1 EarthArXiv Cover Sheet

2 3 **Title**

Timescale-dependent response of vegetation to climate change

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93 Abstract

94

95 Climate and ecosystems are dynamic across timescales, but existing research into climate-driven

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

analysis-based approach that provides unprecedentedly detailed estimates of the timescales at

98 which vegetation tracks climate change, from 10^1 to 10^5 years. We report dynamic similarity of

vegetation and climate at centennial frequencies (146⁻¹ to 17,505⁻¹ years⁻¹). A breakpoint in

100 vegetation turnover (759⁻¹ years⁻¹) matches a breakpoint between stochastic and autocorrelated

climate processes, suggesting ecological dynamics are governed by climate across these regimes.
 However, heightened vegetation turnover at millennial frequencies (4,650⁻¹ years⁻¹) highlights

103 the risk of abrupt ecological responses to climate change, while vegetation-climate decoupling at

104 frequencies shorter than 146⁻¹ years⁻¹ suggests that plant assemblages may continue changing for

105 centuries in response to anthropogenic climate change, with potentially lasting consequences for

106 ecosystem function and biodiversity.

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108 Keywords

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Spectral power continuum, community turnover, climate variability, dynamic equilibrium, nonlinear ecological dynamics, temporal beta diversity, vegetation

112

113 Manuscript Text

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115 The biosphere is a dynamic component of the Earth system that is sensitive to climate variability,

116 with eco-evolutionary processes operating across a broad range of timescales (1-3). Ecologists

117 have long recognized that species and ecological systems differ in their responses to changing

118 climate and that these dynamics are timescale dependent (3-6). However, most studies of

119 climate-driven ecological dynamics have focused on recent baselines and narrow ranges of

timescales, leaving critical gaps in our understanding of how communities respond toenvironmental change across the continuous range of timescales experienced by biota (7, 8).

121 122

123 Recent advances have improved our understanding of climate variability (9, 10) and expanded

124 global networks of ecological and paleontological data across timescales (*11, 12*). These parallel

- advances now enable us to characterize, in ways not previously possible, ecological responses to advances forming as fost alow an d/a and d/a and d/a
- 126 climate forcing as fast, slow, and/or nonlinear (13, 14). Fast ecological dynamics can track

127 climate change (13, 14), while slow dynamics are lagged or decoupled from climate (15-18).

128 Regardless of whether dynamics are fast or slow, ecosystems can linearly or nonlinearly respond 120 to forcing (e.g. (10)) with the notantial for nonlinear responses to lead to shrupt species

129 to forcing (e.g. (19)), with the potential for nonlinear responses to lead to abrupt species 130 compositional changes or other ecological regime shifts (20). Characterizing the nature of

130 compositional changes or other ecological regime shifts (20). Characterizing the nature of 131 ecological dynamics across timescales is urgently required for understanding how and at what

132 rates ecological systems are likely to respond to anthropogenic climate change (21).

133

Here, we focus on the relationship among temperature, precipitation, and vegetation

135 compositional turnover in time series spanning hundreds to hundreds of thousands of years for

the last 600,000 years, with the densest coverage for the last 20,000 years. To study the

relationship between timescales of climate variability and vegetation dynamics, we create and

apply a conceptual and analytical framework rooted in spectral analysis (22), widely used in

139 climate science (9, 23–25). Spectral analysis decomposes the variance in a time series into its

140 constituent frequencies, providing insights into the relative contributions of different timescales

- to the overall variability. Within this framework, vegetation variability is characterized by
- 142 change (or turnover) in species composition within assemblages as measured with the squared
- 143 chord dissimilarity metric (26). Comparing climate and vegetation variability in the frequency
- domain overcomes a fundamental challenge in time-domain analyses: the coupling, decoupling,
- and scaling of climate drivers and ecological responses with time.
- 146
- 147 Through this approach, we generate global power spectra of vegetation variability by averaging
- site-level power spectra for fossil pollen assemblages across a global compilation of 1,321 sites.
- 149 We compare these global vegetation compositional changes to power spectra of temperature and
- 150 precipitation from a climate model simulation of the last 21,000 years (TraCE-21ka) (27, 28). To
- 151 capture lower-frequency climate variability than that covered by the 21,000 year-long
- simulation, we include climate reconstructions that approximate global climate from an Antarctic
- 153 ice core (29) and a proxy-based reconstruction of global surface air temperature of the last two
- 154 million years (*30*). By comparing the global dynamics of climate and vegetation across
- timescales, we assess the coupling of vegetation assemblages to climate variability.
- 156

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

158 159

160 Paired spectral analyses of climate and ecological time series can quantify the dynamic similarity

- 161 of climate and assemblage turnover across timescales (31, 32). In frequency space, timescale and
- 162 frequency are inversely related longer timescales correspond to lower frequencies and short
- 163 timescales correspond to higher frequencies. The dynamics of climate and vegetation can be
- assessed in frequency space by comparing their spectral continua. For many physical systems,
- 165 the exponential coefficient of the power-law relationship (β in S(f) \propto f^{β}) between spectral power 166 (S) and frequency (f) defines the spectral continuum. Within a time series, β characterizes
- 167 memory (i.e. temporal autocorrelation) and how variance is partitioned across frequencies (25).
- 168 If the exponential coefficient (β) of the power-law relationship between frequency and spectral
- 169 power is small ($\beta \sim 0$), variance is equally partitioned among all frequencies (i.e., white noise;
- 170 Figure S1) (25). In contrast, $\beta > 0$ indicates more variance at lower frequencies (longer periods),
- 171 with $\beta = 2$ defining a random walk (i.e., red noise; Figure S1) (25).
- 172

173 There exists a scale break in the spectral continuum of climate variability between short-lived,

- 174 stochastic, weather processes and climate processes that possess increasing variability with
- 175 decreasing frequency (33). This break occurs between 100^{-1} to $1,000^{-1}$ years⁻¹ and separates high
- 176 frequencies that are represented by a low β from low frequencies that are characterized by a high
- 177 β (9, 10). If vegetation composition changes in parallel with climate variability, then variability
- 178 in vegetation turnover should have similar β s and show a similar scaling break (Figure 1A, $\beta_{veg} =$
- 179 β_{clim}). However, the drivers of vegetation compositional change vary in relative importance 180 across frequencies (Figure 1): disturbance, biotic interactions, and demographic processes are
- thought to be more important at high frequencies; dispersal limitation, population dynamics,
- restriction to refugia, and ecosystem transformation dominate at intermediate frequencies; and
- 182 macroevolutionary processes such as speciation and extinction prevail at lower frequencies
- 183 macroevolutionary processes such as speciation and extinction prevail at lower frequencies

(Figure 1)(1, 2)). These processes may modulate vegetation responses to climate and may cause 184

- 185 the continuum of vegetation variability to diverge from climate.
- 186

187 We expect that matching β s for climate and climate and vegetation (i.e. $\beta_{veg} = \beta_{clim}$) are likely to emerge at intermediate frequencies (i.e. millennial to orbital cycles, roughly 1,000⁻¹ to 100,000⁻¹ 188 189 years⁻¹) (13, 14), where plant assemblages are influenced by ecological and biogeographic 190 processes such as environmental filtering, dispersal, restriction to refugia, and local population extirpation (34, 35) (Figure 1). At these intermediate frequencies, the processes determining 191 192 assemblage composition, such as dispersal and ecosystem transformations caused by changing 193 species' abundances, act quickly relative to the pacing of climate variability (13, 14). Here, we 194 use the term 'fast tracking' to refer to cases where vegetation and climate have matching β s, even 195 though our methods do not test for causation. Built upon this expectation of fast tracking at these 196 frequencies, many prior studies have used pollen and other microfossils as paleoclimate proxies

