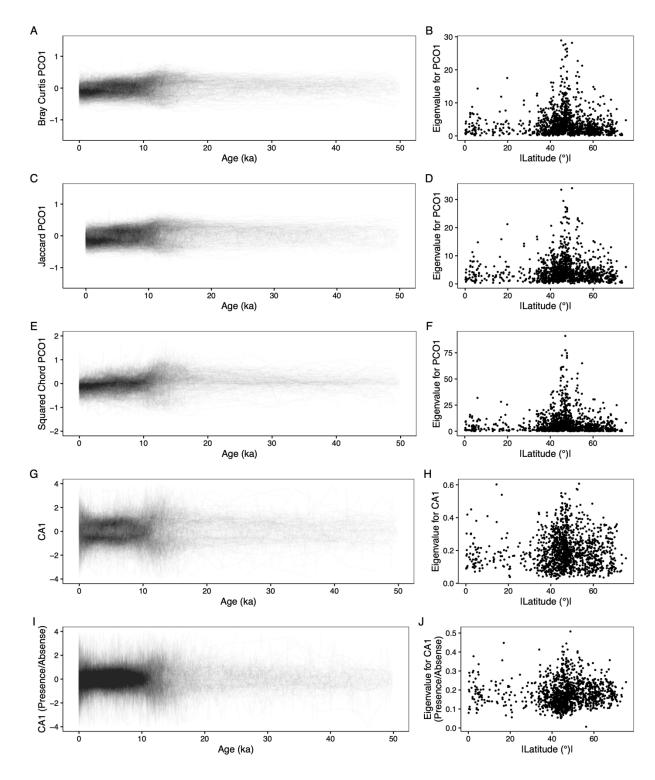
1373

1374 Lastly, we assessed the sensitivity of our results to our choice of averaging across all sites, sites 1375 in the tropics, and sites in the extra-tropics by averaging across biomes from Dinerstein (99)(Fig. 1376 S17, Fig. S16). Results partially align with expectations given the life history of the primary plant functional types that compose each biome. For instance, biomes with grassland ecosystems 1377 1378 such as Montane Grasslands and Shrubland and Tropical and Subtropical Grasslands, Savannas 1379 and Shrublands have smaller β 's than tree dominated biomes like Temperate Broadleaf and 1380 Mixed Forests, Boreal Forests/Taiga, and Mediterranean Forests (Fig. S16). Grasslands have a 1381 shorter lifespan and would be expected to have a lower β at high frequencies unlike treedominated ecosystems which have increasing turnover approaching the median age of tree 1382 1383 longevity (Fig. 2). However, β remains low across most frequencies, not just high frequencies. 1384 This may occur because grass pollen is commonly identifiable to the family level, therefore any changes in grassland composition are not observed by fossil pollen and may lead to low 1385 1386 vegetation turnover at low frequencies (Fig. S16). However, the Tundra and Temperate Conifer Forests do not cohere with these expectations. Temperate Conifer Forests have a low β and a 1387 1388 power spectrum that is characterized by abrupt changes indicated by high spectral power at 1389 ~5,000⁻¹ and ~9,000⁻¹ years⁻¹. In contrast, the Tundra biome has a large β despite being composed primarily of dwarf shrubs and grasses, with short generation times. Despite these two 1390 1391 exceptions, β and power spectra averaged across biomes generally align with ecologic 1392 expectations.

1393



- 1398 (A) All sites used in the spectral analyses, as in Fig. 2A. The probability density of (B) temporal
- 1399 resolution and (C) temporal span for all sites analyzed and all corresponding posterior age
- 1400 estimates. Note, that the Northern Hemisphere is more well-represented than the Southern1401 Hemisphere.
- 1402





1404 Fig. S2

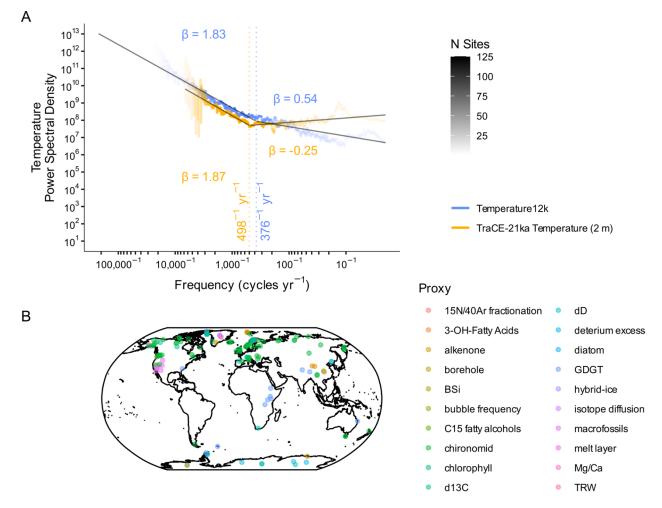
1405 (A, C, E, G, I) The primary dimension of variability from 1) principal coordinates analyses

1406 (PCO) using the (A) Bray-Curtis, (C) Jaccard, and (E) Squared Chord Distance metrics and 2)

1407 (G) correspondence analysis on fossil pollen assemblages for each site analyzed. We also

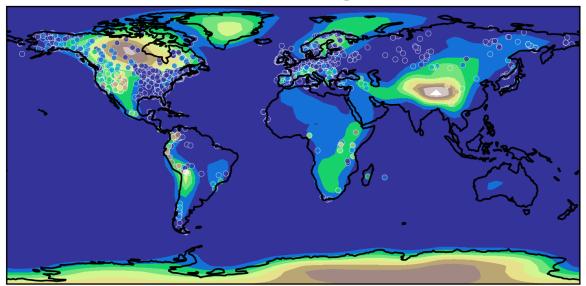
1408 performed correspondence analyses on fossil pollen assemblages after degrading the abundance

- 1409 observations to presence/absence (I). (B, D, F, H, J) Eigenvalues corresponding to PCO1 for
- 1410 each site plotted against the absolute value of the site latitude. For correspondence analyses,
- 1411 eigenvalues do not correspond to variance explained as they do for principal coordinate analyses.
- 1412 Rather, eigenvalues correspond to correlation coefficients between the coordinates for species in
- 1413 the fossil pollen assemblage (i.e. species score) and coordinates for time intervals (i.e. site score) 1414 in the ordination coordinate system. For visual simplicity, the PCO1 and CA1 results for each
- 1414 in the ordination coordinate system. For visual simplicity, the PCO1 and CA1 results for each 1415 site are unscaled by the corresponding eigenvalue. Several scaled time series are presented in
- 1416 Fig. S18. In addition, the right column (B, D, F, H, J) demonstrates that eigenvalues tend to be
- 1417 higher in the high latitudes, causing PCO1 for high-latitude sites to be upscaled, producing
- 1418 greater total spectral power in Fig. S9, relative to the low latitudes. Also for visual simplicity, we
- 1419 only present sites here that span the last 50,000 years; we direct readers to our Zenodo repository
- 1420 (66) where all data are present.
- 1421