- 197 (36–39).
- 198

199 However, the relationship between climate and vegetation dynamics at lower ($< 100,000^{-1}$ years⁻

¹) and higher frequencies (> $1,000^{-1}$ years⁻¹) remains an open question, as does the exact 200

201 frequencies at which the assumption of fast tracking no longer holds (15). High frequencies are 202 particularly crucial for predicting vegetation responses to anthropogenic climate warming, as 203 they allow exploration of how ecological and life-history factors may override the influence of 204 climate variability. The vegetation response at high frequencies may be slow because trees tend 205 to have lifespans of 10^1 to 10^3 years (40). This characteristic may produce low variability in 206 vegetation turnover at high frequencies, but high variability at frequencies corresponding with 207 tree senescence—manifesting as a larger β in vegetation turnover than in climate (Figure 1B, β_{veg} $>\beta_{clim}$). Conversely, disturbance through herbivory, fire, human land use, and disease could 208 209 increase vegetation turnover at high frequencies, thereby causing a smaller β relative to climate 210 (Figure 1B, $\beta_{\text{veg}} < \beta_{\text{clim}}$).

211

212 At low frequencies, vegetation dynamics distinct from intermediate and short frequencies may 213 emerge. Climate tracking could persist, as expected at intermediate frequencies (Figure 1C, β_{veg} 214 $=\beta_{\text{clim}}$, or adaptive evolution could increase species' tolerances to new climate regimes (41),

215 potentially reducing assemblage compositional responses to climate forcing and species'

- 216 sensitivity to environmental changes. As a product of compositional stability, vegetation
- 217 turnover variability would increase minimally as frequencies decrease relative to climate 218
- variations. (Figure 1C, $\beta_{veg} < \beta_{clim}$). Conversely, if vegetation responses to environmental 219
- forcings are characterized by strong non-linearities (42–44), variability in vegetation turnover 220 would be high relative to climate and vegetation turnover variability would increase as frequency
- 221 decreases faster than climate variability (Figure 1C, $\beta_{veg} > \beta_{clim}$) (45).
- 222

223 Spectral continuum of vegetation variability

224

225 To minimize sampling effects when comparing the power spectrum of vegetation variability to

226 that of climate variability, we downsample and low-pass filter the simulated climate time series

227 from TraCE-21ka to match the spatiotemporal characteristics of the fossil pollen archives (see

228 Supplemental Information). Unlike simulated data, climate proxy data cannot undergo this

229 processing, resulting in spatiotemporal characteristics that differ from the fossil pollen records.

- 230 We assess the effects of temporal uncertainty and uneven spatiotemporal coverage of the
- 231 vegetation turnover data on the global power spectra (Figure 2) by resampling sites and their
- 232 corresponding posterior age estimates to produce an ensemble of power spectra, estimates of β ,
- and estimates of the breakpoints in β (see Methods).
- 234

235 We find that the spectral continuum of variability in vegetation turnover carries clear similarities 236 to that of the climate system (Figure 2), yet the relationship to climate variability varies with 237 frequency. The power spectrum of vegetation turnover appears to follow the climate system 238 across the weather-climate breakpoint reported in previous studies (9, 10, 23, 46) and found here 239 (Figure 2, Table S1, 668⁻¹—647⁻¹ years⁻¹ for temperature; 691⁻¹—661⁻¹ years⁻¹ for precipitation; 240 802⁻¹—768⁻¹ years⁻¹ for vegetation turnover), supporting the interpretation that vegetation 241 dynamically tracks the climate system at intermediate frequencies (Figure 1, Figure 2) (13). 242 However, unlike temperature and precipitation in our analyses (Figure 2) or in previous studies 243 (9, 10, 23, 46), the vegetation turnover power spectrum has two additional breakpoints, 244 determined using segmented regressions (47), at 146^{-1} years⁻¹ (95% CI: 150⁻¹, 141⁻¹) and 17,505⁻¹ 245 years⁻¹ (18,162⁻¹, 16,831⁻¹) (uncertainties for all parameters estimated are reported in Table S1). 246 The vegetation turnover power spectra are therefore characterized by four scaling regimes: high frequencies (< 146⁻¹ years⁻¹); high-intermediate frequencies (146⁻¹ to 759⁻¹ years⁻¹); low-247 intermediate frequencies (759^{-1} to $17,505^{-1}$ years⁻¹); and low frequencies (> $17,505^{-1}$ years⁻¹). The 248 249 additional breakpoints in β in the vegetation turnover power spectrum found in the full ensemble 250 (Figure 1) are also found in the spectra of well-resolved individual time series (Figure S2), 251 indicating the patterns are not an artifact of the ensemble approach. Together, these features of 252 the vegetation turnover power spectra provide striking evidence that the relationship between 253 plant communities and climate is timescale-dependent and complex. Ecological communities and 254 climate may co-vary on some timescales but differ in their dynamics on others, which we detail 255 below.

256

257 Timescales of Ecological Dynamics

258 We find evidence of climate and vegetation coupling between the frequencies of 146⁻¹ to 17,505⁻ 259 ¹ years⁻¹ (Figure 2), where the continuum of vegetation turnover and climate variability have 260 261 similar β s. Specifically, β s are near zero at frequencies from 146⁻¹ to 759⁻¹ years⁻¹, and ~2 at frequencies from 759⁻¹ to 17,505⁻¹ years⁻¹. Moreover, the alignment of climate and vegetation 262 turnover breakpoints between 664⁻¹ and 759⁻¹ years⁻¹ provides strong evidence of vegetation and 263 264 climate coupling even across the transition from weather to climate regimes. Although the breakpoint for vegetation turnover is statistically distinguishable from that of temperature and 265 266 precipitation (Table S5), these small differences may reflect the limitations of the approach 267 rather than actual differences in timing. The non-random subset of communities recorded by 268 these vegetation assemblage records, our choice of climate model, or biased local/regional 269 spectral estimates from climate models (46, 48) all could affect the precise location of the 270 breakpoint and lead to an apparent offset. However, if this offset between the vegetation and 271 climate breakpoints is real rather than an artifact, two hypotheses may explain the brief decoupling of climate and vegetation between frequencies of 675⁻¹—664⁻¹ years⁻¹ and 759⁻¹ 272 273 years⁻¹: a lag in vegetation response to the transition from low, β weather to higher β , climate 274 regimes or the greater importance of non-climatic forcing (such as disturbance regimes) at these 275 frequencies.

- 276
- 277 This finding sharpens our understanding of the frequencies at which plant communities rapidly
- 278 and dynamically adjust composition and structure in response to climate forcing (49). Prior
- 279 theory and the observations of orbital signals in pollen records have led to the widespread
- 280 agreement of fast tracking of climate by vegetation composition at frequencies of 1,000⁻¹ to
- 281 100,000⁻¹ years⁻¹ (13, 14). Vegetation turnover from climate warming during the last deglaciation
- 282 illustrates this phenomenon particularly well (50). During this time interval, the climate system 283 was characterized by millennial- to orbital-scale climate variability in temperature and
- 284 precipitation (51, 52), which have been identified as the primary correlates of vegetation
- 285 turnover across these frequencies (49, 50, 53–55). However, whether vegetation rapidly tracks
- climate at sub-millennial frequencies $(10^{-2} \text{ to } 10^{-3} \text{ years}^{-1})$ is unclear (14), and there is evidence 286
- 287 for and against climate disequilibrium at frequencies of 50^{-1} to 200^{-1} years⁻¹ (15, 49). Our work
- 288 thus expands prior knowledge by suggesting climate tracking by vegetation for frequencies as short as 146⁻¹ years⁻¹. 289
- 290

291 Unlike frequencies between 146⁻¹ and 17,505⁻¹ years⁻¹, the highest and lowest frequency bands 292 exhibit climate decoupling. β is 4.58 (4.02, 5.12) for vegetation turnover at the highest 293 frequencies, while for temperature and precipitation, β is -0.28 (-0.33, -0.21) and -0.52 (-0.59, -294 0.47), respectively (Figure 2, Table S1). This finding supports prior observations of higher β s in 295 vegetation turnover at these high frequencies (56) but appears sensitive to the amount of weight 296 given to abundant and rare taxa in the dissimilarity metric and the fossil pollen record under 297 consideration (Figure S3). Some combination of taphonomy, sampling, and ecological processes 298 could explain higher β s in vegetation turnover at these high frequencies. Decadal-scale mixing of 299 lake sediments (57), scale gaps caused by discontinuous sampling of sediments (12), and 300 variable record length may enhance autocorrelation in vegetation variability from these archives 301 (58). In addition, the large ßs at the highest frequencies may be due to the long life spans of some 302 plants (e.g. trees, which are well-represented in fossil pollen assemblages), limiting the ability of 303 the full assemblage to track high frequency climate due to slow turnover times (56). Indeed, the 304 median tree lifespan from the International Tree Ring Data Bank (59, 60) is 246 years (n = 305 4,773) (Figure S4), which may impart a high β as vegetation turnover would increase 306 approaching the frequency of median tree longevity from increasing senescence. Furthermore, 307 anthropogenic land use change may contribute to climate decoupling at high frequencies (61, 308 62), possibly interacting with tree longevity. Finally, a greater β for vegetation turnover at the 309 highest frequencies is consistent with observations of slow vegetation responses to climate 310 variability and evidence of climate debt (16–18, 63). These slow responses are expected to create 311 mismatches between species' climate preferences and ambient climates and thus reduce 312 organismal fitness and ecosystem function.

313

In the low-frequency band (frequencies lower than 17,505⁻¹ years⁻¹, 95% CI: 18,162⁻¹, 16,831⁻¹), 314

- we observe β =-0.28 (-0.47, -0.10) for vegetation turnover power spectra (Figure 2). A low β for 315
- 316 vegetation turnover in the low frequency band contrasts with the climate power spectra, which 317 maintain the long-term climate system β s of ~2-3 due to the influence of astronomical forcing of
- 318 ice sheets (Figure 2) (64, 65). There are two possible explanations for low β s in vegetation
- 319 turnover at these low frequencies. First, a low vegetation turnover β may reflect the saturation of
- 320 community dissimilarity metrics used to compare vegetation assemblages across the time series,
- 321 (Figure S5) which fail to record turnover beyond a complete replacement of the vegetation

322 assemblage (66). If climate change is large enough to have produced multiple assemblage

- turnovers (species assemblage A replaced by B replaced by C), community dissimilarity metrics
- 324 will underestimate the true ecological impact of past climate change producing an apparent
- decrease in vegetation turnover with decreasing frequency. The second potential explanation for
- 326 the low β at frequencies below 17,505⁻¹ years⁻¹ is fast evolutionary adaptation by species to 327 environmental variation that results in vegetation communities appearing relatively resistant to
- environmental variation that results in vegetation communities appearing relatively resistant toclimate forcing. Although local adaptation cannot be excluded, the hypothesis of metric
- 329 saturation appears sufficient to explain the reduced vegetation turnover variability at low
- 330 frequencies (Figure S3).
- 331

332 Non-Linearity in the Climate-Vegetation Relationship

333

High spectral power at $4,650^{-1}$ years⁻¹ is unique to vegetation turnover and is absent in the power spectra of climate proxies and climate simulations (Figure 2, Figure S13) (9, 10). 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 (67) and provide a plausible mechanism for forcing vegetation turnover (37, 49, 68). However, global compilations of Holocene climate records lack high spectral power at any of these frequencies (69), as do our power spectra of temperature and precipitation (Figure 2).

- 340 This disconnect at the global scale (and in the subset of sites we investigated) between climate
- 341 and vegetation turnover leads us to hypothesize that relatively subtle or regional millennial-scale
- climate variations are amplified in the vegetation signal by non-linear ecological dynamics (42, 70).
- 343 344

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

our records span the last 20,000 years with fewer long records exceeding that duration (186 sites,
 Figure S6, Table S2). The relatively low number of sites sampled could bias our spatial and

- 348 environmental coverage at low frequencies, producing a spurious peak in spectral power. Despite
- 349 these potential artifacts, evidence for nonlinear responses in vegetation assemblages to small
- as on the environmental changes is well-documented (42). Our observations suggest slow vegetation
- responses to climate variability at high frequencies alongside high turnover at 4,650⁻¹ years⁻¹,
- demonstrating how gradual vegetation changes can lead to abrupt, nonlinear shifts in vegetation
- assemblages. 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 communities over the coming decades of warming (71, 72).
- 356

357 Latitudinal Gradient in Assemblage Dynamics

358

359 We find that the relationship between vegetation turnover variability and climate variability

- 360 differs across latitudes. Climatically, the high latitudes experience greater temperature variability
- than the tropics at all frequencies, while the tropics experience greater precipitation variability
- 362 (Figure 3) (9). Vegetation turnover appears to resemble temperature, in that tropical sites (<
- 23.5°) have less vegetation variability than extra-tropical sites (> 23.5°), although the power
- 364 spectra have overlapping confidence bounds across most of frequency space (Figure 3A). This
- overlap is caused mostly by larger differences among tropical vegetation turnover power spectra. At frequencies of 696^{-1} (722⁻¹, 680^{-1}) to $14,289^{-1}$ (15,017⁻¹, 13,797⁻¹) years⁻¹, extra-tropical sites
- 366 At frequencies of 696^{-1} (722⁻¹, 680^{-1}) to $14,289^{-1}$ (15,017⁻¹, 13,797⁻¹) years⁻¹, extra-tropical 367 have a β of 2.21 (2.17, 2.26) that is similar to those of temperature and precipitation, while

368 tropical sites appear to have a β of 1.20 (1.14, 1.29) (Figure 3). Thus, there is the possibility that

- 369 tropical vegetation assemblages are less sensitive to climate forcing across the frequencies
- 370 investigated, are sensitive to climate forcings other than temperature and precipitation, are
- 371 affected more by non-climatic factors, or are more stable and resistant to turnover. Along these
- 372 lines, recent observations show that while net primary production in low latitudes is constrained
- 373 by solar radiation and precipitation, high northern latitude productivity is limited by temperature 374
- (73), suggesting these latitudinal differences in β could result from spatially variable climate
- 375 controls on vegetation variability.
- 376