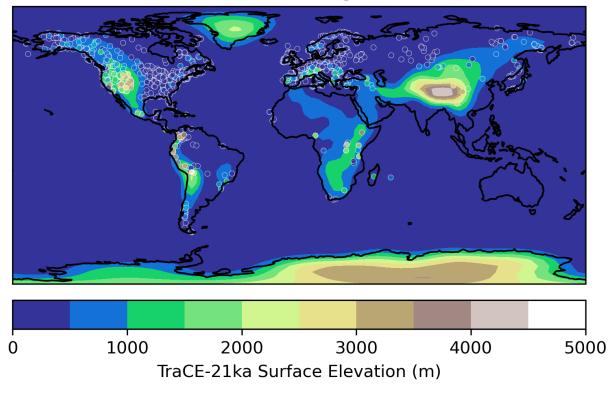


1423 Fig. S3

1424 (A) The averaged power spectrum for non-pollen temperature estimates from Temperature 12k 1425 (yellow). The averaged power spectrum of temperature variability for TraCE-21ka (blue) is 1426 estimated after degrading TraCE-21ka to match the time-averaged and spatial characteristics of 1427 the Temperature12k sites. Power spectra line opacity indicates the number of sites that resolve 1428 each frequency. Note the similar β at low frequencies and the similar break location between the 1429 high frequency and low frequency scaling regimes. (B) The Temperature12k sites are colored by 1430 proxy. 21 ka Average

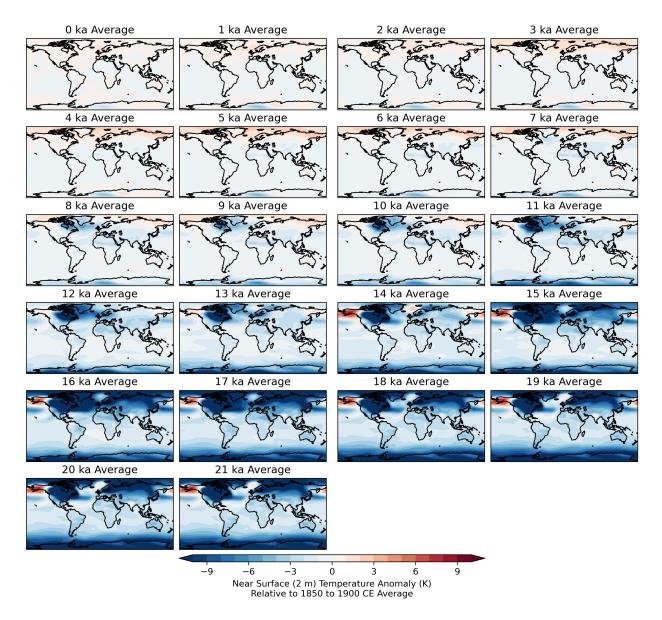


0 ka Average



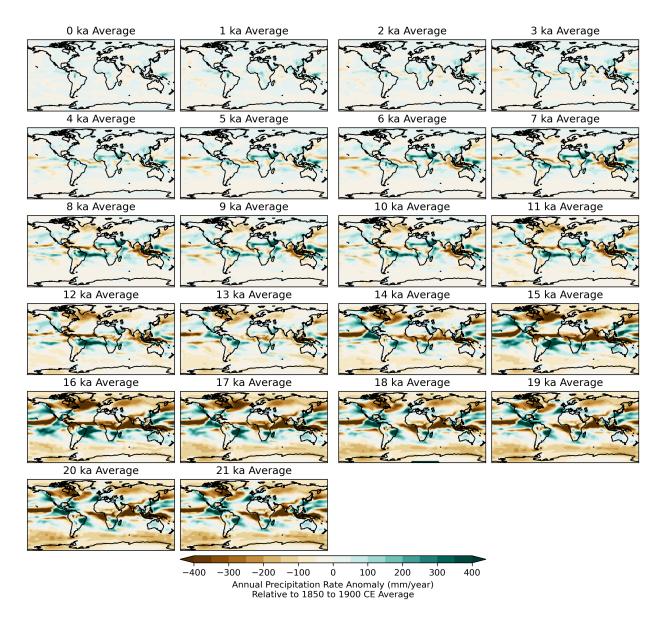
- 1431
- 1432 Fig. S4
- 1433 Surface elevation for the TraCE-21ka simulations averaged for 21ka and 0ka, calculated using
- 1434 the surface geopotential (PHIS in CCSM3). The change in topography in North America and
- 1435 Antarctica from 21ka to 0ka is associated with a loss of the Laurentide Ice Sheet and a reduction

- in ice volume in Antarctica. TraCE-21ka is simulated with ice sheet topography from the ICE-5G reconstruction (100).

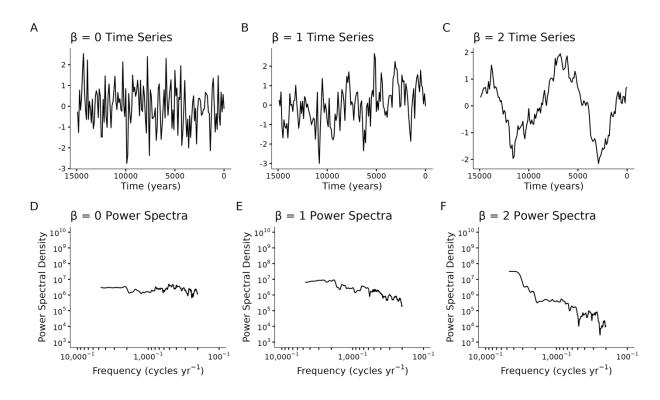


1439 Fig. S5

- 1440 Near surface temperature anomalies for TraCE-21ka relative to an 1850 to 1900 CE baseline
- 1441 averaged every 1,000 years.
- 1442



- 1443
- 1444 Fig. S6
- 1445 As in Fig. S5 but for the total annual precipitation rate.
- 1446