377 Conclusions

378

379 Our novel and adaptable theoretical framework based on spectral analyses provides a new

- 380 pathway forward to disentangle a fundamental question in ecology: how closely are ecological
- 381 dynamics coupled or decoupled with environmental drivers across timescales? The methods
- 382 shown here are flexible and adaptable to all ecological systems with observational data across a 383 range of timescales.
- 384
- 385 Through this framework, we show that the relationship between vegetation turnover and climate variability is non-linear and timescale-dependent over frequencies from 10⁻¹ to 100,000⁻¹ years⁻¹.
- 386 We show evidence for vegetation tracking climate change at frequencies of 146⁻¹- 17,505⁻¹ years⁻ 387
- 388 ¹, which is a narrower range of frequencies than previously theorized (13). This time period of
- 389 fast vegetation tracking spans across the theorized (33) and observed scaling break (9, 10) that
- 390 separates weather and climate variability, which in turn suggests that a foundational shift of
- 391 ecological variability from more red-noise to more white-noise at frequencies of ca. 700⁻¹ years ⁻¹
- 392 is directly governed by coupled atmosphere-ocean processes. Modes of heightened variability in
- 393 vegetation relative to climate at millennial frequencies underscore the risk of nonlinear and
- 394 abrupt vegetation responses to current climate change. Conversely, the decoupling of vegetation and climate variability at higher frequencies (higher than 146⁻¹ years⁻¹) is consistent with, and 395
- 396 reinforces, concerns that biotic processes will be slow to respond to contemporary climate
- 397 warming and changing climate variability (15). Consequently, the fast rate of anthropogenic
- 398 climate change likely will outstrip the response time of plant communities in the next century,
- 399 leading to delayed and widespread ecological transitions that challenge predicting vegetation
- 400 responses to current warming.
- 401

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403

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- 422 the manuscript.423

424 Data Availability Statement

425

426 Data and code needed to reproduce all analyses are available on Zenodo (74).427

- 428 Author Contributions
- 429
- 430 DF and PMH developed the research questions and study design. DF, SRM, EES, JWW, and
- 431 PMH co-developed the theoretical framework. DF performed all analyses with help from SRM
- and EES. DF led writing with support from SRM, EES, JWW, and PMH. The ideas for this
- 433 paper originated from discussions in the BioDeepTime working group. All authors reviewed and
- 434 contributed to the article.
- 435
- 436 Figures



- 438 **Figure 1.** A conceptual framework for interpreting the relationship between vegetation and
- 439 climate using power spectra through the power-law scaling relationship between spectral power
- and frequency (S(f) \propto f^{- β}). The blue line corresponds to β for climate variability and the green
- 441 line corresponds to β for vegetation compositional turnover. The breakpoint in climate spectral
- 442 power in all three panels is based on prior work that indicates a breakpoint in climate variability
- 443 at approximately 100^{-1} to $1,000^{-1}$ years⁻¹ (9, 10). Key phenomena include the slope (β , i.e.
- 444 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 composition exhibits linear responses to climate across all frequencies and so the
- 446 (A) vegetation composition exhibits linear responses to chinate across an frequencies and so in 447 slope of vegetation spectral power parallels that of climate (13). (C) Vegetation tracks
- 447 slope of vegetation spectral power parallels that of climate (15). (C) vegetation tracks 448 climate across high and intermediate frequencies but is decoupled at low frequencies from
- 449 processes like evolutionary adaptation (lower β for vegetation) or non-linear amplification
- 450 through processes such as threshold responses (higher β for vegetation). Other scenarios and
- 451 ecological processes are possible beyond those shown here.





453 Figure 2. The spectral continuum of (A) vegetation turnover (green), (B) temperature (blue, red, 454 pink), and (C) precipitation (light blue) variability based on the median from an ensemble of 455 spectral power estimates. Power spectra line opacity indicates the number of ensemble members

that resolve each frequency with the corresponding legend for all plots in (C). β in the high 457 frequency band was fit to the maximum frequency that yielded an unbiased estimate

- 458 (Supplementary Information). Solid gray lines correspond to β from ordinary least squares

459 regressions of log-spectral power and log-frequency. Vertical dashed lines correspond to

breakpoints identified in the spectral continuum. Climate estimates from TraCE-21ka have been

downsampled in space and time and low-pass filtered to match the temporal characteristics of the

- 462 fossil pollen abundances. Uncertainties for β and breakpoints and permutation tests comparing
- these parameters are reported in the Supplementary Information (Table S1, Table S4 S5).
- 464 465
- 10¹¹β = -0.15 10¹⁰ 10⁹ Vegetation Turnover Power Spectral Density β = 2.21 10⁸ β = -0.46 $\beta = 4.51$ 10⁷ 10⁶ 10⁵ β = 1.2 $\beta = -0.5$ 10⁴ 10³ g 10² 100,000 10,000 1,000 100^{-1} Frequency (cycles yr⁻¹) 10⁹ B β = 3.15 10⁸ Near Surface Temperature (2 m) Power Spectral Density 10⁷ 10⁶ β = -0.29 10⁵ 10⁴ β = 3.08 10³ 10² 10¹ $\beta = 0.99$ c 665 10⁰ 100.000 10.000 100 1.000 Frequency (cycles yr⁻¹) 10⁷ C 10⁶ $\beta = 2.46$ Annual Precipitation Rate Power Spectral Density 10⁵ $\beta = 0.49$ 10⁴ 10³ 10² β = 2.52 10¹ $\beta = -0.99$ 10⁰ 10 10 100.000 10.000 1.000 100 Frequency (cycles yr⁻¹) Tropics (< 23.5°) Spatial Average - Extra-tropics (> 23.5°) -Ensemble Count 250 500 750 1000

466 467 **Figure 3.** The continuum of (A) vegetation turnover, (B) near-surface temperature, and (C) 468 annual precipitation rate variability, averaged for the extra-tropics (blue, $> 23.5^{\circ}$) and tropics 469 (red, $< 23.5^{\circ}$) based on the median from an ensemble of spectral power estimates. Power spectra 470 line opacity indicates the number of ensemble members that resolve each frequency. β in the

- 471 high frequency band was fit to the maximum frequency that yielded an unbiased estimate
- 472 (Supplementary Information). Vertical dashed lines correspond to breakpoints identified in the
- 473 spectral continuum and are colored by the corresponding spatial average. All climate estimates
- are from TraCE-21ka and have been downsampled as in Figure 1. Uncertainties for β and
- breakpoints and permutation tests comparing these parameters are reported in the Supplementary
- 476 Information (Table S1, Table S6 S9).
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 863 864 865 866 867 868 869 870 871 872 873 874 875 876 877 878 	We es as lac albeit <i>Picea</i> morph Addit sourc assem produ the w transf analy poller Chevy comp	stimate vegetation turnover from fossil pollen abundances stored in geologic archives, such ustrine sediments (36). Fossil pollen tracks plant assemblage composition through time, with some biases and limitations. Taxonomic resolution is often to the genus level (e.g.), though species-level identification is possible (e.g. <i>Alnus rugosa</i>) for some fossil pollen hotypes, and only family-level identification is possible for others (e.g. Poaceae). ionally, some taxa overproduce pollen and others underproduce pollen relative to the e vegetation assemblage. For instance, pine (<i>Pinus</i>) is often overrepresented in pollen ablages while fir (<i>Abies</i>) tends to be underrepresented (78). Our analyses account for these ction biases by including metrics that downweigh abundant fossil pollen taxa and increase eight of rarer taxa (e.g. squared chord dissimilarity metric incorporates a square root form and we square root transform the fossil pollen assemblages before correspondence sis). When these biases are considered and accounted for in analyses, as we do here, fossil n is an effective representation of the source plant assemblage. We refer the reader to alier et al. (36) for a comprehensive review of fossil pollen as a proxy for plant assemblage osition.
879	We ga	athered fossil pollen abundance data from the Neotoma Paleoecology Database (11) in May

2022, which was included as a part of the BioDeepTime database (12). 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. (61),
- 883 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.
- 885 (61), which produced an additional 181 fossil pollen records, hereafter referred to as "sites".
- 886 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
 points in each assemblage time series).
- 890

We created age-depth models using Bchron (79, 80) to improve upon existing Neotoma age
estimates, which sometimes rely on age-depth models that can underestimate error. Bchron uses
information from sparse but specific ages for depths in sedimentary archives for the sites to
develop a continuous model of sedimentation from which ages at every depth can be estimated
(80). 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-

- depth relationship in a sedimentary archive to be propagated to all analyses. Age controls
- included radiocarbon years, varve years, biostratigraphic markers, and core-top age.
- 899
- Bchron models were run with default parameters (80), except for the radiocarbon calibration
- 901 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
- 903 Northern Hemisphere were calibrated using IntCal20 (81) and sites in the Southern Hemisphere
- 904 were calibrated using SHCal20 (82). Non-radiocarbon ages were incorporated into Bchron as
- calendar years before 1950, with Gaussian errors. Chronological controls with no given age
- 906 uncertainties, often the case with biostratigraphic ages, were assigned a Gaussian, one standard 907 deviation, age error that was 10% of the age estimate (e.g. for an age estimate of 1,000 years
- 908 with no assigned error, the ages followed a $N(1000, 100^2)$ distribution in Bchron). From our
- 909 compilation, 19 sites had only one chronological control and were excluded from further
- 910 analyses. Additionally, Bchron failed to initialize for five sites that were also excluded.
- 911
- 912 After creating new age-depth models, we harmonized the taxonomy across these sites using taxa
- 913 lists from Flantua et al. (83). We were not able to match taxa in Flantua et al. (83) for 21 sites, so
- 914 these sites were removed from further analyses. Of these removed sites, 16 were in Oceania and
- 915 Australia because the taxonomy harmonization lists from Flantua et al. (83) do not include these
- 916 regions (Table S2). Lastly, one site (Foy Lake, Table S2) contained negative abundances for
- 917 some fossil pollen counts and was removed from further analyses. Five sites had issues with both
- 918 chronological controls and taxonomy harmonization, therefore the final compilation of fossil
- 919 pollen abundances included 1,321 datasets with good spatiotemporal coverage (Table S2).
- 920 Sites span the Southern Hemisphere midlatitudes to the Northern Hemisphere Arctic, with the
- 921 densest sampling between 40° N and 50° N, and the least dense sampling between 20° S and 50°
- 922 S (Figure S6). The Northern Hemisphere is better represented across sites than the Southern
- 923 Hemisphere. Temporally, these records span the last 600,000 years, with one site spanning an
- 924 interval from 1.4 to 1.5 Ma, and they are heavily concentrated in the last 20,000 years (Figure
- 925 S6). Based on the median age-depth model for each site, 389 sites have a temporal span less than
- 10,000 years, 746 sites have a temporal span between 10,000 to 20,000 years, 72 have a temporal
- span between 20,000 to 30,000 years, 43 have a temporal span between 30,000 to 40,000 years,

17 have a temporal span between 40,000 to 50,000 years, 19 have a temporal span between

50,000 to 60,000 years, seven have a temporal span between 60,000 to 70,000 years, six have a

temporal span between 70,000 to 80,000 years, three have a temporal span between 80,000 to

931 90,000 years, one has a temporal span between 90,000 to 100,000 years, and 18 have a temporal

- span greater than 100,000 years. Of this final compilation, seven sites had different fossil pollen
- 933 assemblages at identical depths (Dataset IDs: 22,636, 22,759, 3,973, 4,196, 4,197, 4,7595, 525 in
- Table S2). For each duplicate depth, we retained the first entry.
- 935
- 936 Tree Longevity Estimates 937

We estimated tree longevity with observations from all taxa available in the International Tree Ring Data Bank (ITRDB) (59, 60). 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

941 chronology, to minimize underestimation and overestimation of longevity (40). We used the

- 942 longest tree ring record in a collection to estimate longevity for that collection and report the
- median across all collections in the main text (84). The spatial distribution of the ITRDB is
- comparable to the fossil pollen sites, which have the greatest density of tree ring width records in
- North America and Europe and comparatively fewer records in the Southern Hemisphere (Figure
- 946 S6) (60). The ITRDB lacks records in the tropics, but our median estimate of tree longevity (246
- 947 years) agrees with a compilation of tree ring width records from the tropics (40).
- 948
- 949 Spectral Analysis
- 950

951 We used Thomson's multitaper method (MTM) (22) to estimate the power spectra of fossil 952 pollen turnover using the astrochron R-package (R version 4.4.1, astrochron version 1.4) (85, 953 86). MTM is a Fourier-based method that reduces spectral bias (e.g., spectral leakage) through the application of multiple orthogonal data "tapers" that weigh a time series according to Slepian 954 955 functions (22), of which we used five 3π prolate tapers. The application of Slepian data tapers 956 imparts several positive attributes to MTM when compared to the standard discrete Fourier 957 transform: a reduction in spectral leakage and optimal bias protection for a specified bandwidth 958 resolution, and leveraging of the multiple tapers to provide a statistical sample for estimation of 959 spectral power and its uncertainty (22). We scale spectral estimates from MTM by energy per 960 unit frequency to return power spectral density, hereafter referred to as the power spectrum (9). 961 An underlying assumption in these analyses, and all spectral analyses, is that a single power

- 962 spectrum is a good representation of the entire time series.
- 963

964 We further processed the fossil pollen abundances to meet the MTM requirements of a 965 univariate, regularly sampled time series. We addressed the requirement of a single time series 966 by using principal coordinate analysis (PCO) (87) on fossil pollen dissimilarity matrices to 967 reduce the dimensionality of the fossil pollen abundances. Pollen dissimilarity matrices were 968 calculated for each individual time series using the squared chord distance metric (26), which 969 consistently outperforms other distance metrics in distinguishing between two distinct fossil 970 pollen assemblages (26, 88). We retained the primary (PCO1) and secondary (PCO2) dimensions 971 of variability for further analysis via MTM and presented the results from the primary dimension

- 972 of variability in the main manuscript.
- 973

974 We sought to identify latitudinal differences in fossil pollen dissimilarity, for comparison with 975 climate variables which are known to have a variance structure that varies by latitude (9). To that 976 end, we multiplied PCO1 by the square root of its corresponding eigenvalue. This procedure 977 scales PCO1 for each fossil pollen assemblage by the variance explained by that dimension. That 978 is, a fossil pollen assemblage where PCO1 explains a substantial amount of compositional 979 variance will have a large eigenvalue corresponding to PCO1 and PCO1 will be up-weighted, 980 producing high spectral energy across all frequencies. In contrast, a fossil pollen assemblage 981 where PCO1 explains little variance will have a small eigenvalue corresponding to PCO1 and 982 PCO1 will be down-weighted. Total spectral energy (i.e. area under a power spectral density spectrum) is equal to the variance of the time series (Parseval's theorem). Therefore, any spatial 983 984 patterns in the variance explained by PCO1 are imprinted onto the time series and will produce 985 high spectral power when PCO1 is up-weighted and low spectral power when PCO1 is down-986 weighted. This effect carries forward to spatially averaged power spectra (i.e. tropical and extra-987 tropical averaged power spectra) thereby enabling an assessment of whether there are spatial 988 patterns in fossil pollen turnover.