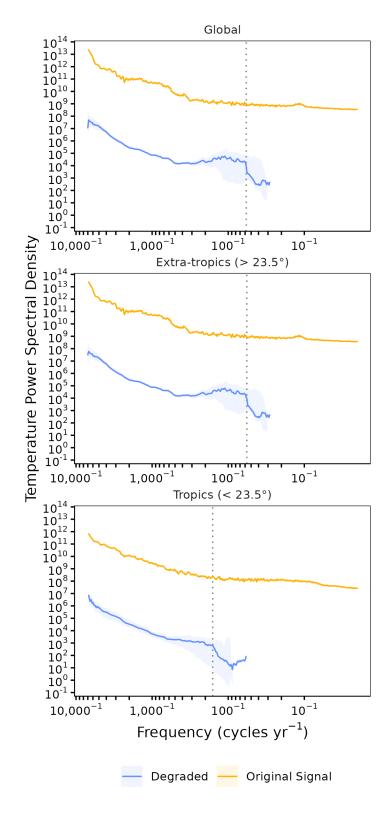




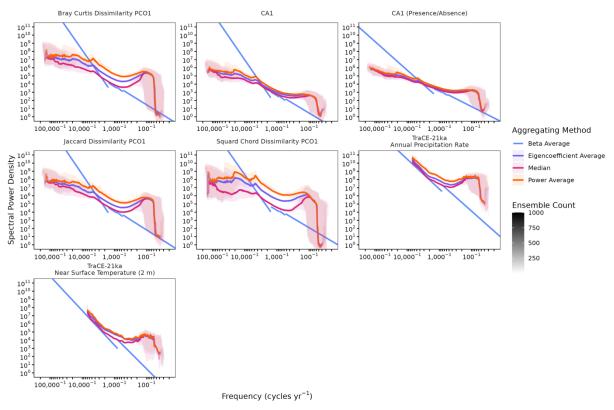
1448 Fig. S7

1449 (A-C) Synthetic time series with arbitrary units demonstrating a β of (A) 0, (B) 1, and (C) 2. (D-

1450 F) The corresponding power spectra for the synthetic time series in (A-C).



- 1454 Spectral power for near-surface temperature for TraCE-21ka at each fossil pollen site where the
- 1455 temperature time series is resolved annually (yellow) and degraded (blue) to match the temporal
- 1456 characteristics of the fossil pollen assemblage. For degradation, each annually-resolved
- 1457 temperature time series corresponding to the nearest grid cell to the fossil pollen site being
- analyzed was temporally subsampled to match the fossil pollen abundances and then smoothed
- 1459 using a low-pass filter with a timescale twice the mean resolution of the fossil pollen abundances
- 1460 (33). The frequency associated with a spurious drop in spectral power in the degraded power
- spectra, not present in the annually resolved power spectra, is defined as the highest resolvable
- 1462 frequency for (A) global, (B) extra-tropical, and (C) tropical spectral power estimates and
- 1463 marked with a dashed line. These frequencies are 58^{-1} years⁻¹, 57^{-1} years⁻¹, and 160^{-1} years⁻¹,
- 1464 respectively. Confidence intervals derive from the Monte-Carlo resampling procedure outlined in
- 1465 Uncertainty Estimation.



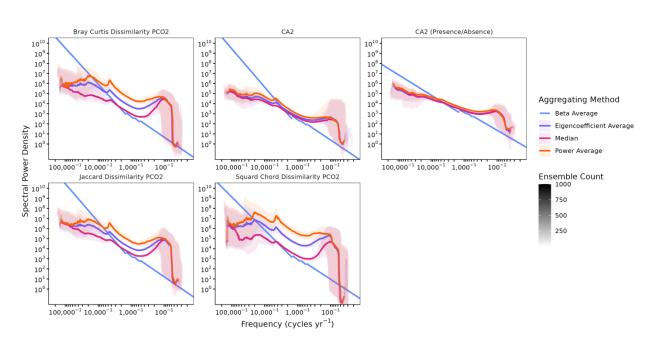
1467

1469 Sensitivity tests for the continuum of ecological variability, in which the dimensionality-1470 reduction methods and spectral-averaging methods are varied. Power spectra line opacity 1471 indicates the number of ensemble members that resolve each frequency. Results are presented for 1472 the primary dimension of variability from dimensionality reduction on fossil pollen assemblages. 1473 For the power average approach, we bin by frequency and then average the spectral power values 1474 across sites. For the eigencoefficient average approach, we bin by frequency and average the five 1475 MTM eigencoefficients corresponding to each data taper, across sites. We calculate spectral power following Equation 1. For the β average approach, we estimate β through an ordinary least 1476 1477 squares regression between spectral power and frequency at a single site. We then average across 1478 sites to produce a global estimate of β . This procedure only retains β , not spectral power. 1479 Therefore, for the β average method only the resulting β fit is presented. The separate lines for β 1480 average correspond to β in four frequency bands. The breakpoint of these two lines indicates the 1481 calculated average break location averaged across sites. All sensitivity analyses were performed 1482 with the Monte Carlo resampling procedure detailed in Uncertainty Estimation with the shaded 1483 area corresponding to the 95% confidence interval. Note, that all averaged power spectra based

- 1484 on PCO1 (the first axis of Principal Coordinates Analysis) of the site-level community 1485 dissimilarity matrix demonstrate a decrease in β after the common ~17,000⁻¹ years⁻¹ breakpoint
- 1486 ($\beta = 0.57$ for Bray-Curtis PCO1, $\beta = 0.72$ for Jaccard PCO1, $\beta = -0.08$ for Squared Chord
- 1487 PCO1). This decrease is greatest in the squared chord dissimilarity metric which outperforms all
- other metrics for distinguishing modern fossil pollen assemblages that source from different
 ecosystems (i.e. is the most sensitive dissimilarity metric) (63, 64). In contrast, CA1 (the first
- 1490 axis of Correspondence Analysis), which cannot saturate like metric-based approaches, shows no

- 1491 such decrease in β . The averaged power spectra for CA1, which represents the primary
- 1492 dimension of variation in fossil pollen assemblages (not the dissimilarity matrix), has a higher β
- 1493 ($\beta = 0.87$ for frequencies lower than the 18,395⁻¹ years⁻¹ breakpoint) and more consistent β s
- 1494 across all frequencies, demonstrating that the decrease in β observed at low frequencies for PCO-
- 1495 based approaches is caused by metric saturation.
- 1496



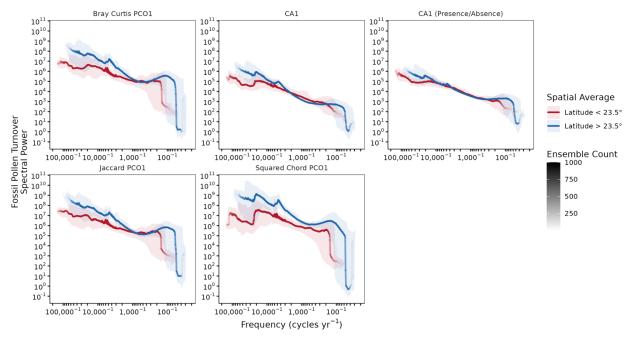


1499

1500 Fig. S10

1501 As in Fig. S9, for the secondary dimension of variability from dimensionality reduction on fossil

1502 pollen assemblages.



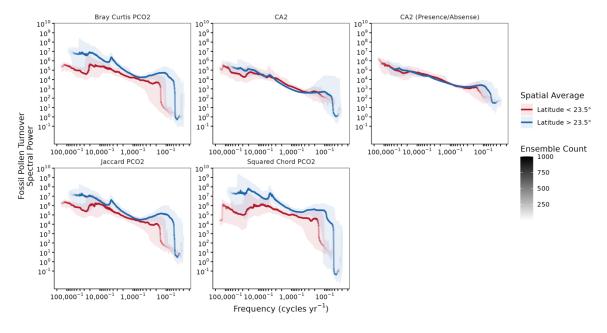
1506 Sensitivity tests for latitudinal averaged power spectra for PCO1 of fossil pollen assemblages

1507 where the dimensionality reduction method is varied. All power spectra were generated by

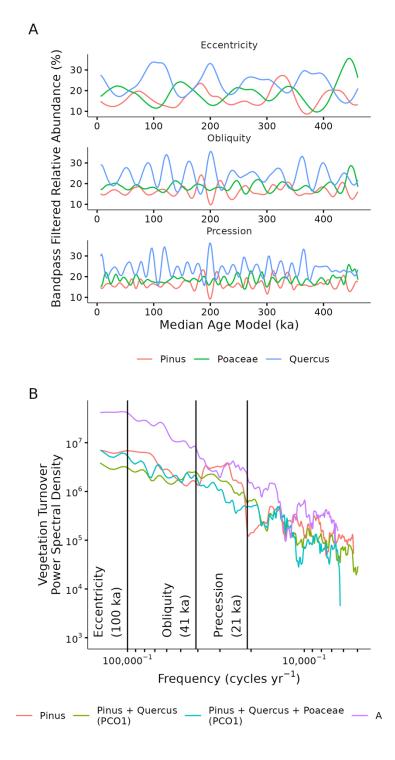
1508 averaging spectral power after binning by frequency. Power spectra line opacity indicates the

1509 number of ensemble members that resolve each frequency.

1510



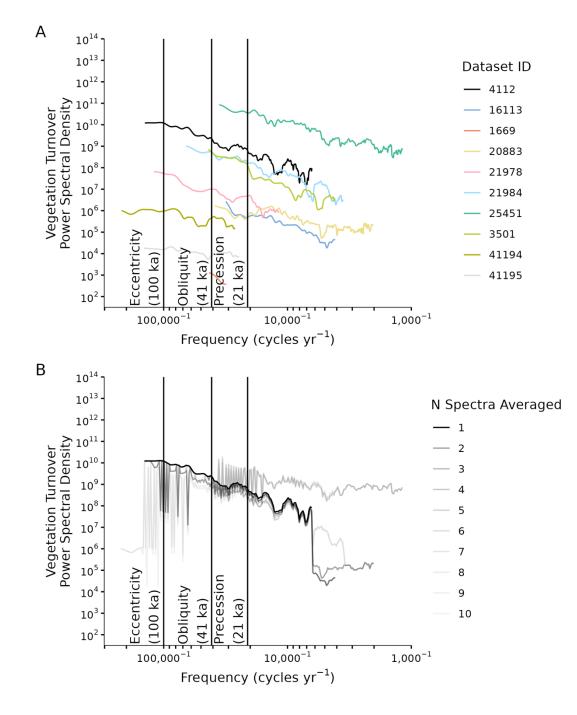
- 1512 Fig. S12
- 1513 As in Fig. S11 but for PCO2 from fossil pollen assemblages.
- 1514





(A) Taner filtered relative abundance of the three most abundant taxa at Ioannina (Dataset ID: 4112) for the precession (21,000 year), obliquity (41,000), and eccentricity (100,000 year)
Milankovitch cycles: *Pinus* (red), *Quercus* (blue), and Poaceae (green). A filter window from 25,000⁻¹ to 18,000⁻¹ years⁻¹ was used to isolate the precession signal. A filter window from 45,000⁻¹ to 35,000⁻¹ years⁻¹ was used to isolate the obliquity signal. A filter window from

- 1522 120,000⁻¹ to 80,000⁻¹ years⁻¹ was used to isolate the eccentricity signal. Note, that *Pinus*,
- 1523 Poaceae, and *Quercus* are out of phase for each Milankovitch cycle. (B) The effect of these out
- 1524 of phase relative abundance changes on periodic signals in the relative abundance and primary
- dimension of variability at site Ioannina. The red line corresponds to MTM performed on *Pinus*
- 1526 pollen relative abundance, not the primary mode of variability from PCO since more than one
- taxa is needed to generate a dissimilarity matrix. The green line corresponds to MTM performed
- on the primary dimension of variability of the dissimilarity matrix calculated with *Pinus* and
- 1529 *Quercus* relative abundances. For the blue line, Poaceae was added when calculating the 1530 dissimilarity matrix. In all instances, the out of phase behavior in (A) causes the periodic signal
- present in *Pinus* relative abundance near the obliquity band to diminish. MTM on PCO1 of the
- 1532 dissimilarity matrix of all taxa at Ioannina corresponds to the purple line.
- 1533



1535 Fig. S14

1536 (A) Spectral power from the ten longest records from our Neotoma compilation. High spectral

power at all Milankovitch bands is particularly well expressed at ODP Site 658 (41194) and

1538 Páramo de Agua Blanca (21978). (B) The effect of averaging spectral power across these sites,

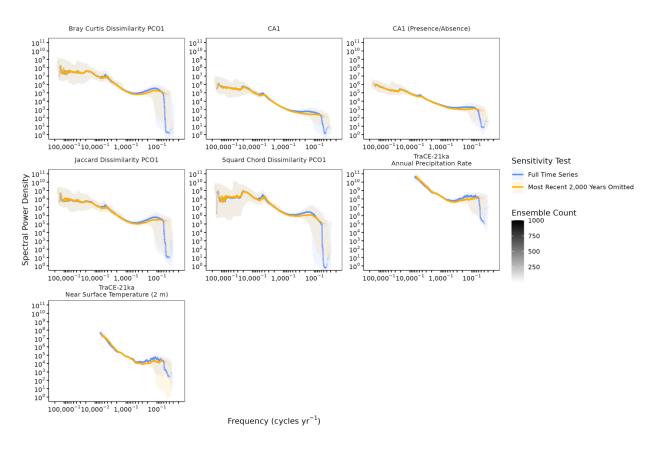
1539 each with a unique sampling resolution and temporal span. Here, the averaging is a running

1540 mean from the site order in A. For instance, "N Spectra Averaged" of one is the Ioannina (4112)

record; a value of two is the average of Ioannina (4112) and Grays Lake (16113); a value of three

1542 is the average of Ioannina (4112), Grays Lake (16113), and Lake Louise (1669). We use the

- median Bchron age model in these analyses and do not employ the resampling procedure of the main manuscript.
- 1545



1548 Sensitivity tests for the continuum of vegetation turnover and climate variability based on the

1549 median of an ensemble of spectral power estimates after removing any observations younger

1550 than 2,000 years, to assess the influence of anthropogenic land use change. The blue line