989

990 Temporal sampling that is evenly spaced (i.e. identical temporal distance between all consecutive 991 samples) is required by MTM, but this condition is rarely met by proxy data extracted from

992 geologic archives and is not met by any of our fossil pollen sites. Therefore, we interpolated

993 PCO1 of all fossil pollen assemblages using a linear interpolation approach adapted from (89).
994 This approach aims to determine an optimal interpolation resolution and minimize energy loss at

high frequencies by comparing the PCO1 power spectra to the power spectra of a power law process where $\beta = 1$. The optimal interpolation resolution is identified when the ratio between

997 the theoretical and empirical power spectra crosses 0.7 (89). This approach objectively 998 determines an optimal interpolation 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 present in the Zenodo data repository (74)).

1001

1002 We estimated the power spectra of global ecological turnover by performing MTM on PCO1 for 1003 individual sites after subtracting the mean from each site-level PCO1 time series, binning 1004 spectral power by log10(frequency), and then averaging spectral power across sites within each 1005 such bin. This choice was made to avoid convoluting temporal and spatial variance in the 1006 eigenvector decomposition of the community dissimilarity matrix, as would have occurred if we 1007 considered all sites and samples together. By averaging power spectra across sites, we leverage both short, highly-sampled records to resolve high frequencies and long, sparsely-sampled 1008 1009 records to resolve low frequencies - characteristics that would be difficult to achieve using any 1010 single site's power spectrum alone. For averaging site-level power spectra, we used a bin size of 1011 0.01 in log10(frequency) coordinates, which equates to $22,000^{-1}$ years⁻¹ near the smallest frequencies (e.g. $10^{-6} - 10^{-5.99}$ years⁻¹) and <1 year near the largest frequencies (e.g. $10^{0.99} - 10^{11}$ 1012 vears⁻¹). 1013

1014

1015 After estimating the spectra of global vegetation turnover we evaluated the continuum of global

1016 vegetation turnover for specific frequency bands using an ordinary least squares linear regression

1017 in log-log space for frequencies resolved by at least two sites (9, 10). Prior to the regression, we

1018 smoothed the spatially averaged power spectra using a Gaussian kernel in log10 frequency

1019 coordinates with a width of 0.03 (23, 90). Using the smoothed global estimate of spectral power

1020 for global vegetation turnover, frequency is a predictor of spectral power and the resulting slope 1021 is the β exponent in the S(f) \propto f^{- β} power law relationship (9, 10). To determine the frequency bands of distinct temporal scaling regimes in spectral power for global vegetation turnover we 1022 1023 identified breakpoint locations in the log-log relationship between spectral power and frequency 1024 through piecewise linear regressions in the segmented R package (version 2.1.2) (47). We 1025 constrained segmented regressions to identify three breakpoints (low, intermediate, and high frequencies) for fossil pollen turnover and one breakpoint for simulated temperature and 1026 precipitation. The number of breakpoints was based on prior expectations for climate (9, 10) and 1027 1028 visual inspection for fossil pollen. Although the number of breakpoints is constrained in the 1029 segmented regressions, the location of these breakpoints depends on the power spectrum. For 1030 vegetation turnover, β was then fit across the four frequency ranges between the three identified breakpoints: (1) the lowest frequency resolved and the low frequency breakpoint, (2) the low 1031 1032 frequency breakpoint and the intermediate frequency breakpoint, (3) the intermediate frequency 1033 breakpoint and high frequency breakpoint, and (4) the high frequency breakpoint to the highest 1034 frequency that produces unbiased estimates of β (see *Estimating the Highest Resolvable* 1035 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 1036 years⁻¹, β was fit between (1) the lowest frequency resolved and 4,000⁻¹ years⁻¹, (2) from 4,000⁻¹ 1037 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 1038 1039 highest frequency that produces unbiased estimates of β . For temperature and precipitation, we 1040 fit β between the lowest frequency resolved and the one breakpoint identified and again from the 1041 one breakpoint identified to the highest frequency that produces unbiased estimates of β .

1042

1043 Recently, methods for estimation of temporal scaling in time series were compared for their 1044 ability to reproduce β in synthetic paleoclimate time series with known β and performed 1045 reasonably well (58). In these analyses, MTM emerged biased towards larger β values when

1046 evaluating the full frequency range, compared to other spectral transformation methods (58).

- 1047 However, MTM showed little bias at long timescales (greater than nine times the mean
- 1048 resolution), moderate bias at intermediate timescales (greater than 4 times the mean resolution),
- and generally outperformed competing methods such as spectral transformation from the Lomb-
- 1050 Scargle periodogram when β is high and the input data is irregularly sampled (58). Only Haar 1051 structure functions more accurately estimated β from the synthetic dataset, but the approach is
- 1052 limited to $-1 < \beta < 3$ (58) and does not allow for the identification/influence of
- 1053 quasiperiodic/periodic signals that may bias estimates of the spectral continuum (91).
- 1054 Additionally, MTM has seen broad use in paleoclimatology (9, 23, 92) and atmospheric sciences
- 1055 (93, 94) for estimating β , providing baseline estimates for comparison with our study.
- 1056

1057 TraCE-21ka and Proxy Paleoclimate Estimates

1058

1059 TraCE-21ka is a series of fully coupled climate model experiments that simulate the effect of

1060 transient climate forcings of the most recent deglaciation with the Community Climate System

1061 Model, version 3 (27, 28). TraCE-21ka includes transient changes in ice sheet topography,

1062 meltwater forcing, orbital configuration, and greenhouse gas concentration that matched then-

1063 current proxy reconstructions (27, 28). These climate simulations have been pillars of

1064 paleoclimatological research and have undergone substantial comparisons against proxy

1065 reconstructions and generally perform well (27, 28, 52, 95–97). Unlike proxy-based climate

reconstructions, TraCE-21ka offers full fields that are annually resolved and well-suited forcomparison against spectral estimates from fossil pollen.

1068

1069 TraCE-21ka has known deficiencies such as seasonal precipitation biases in North America (95) 1070 and imperfect greenhouse gas and meltwater forcings (98–100). What's more, all climate models

- 1071 overestimate high frequency climate variability and underestimate low frequency climate
- 1072 variability at local and regional scales (48), 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
- 1075 the last deglaciation, which are widely used to assess ecological relationships to paleoclimate
- 1076 (45, 101, 102). Recently, the TraCE-21ka experiments were the first climate simulations to show 1077 a scaling break in the continuum of mean global temperature that is expected to exist given
- 1078 physical principles (10).
- 1079

1080 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 1081 1082 temperature, simulated precipitation, and vegetation turnover and degraded the TraCE-21ka 1083 climate simulation to match the spatial and temporal characteristics of the fossil pollen sites. 1084 Specifically, we subsampled TraCE-21ka spatially to get the nearest grid cell for every fossil 1085 pollen site and applied a low-pass filter with a characteristic timescale of twice the mean 1086 resolution of the corresponding fossil pollen record to guard against aliasing of high-frequency 1087 variance (23, 58). We then downsampled these low-pass filtered climate time series temporally, 1088 retaining only the years with fossil pollen data. This process produced a dataset of simulated temperature and precipitation that matched fossil pollen abundances in space and time with 1089 similar temporal characteristics (i.e. low-pass smoothing induced by sedimentation). Finally, we 1090 1091 interpolated the simulated temperature and precipitation to a regular temporal grid using the same methodology applied to the fossil pollen data (89). All spectral analyses for TraCE-21ka 1092 1093 were performed on these spatiotemporally subsampled and interpolated temperature and 1094 precipitation time series.