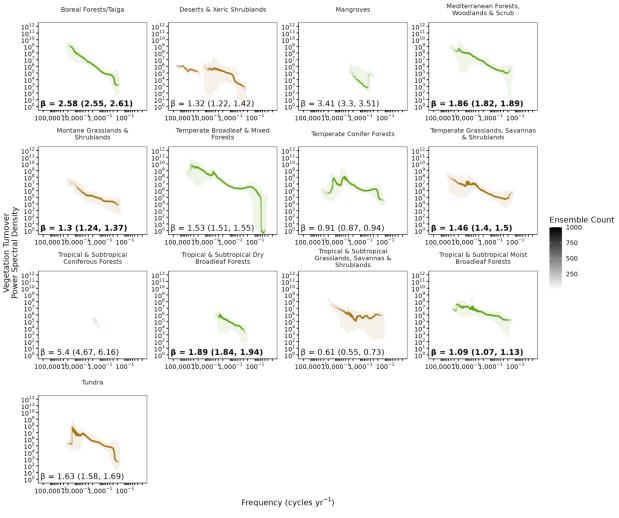
1551 corresponds to results from Fig. 2 and Fig. S9 and the yellow line corresponds to the sensitivity

1552 test. Power spectra line opacity indicates the number of ensemble members that resolve each

1553 frequency. Note, that the confidence intervals for the power spectra overlap across all of

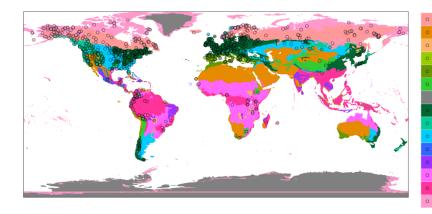
1554 frequency space suggesting a limited influence of anthropogenic land use change.

1555



1557 **Fig. S16**

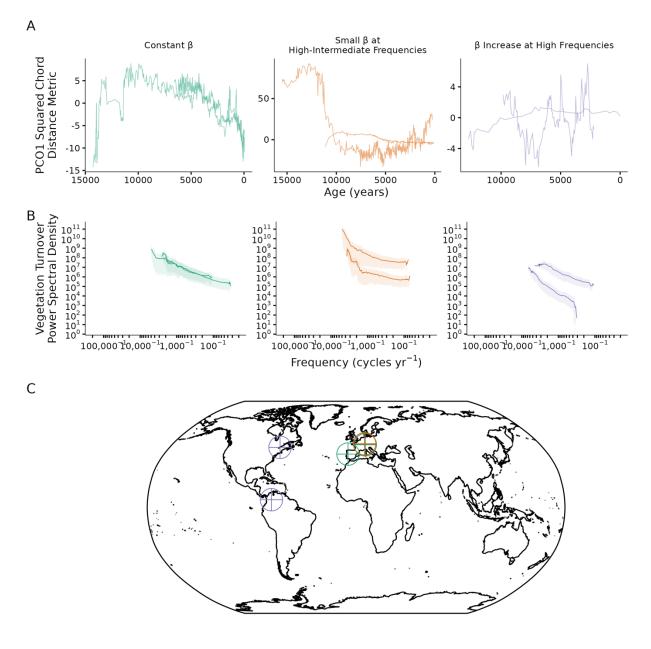
1558 Power spectra for vegetation turnover averaged across biomes, unlike the global, tropical, and 1559 extra-tropical averages in Fig. 2 and Fig. 3. Line coloring corresponds to biomes that have a 1560 large proportion of grasses (brown) or a large proportion of trees (green). β was estimated across 1561 each, entire power spectra (i.e. no breakpoint identification) and the bold text corresponds to power spectra where a single β estimate fits the power-law scaling relationship between spectral 1562 1563 power and frequency well. For instance, vegetation turnover in the Tropical & Subtropical 1564 Grasslands, Savannas & Shrublands biomes have two scaling regimes. Frequencies lower than $\sim 2.000^{-1}$ years⁻¹ have a large increase in spectral power with decreasing frequency. In contrast, 1565 frequencies higher than $\sim 2,000^{-1}$ years⁻¹ have uniform spectral power. For this reason, a single β 1566 1567 value poorly represents the non-linear scaling relationship. Note, that the gap in the power 1568 spectrum of Deserts & Xeric Shrublands is caused by the power spectra of two long records at 1569 coarse resolution (ODP658, Dataset ID: 41194, 41195, off the western coast of the Sahara Desert 1570 in Fig. S17, Data S1) being averaged with short, comparatively high resolution records. A lack of 1571 sites with intermediate resolution and temporal span in the Deserts & Xeric Shrubland biome 1572 causes a gap spectral power when all sites in the biome are averaged together. 1573



Boreal Forests/Taiga Deserts & Xeric Shrublands Flooded Grasslands & Savannas Mangroves Mediterranean Forests, Woodlands & Scrub Montane Grasslands & Shrublands No Biome Assigned Temperate Broadleaf & Mixed Forests Temperate Conifer Forests Temperate Grasslands, Savannas & Shrublands Tropical & Subtropical Coniferous Forests Tropical & Subtropical Grasslands, Savannas & Shrublands Tropical & Subtropical Grasslands, Savannas & Shrublands Tropical & Subtropical Grasslands, Savannas & Shrublands Tropical & Subtropical Moist Broadleaf Forests Tundra

- 1575
- 1576 **Fig. S17**
- 1577 Biome classifications for each site in our compilation based on ecoregions determined by
- 1578 Dinerstein et al (99).
- 1579

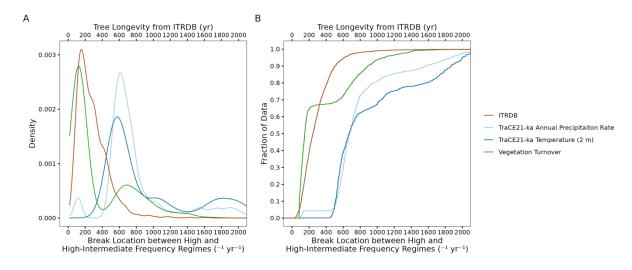




1582 Fig. S18

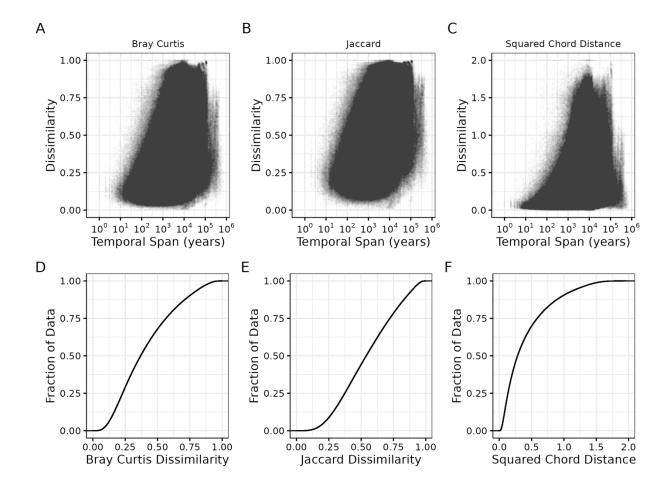
- 1583 (A) Individual records of vegetation turnover from the 1,321 site compilation that are selected to 1584 demonstrate characteristics of the global average power spectra that are presented in Fig. 2 and 1585 Fig. 3. Sites that demonstrate a constant β at millennial frequencies are colored in green and 1586 correspond to the globally averaged spectrum of vegetation turnover from 797⁻¹ to 18,012⁻¹
- 1587 years⁻¹ (Dataset IDs: 40999, 41909). Sites that have a low β at high-intermediate frequencies are
- 1588 colored in orange and correspond to the globally averaged spectrum of vegetation turnover from
- 1589 149⁻¹ to 797⁻¹ years⁻¹ (Dataset IDs: 40958, 42692). Sites that demonstrate a high β at the highest
- 1590 frequencies are colored in purple and correspond to the globally averaged spectrum of vegetation 1591 turnover for frequencies higher than 149⁻¹ years⁻¹ (Dataset IDs: 219, 21702). (B) The power

- 1592 spectra for the vegetation turnover time series in (A). (C) The location of sites presented in (A).
- 1593 The colors correspond to different spectral characteristics that are highlighted in the main text.
- 1594 Note, that all sites demonstrate a decrease in β at multimillennial timescales present in the global
- 1595 average at frequencies lower than 18,012⁻¹ years⁻¹. Note, in (A) the PCO1 time series are scaled
- 1596 by the corresponding eigenvalue, unlike in Fig. S2.
- 1597
- 1598



1599

1601 (A) Probability density distributions and (B) empirical cumulative distributions for the ensemble of breakpoints estimated for globally averaged power spectra between the low-intermediate and 1602 high-intermediate frequency band for fossil pollen (green) from our Monte Carlo resampling 1603 1604 approach, compared to tree longevity estimates from the International Tree Ring Data Bank (brown). Break locations for TraCE-21ka near-surface temperature (blue) and TraCE-21ka 1605 1606 precipitation (light blue) correspond to one break location, previously reported (5, 6), at frequencies between 100⁻¹ to 1,000 years⁻¹. Tree longevity from the International Tree Ring Data 1607 1608 Bank corresponds to the top horizontal axis. All pollen results presented are from PCO1 using 1609 the squared chord distance metric and averaged by spectral power. 1610



1613 Fig. S20

1614 (A-C) Measured vegetation assemblage dissimilarity, for all sites in the global fossil pollen

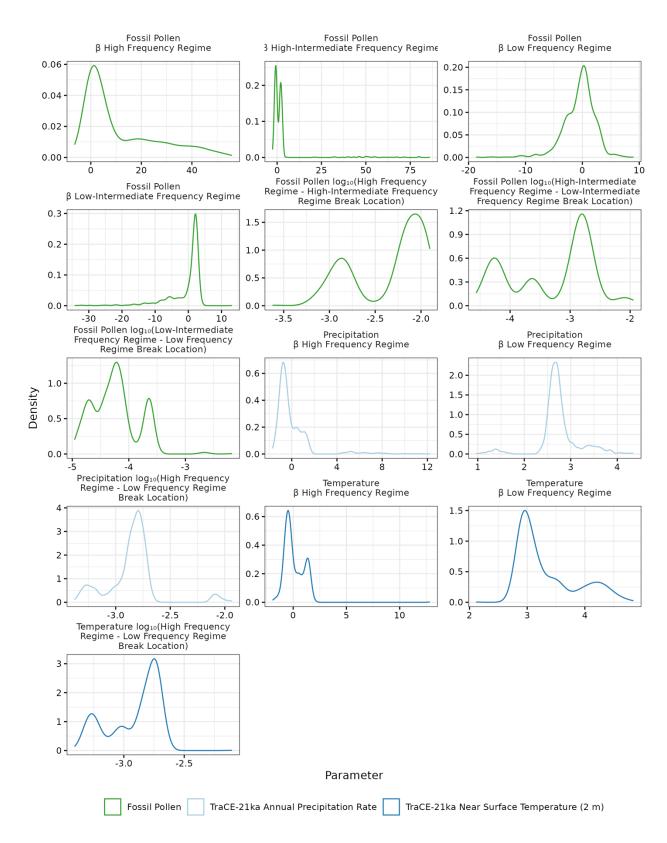
1615 compilation. Dissimilarity was calculated only for assemblages from the same site and was not

1616 calculated for assemblages from different sites. Within each site, all possible pairs of fossil

1617 pollen assemblages were compared using the (A) Bray Curtis, (B) Jaccard, and (C) Squared

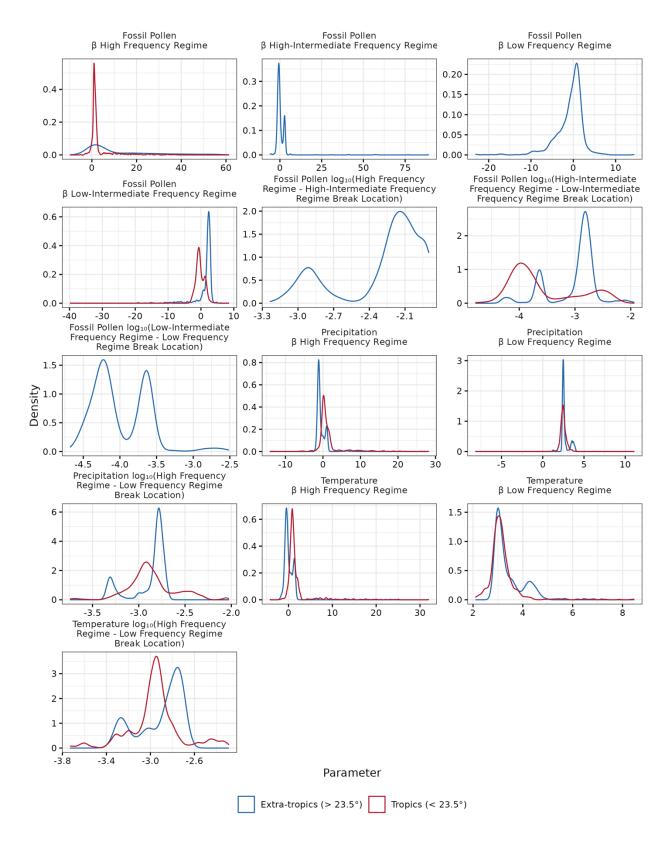
1618 Chord Distance metrics with the corresponding temporal span between the samples being

1619 compared retained. (D-F) The empirical cumulative distribution of all points shown in the top1620 row of plots.



1625 Each plot corresponds to the probability density function for all breakpoint and β parameter

- 1626 estimates in Fig. 2 and Table S1. Colors correspond to parameter estimates for fossil pollen
- 1627 (green), TraCE-21ka annual precipitation rate (light blue), and TraCE-21ka near-surface
- 1628 temperature (blue).
- 1629



- **Fig. S22**
- As in Fig. S21 but for breakpoint and β estimates in Fig. 3. Colors correspond to the spatial average with red indicating the tropics (< 23.5°) and blue indicating the extra-tropics (> 23.5°).