1094

1096 For subsampling of the TraCE-21ka simulations, we excluded those fossil pollen samples that

- 1097 were outside of the temporal coverage of TraCE-21ka. Fossil pollen sites that did not contain any
- 1098 fossil pollen assemblage observations within the last 21,000 years were excluded and not
- 1099 represented in the spectral estimates of the TraCE-21ka simulations.
- 1100

1101 To capture climate variability outside of the last 21,000 years we supplement our analysis of 1102 TraCE-21ka with two proxy records that approximate global climate variability for the last two

- 1102 million years. We use temperature reconstructions from the EPICA Dome C ice core in
- 1104 Antarctica (28). Temperature reconstructions from Antarctic ice cores primarily track global
- 1105 greenhouse gas concentrations and therefore global temperature changes (103). We also use
- 1106 global average surface temperature (GAST) reconstructions from Snyder (*30*). This estimate of
- 1107 GAST is based on proxy-based sea surface temperature reconstructions (SST) that are scaled to
- 1108 surface temperatures with a value determined by examining SST-surface air temperature
- 1109 differences from the Paleoclimate Modelling Intercomparison Project (PMIP) model simulations.
- 1110 Comparisons between GAST reconstructions, EPICA Dome C, and greenhouse gasses
- 1111 demonstrate that both sets of proxy records used here well approximate global climate evolution

- (30). Variations in ocean circulation emerge in EPICA Dome C oxygen isotopes (104) but as a
- second-order feature imposed on greenhouse gas-controlled temperature changes. The spectral
- 1114 continuum of temperature variability at EPICA Dome C and global surface air reconstructions 1115 were fit between 100^{-1} -15,000⁻¹ years⁻¹ (9) and 2,000⁻¹-100,000⁻¹ years⁻¹ (10), respectively.
- 1115
- 1117 Benchmarking TraCE-21ka Simulated Climate Variability Against Temperature12k
- 1118

1119 We compared TraCE-21ka to the Temperature12k database (105), a global compilation of proxy

- temperature reconstructions that span the last 12,000 years. Though, several proxy
 reconstructions within Temperature12k extend well beyond the last 12,000 years. We first
- filtered the Temperature 12k database to remove all pollen-based temperature estimates and then
- estimated the continuum of global temperature variability in the same framework defined in the
- 1124 TraCE-21ka and Proxy Paleoclimate Estimates and Spectral Analyses section. That is, we
- 1125 estimated power spectra for Temperature12k at a site level, and then averaged across sites to
- 1126 produce a globally averaged power spectrum. For TraCE-21ka, we performed the same
- 1127 procedure after spatiotemporally subsampling and low-pass filtering the temperature simulations.
- 1128 Six of the non-pollen temperature estimates in Temperature12k failed spectral analyses for
- 1129 various reasons (Table S3). No similar comparisons are made for precipitation due to the lack of
- an analogous database to Temperature12k. However, low-frequency precipitation variability in
- 1131 TraCE-21ka likely results from thermodynamic effects of temperature changes (Clausius-
- 1132 Clapeyron relationship) given the nearly identical power spectra presented in Figure 2.
- 1133
- 1134 We find that TraCE-21ka can accurately simulate the three key features of the temperature
- 1135 continuum: 1) a high β at low frequencies (climate regime), 2) a low β at high frequencies
- 1136 (weather regime), and 3) a breakpoint in the scaling relationship between spectral power and 1137 frequency (Figure S13). In the low frequency, climate, regime β for Temperature12k is 1.83 and
- 1138 TraCE-21ka simulates a β of 1.87. In the high frequency, weather, regime Temperature12k has a
- 1139 β of 0.54 while TraCE-21ka has a β of -0.25. The location of the break in the scaling relationship
- for Temperature 12k is 376^{-1} years⁻¹ and 498^{-1} years⁻¹ for TraCE-21ka. These results demonstrate
- 1141 that TraCE-21ka performs well, despite the general struggle of climate models to accurately
- 1142 simulate temporal persistence in the high frequency, weather, regime. Much like other
- 1143 comparisons between empirical climate observations against climate models, TraCE-21ka poorly
- simulates temporal persistence in temperature variability (i.e. lower β in TraCE-21ka) in the high
- 1145 frequency regime (48). Despite this deficiency, TraCE-21ka captures the key features of the
- temperature continuum and is well-suited as a climate benchmark against which we can compare
- 1147 our globally averaged power spectra of vegetation turnover.
- 1148
- 1149 Estimating the Highest Frequency for Unbiased Estimates of β
- 1150
- 1151 In light of the limitations and biases of MTM for estimating β (58), we sought to estimate the
- 1152 highest frequency that produces unbiased estimates of β for each of our spatially averaged power
- spectra. We used the undegraded, annually resolved TraCE-21ka near-surface temperature time
- series, from the closest grid cell corresponding to each fossil pollen site, as a target signal with a
- 1155 known power spectrum. We then temporally degraded the TraCE-21ka near-surface temperature
- as outlined in the *TraCE-21ka and Proxy Paleoclimate Estimates* section and compared these

1157 degraded power spectra to the target, annually resolved signal to estimate the highest frequency

1158 where estimates of β are unbiased by sedimentary processes.

1159

1160 In our analyses and prior work (10), annually resolved near-surface temperature estimates from TraCE-21ka produce a power spectrum where spectral power is evenly distributed in a high 1161 1162 frequency band (> 831⁻¹ year⁻¹ from Figure 2). At frequencies lower than this breakpoint, temperature variability increases with frequency (10) (Figure S16). This pattern holds when 1163 1164 averaged across all fossil pollen sites (global estimate in Figure S16), the extra-tropics (extratropical estimate in Figure S16), and the tropics (tropical estimate in Figure S16). Built upon the 1165 1166 expectation that sedimentary processes such as sediment mixing (57), and sampling resolution, can decrease spectral power at the highest frequencies and increase β (58), we use the even 1167 distribution of spectral power in the high frequency band of the undegraded TraCE-21ka 1168 temperature power spectrum as the metric to identify when estimates of β become biased by 1169 1170 sedimentary processes. We find that high frequency spectral power decreases in the degraded TraCE-21ka power spectra and β increases in all spatial averages (Figure S16). However, the 1171 temporal characteristics of fossil pollen sites in each spatial average vary, leading to a spurious 1172 1173 decrease in spectral power and an increase in β at the highest frequencies that varies across the 1174 spatial averages. The high latitudes are well represented in our fossil pollen compilation with several short, fossil pollen records with very high resolution (Figure S6). Therefore, in the 1175 1176 degraded global and extra-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 (Figure S16). Above 1177 this frequency, there is a spurious decrease in spectral power and an increase in β (Figure S16). 1178 1179 In contrast, tropical fossil 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 1180 increase in β begins to 160⁻¹ years⁻¹ (Figure S16). Therefore, we fit β to frequencies lower than 1181 58⁻¹, 57⁻¹, and 160⁻¹ years⁻¹, in all analyses for global, extra-tropical, and tropical power spectra, 1182 respectively. 1183

1184

1185 Statistical Comparisons between Estimated Parameters from Spectral Analyses

We compared all estimated parameters (β, break location) from our ensembles of averaged

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 two groups is statistically significant, without making assumptions about the underlying 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 process works as follows:

- 1194
- 1195 1. We calculated the observed difference in medians between the two groups.
- 11962. We then randomly reassigned the data points to the two groups and recalculated the difference in medians.
- 1198
 3. This process is repeated 10,000 times to create a distribution of possible differences 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.