				β			Breakpoint
					High	High-	
					Frequency	Intermediate	Low-
					Band -	Frequency	Intermediate
					High-	Band - Low-	Frequency
		High-	Low-		Intermediate	Intermediate	Band – Low
	High	Intermediate	Intermediate	Low	Frequency	Frequency	Frequency
	Frequency	Frequency	Frequency	Frequency	Band (⁻¹	Band (⁻¹ years ⁻	Band (⁻¹
	Band	Band	Band	Band	years ⁻¹)	1)	years ⁻¹)
Global	4.34*†	0.35*†	$1.78^{*\dagger}$	-0.08†	149*	797*	18,012*
	(3.64, 4.96)	(0.02,	(1.67,	(-0.23,	(154,	(862,	(18,952,
		0.83)	1.87)	-0.06)	145)	797)	17,254)
Extra-	4.34*†	-0.36*†	2.20*†	-0.05†	148*	712*	13,885*
tropics	(3.79,	(-0.43,	(2.16,	(-0.24,	(153,	(730,	(14,495,
(> 23.5°)	4.93)	-0.28)	2.26)	0.11)	142)	698)	13,160)
Tropics	1.30*†			-0.43*†			6,877*
(< 23.5°)	(1.21, 1.38)			(-0.51,			(7,499,
(2010)	())			-0.38)			6,383)
1636				· · ·	1		

TraCE-21ka near-surface Temperature (2 m)

		β	Breakpoint
		Low Frequency Band	High Frequency Band - Low
	High Frequency Band	(Climate Regime)	Frequency Band. (⁻¹ years ⁻¹)
Global	-0.24*†	3.10*†	672*
	(-0.29,	(3.07,	(693,
	-0.18)	3.13)	649)
Extra-	-0.26*†	3.14*†	674*
tropics (>	(-0.30,	(3.11,	(691,
23.5°)	-0.21)	3.17)	649)
Tropics (<	0.94*†	3.08*†	894*
23.5°)	(0.91,	(3.06,	(909,
,	1.00)	3.10)	886)
1637		· · · ·	

TraCE-21ka Annual Precipitation Rate

		В	Breakpoint
		Low Frequency Band	High Frequency Band - Low
	High Frequency Band	(Climate Regime)	Frequency Band (⁻¹ years ⁻¹)
Global	-0.53*†	2.696*†	676*
	(-0.58,	(2.68,	(691,
	-0.49)	2.705)	660)
Extra-	-0.99*†	2.52*†	628*
tropics (>	(-1.01,	(2.51,	(632,
23.5°)	-0.96)	2.53)	618)
Tropics (<	0.47*†	2.47*†	795*
23.5°)	(0.41,	(2.45,	(814,
	0.53)	2.48)	776)

1639 **Table S1**

1640 Parameter estimates and corresponding 95% confidence intervals (in parentheses) for Fig. 2 and

1641 Fig. 3. * indicates that the estimated parameter is statistically distinct from 0 based on the

1642 bootstrapped confidence interval. For estimates of β , [†] indicates that β is statistically distinct

1643 from 2 (i.e. red noise) based on the bootstrapped confidence interval (for methods, see section

1644 Statistical Comparisons between Estimated Parameters from Spectral Analyses).

	Vegetation Turnover High Frequency Band - High-Intermediate Frequency Band Break Location	Vegetation Turnover High- Intermediate Frequency Band - Low- Intermediate Frequency Band Break Location	Vegetation Turnover Low- Intermediate Frequency Band - Low Frequency Band Break Location	TraCE-21ka Temperature High Frequency Band - Low Frequency Band Break Location	TraCE-21ka Annual Precipitation Rate High Frequency Band - Low Frequency Band Break Location
Vegetation Turnover High Frequency Band - High-Intermediate Frequency Band Break Location					
Vegetation Turnover High-Intermediate Frequency Band - Low- Intermediate Frequency Band Break Location	< 0.001***				
Vegetation Turnover Low-Intermediate Frequency Band - Low Frequency Band Break Location	< 0.001***	< 0.001***			
TraCE-21ka Temperature High Frequency Band - Low Frequency Band Break Location	< 0.001***	< 0.001***	< 0.001***		
TraCE-21ka Annual Precipitation Rate High Frequency Band - Low Frequency Band Break Location	< 0.001***	< 0.001***	< 0.001***	0.693	

Table S2

P-values of permutation tests comparing break locations from Fig. 2 where *** corresponds to values <0.001, ** indicates values between 0.001 and 0.01, and * indicates values between 0.01 and 0.05.

	Vegetation Turnover β High Frequency Band	Vegetati on Turnove r β High- Interme diate Frequen cy Band	Vegetati on Turnove r β Low- Interme diate Frequen cy Band	Vegetat ion Turnov er β Low Freque ncy Band	TraCE- 21ka Tempera ture β High Frequen cy Band	TraCE- 21ka Tempera ture β Low Frequen cy Band	TraCE- 21ka Annual Precipita tion Rate β High Frequen cy Band	TraCE- 21ka Annual Precipita tion Rate β Low Frequen cy Band
Vegetation Turnover β High Frequency Band								
Vegetation Turnover β High- Intermediate Frequency Band	< 0.001***							
Vegetation Turnover β Low- Intermediate Frequency Band	< 0.001***	< 0.001** *						
Vegetation Turnover β Low Frequency Band	< 0.001***	0.0543	< 0.001** *					
TraCE-21ka Temperature β High Frequency Band	< 0.001***	< 0.001** *	< 0.001** *	0.0171 **				
TraCE-21ka Temperature β Low Frequency Band	< 0.001***	< 0.001** *	< 0.001** *	< 0.001* **	< 0.001** *			
TraCE-21ka Annual Precipitation Rate β High Frequency Band	< 0.001***	< 0.001** *	< 0.001** *	< 0.001* **	< 0.001** *	< 0.001** *		
TraCE-21ka Annual Precipitation Rate β Low Frequency Band	< 0.001***	< 0.001** *	< 0.001** *	< 0.001* **	< 0.001** *	< 0.001** *	< 0.001** *	

Table S3

P-values of permutation tests comparing β from Fig. 2 where *** corresponds to values <0.001, ** indicates values between 0.001 and 0.01, and * indicates values between 0.01 and 0.05.

	Latitude $> 23.5^{\circ}$ Vegetati on Turnove r β High Frequen cy Band	Latitude > 23.5° Vegetatio n Turnover β High- Intermedi ate Frequenc y Band	Latitude > 23.5° Vegetatio n Turnover β Low- Intermedi ate Frequenc y Band	Latitude > 23.5° Vegetati on Turnove r β Low Frequen cy Band	Latitude > 23.5° TraCE- 21ka Temperat ure β High Frequenc y Band	Latitude > 23.5° TraCE- 21ka Temperat ure β Low Frequenc y Band	Latitude > 23.5° TraCE- 21ka Annual Precipitat ion Rate β High Frequenc y Band	Latitude > 23.5° TraCE- 21ka Annual Precipitat ion Rate β Low Frequenc y Band
Latitude > 23.5° Vegetation Turnover β High Frequency Band								
Latitude > 23.5° Vegetation Turnover β High- Intermediate Frequency Band	< 0.001** *							
Latitude > 23.5° Vegetation Turnover β Low- Intermediate Frequency Band	< 0.001** *	< 0.001***						
Latitude > 23.5° Vegetation Turnover β Low Frequency Band	< 0.001** *	< 0.001***	< 0.001***					
Latitude > 23.5° TraCE- 21ka Temperature β High Frequency Band	< 0.001** *	0.008**	< 0.001***	< 0.001** *				

Latitude > 23.5° TraCE- 21ka Temperature β Low Frequency Band	< 0.001** *	< 0.001***	< 0.001***	< 0.001** *	< 0.001***			
Latitude > 23.5° TraCE- 21ka Annual Precipitation Rate β High Frequency	< 0.001** *	< 0.001***	< 0.001***	< 0.001** *	< 0.001***	< 0.001***		
Frequency Band Latitude > 23.5° TraCE- 21ka Annual Precipitation Rate β Low Frequency Band	< 0.001** *	< 0.001***	< 0.001***	< 0.001** *	< 0.001***	< 0.001***	< 0.001***	

Table S4

P-values of permutation tests comparing β for the extra-tropics from Fig. 3 where *** corresponds to values <0.001, ** indicates values between 0.001 and 0.01, and * indicates values between 0.01 and 0.05.

Latitude > 22.5° Vecetation	Latitude > 23.5° Vegetation Turnover High Frequency Band - High-Intermediate Frequency Band Break Location	Latitude > 23.5° Vegetation Turnover High- Intermediat e Frequency Band - Low- Intermediat e Frequency Band Break Location	Latitude > 23.5° Vegetation Turnover Low- Intermediat e Frequency Band - Low Frequency Band Break Location	Latitude > 23.5° TraCE- 21ka Temperatur e High Frequency Band - Low Frequency Band Break Location	Latitude > 23.5° TraCE- 21ka Annual Precipitatio n Rate High Frequency Band - Low Frequency Band Break Location
Latitude > 23.5° Vegetation Turnover High Frequency Band -					
High-Intermediate Frequency					
Band Break Location					
Latitude $> 23.5^{\circ}$ Vegetation	< 0.001***				
Turnover High-Intermediate					
Frequency Band - Low-					
Intermediate Frequency Band					
Break Location					
Latitude $> 23.5^{\circ}$ Vegetation	< 0.001***	< 0.001***			
Turnover Low-Intermediate					
Frequency Band - Low					
Frequency Band Break Location					
Latitude > 23.5° TraCE-21ka	< 0.001***	< 0.001***	< 0.001***		
Temperature High Frequency					
Band - Low Frequency Band					
Break Location					
Latitude > 23.5° TraCE-21ka	< 0.001***	< 0.001***	< 0.001***	< 0.001***	
Annual Precipitation Rate High					
Frequency Band - Low					
Frequency Band Break Location					

Table S5

- P-values of permutation tests comparing break locations for the extra-tropics from Fig. 3 where *** corresponds to values <0.001, ** indicates values between 0.001 and 0.01, and * indicates values between 0.01 and 0.05.

	Latitude < 23.5° Vegetation Turnover High Frequency Band – Low Frequency Band Break Location	Latitude < 23.5° TraCE-21ka Temperature High Frequency Band - Low Frequency Band Break Location	Latitude < 23.5° TraCE-21ka Annual Precipitation Rate High Frequency Band - Low Frequency Band Break Location
Latitude < 23.5°			
Vegetation Turnover High			
Frequency Band – Low			
Frequency Band Break			
Location			
Latitude < 23.5° TraCE-	< 0.001***		
21ka Temperature High			
Frequency Band - Low			
Frequency Band Break			
Location			
Latitude < 23.5° TraCE-	< 0.001***	< 0.001***	
21ka Annual Precipitation			
Rate High Frequency			
Band - Low Frequency			
Band Break Location			

Table S6

P-values of permutation tests comparing break locations for the tropics from Fig. 3 where *** corresponds to values <0.001, ** indicates values between 0.001 and 0.01, and * indicates values between 0.01 and 0.05.

	Latitude < 23.5° Vegetation Turnover β High Frequency Band	Latitude < 23.5° Vegetation Turnover β Low Frequency Band	Latitude < 23.5° TraCE-21ka Temperature β High Frequency Band	Latitude < 23.5° TraCE-21ka Temperature β Low Frequency Band	Latitude < 23.5° TraCE-21ka Annual Precipitation Rate β High Frequency Band	Latitude < 23.5° TraCE-21ka Annual Precipitation Rate β Low Frequency Band
Latitude < 23.5°						
Vegetation						
Turnover β High						
Frequency Band						
Latitude < 23.5°	< 0.001***					
Vegetation						
Turnover β Low						
Frequency Band						
Latitude < 23.5°	< 0.001***	<				
TraCE-21ka		0.001***				
Temperature β High						
Frequency Band						
Latitude < 23.5°	< 0.001***	<	< 0.001***			
TraCE-21ka		0.001***				
Temperature β Low						
Frequency Band						
Latitude < 23.5°	< 0.001***	<	< 0.001***	< 0.001***		
TraCE-21ka Annual		0.001***				
Precipitation Rate β						
High Frequency						
Band						
Latitude < 23.5°	< 0.001***	<	< 0.001***	< 0.001***	< 0.001***	
TraCE-21ka Annual		0.001***				
Precipitation Rate β						
Low Frequency						
Band	l		l	l	l	

1673 **Table S7**

1674 P-values of permutation tests comparing β for the tropics from Fig. 3 where *** corresponds to 1675 values <0.001, ** indicates values between 0.001 and 0.01, and * indicates values between 0.01

1676 and 0.05.

1677

Site Name	Dataset ID	Failure Reason
Challa Lake	hXPNKEOsFdftFMmUvYYv	No age information in
		Temperature12k
Lake Malawi	Ff4CF5LsHT00394MMeFt	Not enough RAM for
		linterpLH13 interpolation
		algorithm
Midden Cluster 3	yCebthVVgiBnTTu63yvd	No resolvable frequencies
		determined by linterpLH13
		interpolation algorithm
Midden Cluster 5	Mq5F6F6nmLYKNlACGome	No resolvable frequencies
		determined by linterpLH13
		interpolation algorithm
Middel Cluster 6	39OKoIAcvAICa26B8Oiy	No resolvable frequencies
		determined by linterpLH13
		interpolation algorithm
Soylegrotta	Ipsz1iUTCMtvZqRnxzs8	No resolvable frequencies
		determined by linterpLH13
		interpolation algorithm

Table S8

Temperature12k sites that failed spectral analyses and the corresponding reason.

1689 Data S1 (separate file)

- 1690 The list of sites considered in this study including those that were filtered out for issues with
- 1691 taxonomy harmonization, data quality (negative abundances), or chronological issues that
- 1692 prevented developing age models.