- 1203
- This approach allows us to assess whether the observed differences in our spectral parameters are
 likely to have occurred by chance. We report the results of all these comparisons in Table S4 to
 Table S9.
- 1200

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

- 1214
- 1216 Methodological Constraints on Milankovitch Signal Detection

1217 1218 Milankovitch cycles are a primary control of global climate (106, 107) and have been identified 1219 in fossil pollen records that span the last 2,000,000 years (108, 109). Our analyses demonstrate increased spectral power associated with precession cycles at 21,000⁻¹ years⁻¹ in all spatially 1220 averaged power spectra but high spectral power in the obliquity band (41,000⁻¹ years⁻¹) is 1221 missing and high spectral power in the eccentricity band (100,000⁻¹ years⁻¹) is only present in the 1222 1223 vegetation turnover power spectrum for tropical sites (Figure 3). We find that these missing 1224 periodicities result from 1) our dimensionality reduction procedure (i.e. PCO), 2) the spatial scale 1225 of our compilation, 3) few sites that span enough time to resolve variability in the Milankovitch 1226 bands, and 4) variable temporal resolution of the data at each of these few sites.

1227

1228 Individual taxa or groups of taxa often demonstrate periodicity (as seen with arboreal pollen in 1229 (108) and (109)), but when all taxa are included in the dissimilarity matrix for PCO, as we do 1230 here, the periodicity becomes less pronounced. The Ioannina dataset demonstrates this well 1231 (Dataset ID: 4112) (110). Arboreal pollen at Ioannina has a strong cyclical pattern (110), but this 1232 is weakened when all taxa are included to create the dissimilarity matrix for PCO (Figure S15). 1233 The power spectrum at Ioannina does have somewhat higher spectral power in the Milankovitch 1234 bands but is lower than expected from the arboreal pollen abundance (Figure S15) (110). 1235 Variable phase response across taxa can also diminish the expression of periodic signals in the 1236 leading component (e.g., from PCO)

1230

1238 Furthermore, when averaging across a global compilation of sites with variable temporal data 1239 resolution, 41,000 and 100,000 year periodicities decrease in amplitude, even though individual 1240 sites demonstrate periodicity in these bands (e.g. ODP Site 658 (41194) and Páramo de Agua 1241 Blanca (21978) in Figure S15A). As site-level power spectra are averaged to form an estimate of 1242 the global power spectrum, high spectral power in the Milankovitch bands decreases even though it is present at individual sites (Figure S15B). We hypothesize that high spectral power at 21,000⁻ 1243 1244 ¹ years⁻¹ remains because we have more sites with a temporal span and sufficient data resolution 1245 that can resolve the 21,000 year periodicity, as compared to the 41,000 and 100,000 year

- 1246 periodicities (Table S2). The limited number of observations from high latitudes (> 65 °N),
- 1247 where obliquity effects are expected to be the dominant mode of variability (111), may also
- 1248 explain why we detect precession but not 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 1249 1250 (112), which may also partly explain a clear precession signal and the absence of obliquity and eccentricity signals. 1251

1252

1253 Uncertainty Estimation

1254

1255 We quantified uncertainty in our estimates of spectral power and the spectral continuum through 1256 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 1257 1258 posterior age estimate for MTM. We then downsampled TraCE-21ka accordingly, as described 1259 in the TraCE-21ka and Proxy Paleoclimate Estimates section, and then performed MTM as 1260 described in the Spectral Analysis section. We repeated this procedure 1,000 times, which produced an ensemble of 1,000 estimates of global spectral power, β , and breakpoint locations, 1261 for climate and fossil pollen turnover, from which we reported the median and 95% confidence 1262 1263 interval (Figure S8, Figure S9, Table S1). All sampling was performed using a uniform distribution without replacement. This uncertainty estimation procedure assesses the influence of 1264 1265 age model uncertainty and site selection on the global and latitudinally averaged power spectra.

- 1266
- 1267 Sensitivity Tests

as well.

1268

1269 We assessed the sensitivity of our results to our choice of fossil pollen dimensionality reduction 1270 and power spectra estimation methods (Figure S3, Figure S10, Figure S11, Figure S12). For 1271 dimensionality reduction, we tested alternative methods to reduce fossil pollen dimensionality and also tested various community dissimilarity metrics. In these sensitivity tests, we calculated 1272 community dissimilarity using the Bray Curtis and Jaccard dissimilarity metrics. We also 1273 1274 performed correspondence analysis after square root transforming the fossil pollen assemblages, which, unlike PCO, does not assume linearity (113). Lastly, to test the sensitivity of our analyses 1275 to fossil pollen analytical accuracy, we degraded the percent abundance fossil pollen 1276 observations to presence/absence, though the Jaccard distance metric is presence/absence based 1277

1278

1279

1280 Changing the dissimilarity metric and the dimension of variability analyzed had limited impacts 1281 on our conclusions, however, correspondence analyses produced results with the least total 1282 spectral power (Figure S3, Figure S10). We hypothesize that this occurs because PCO assumes linearity in the species-matrix decomposition while correspondence analysis does not assume 1283 linearity (113). Correspondence analysis also produced slightly different results for latitudinally 1284 1285 averaged power spectra because of the scaling procedure we implemented (Figure S11, Figure 1286 S12). The eigenvalues in correspondence analyses do not indicate variance explained as they do 1287 in PCO. Rather, eigenvalues correspond to correlation coefficients between the coordinates for species in the fossil pollen assemblage (i.e. species score) and coordinates for time intervals (i.e. 1288 1289 site score) in the ordination coordinate system. However, our scaling procedure, which assumes 1290 that the eigenvalues correspond to variance explained, is incompatible with correspondence

1291 analysis. Nevertheless, we include sensitivity tests for correspondence analysis to assess the

- 1292 assumption of linearity in PCO and the influence of metric saturation on our results. We chose to
- 1293 present the first dimension from PCO using the squared chord distance metric because of strong

support for the efficacy of the squared chord distance metric to discriminate fossil pollenassemblages that source from distinct ecosystems (26, 88).

1296

1297 We also tested different methods for estimating the global spectral continuum of vegetation turnover by taking the mean of MTM adaptive spectral power (as shown in the main text), taking 1298 1299 the median of MTM adaptive spectral power, averaging MTM spectral eigencoefficients, and 1300 averaging β for each site. The methodology for median estimates of MTM adaptive spectral 1301 power was identical to the main manuscript except we took the median, not the mean as in the 1302 main text. The procedure for returning a global average of spectral power by averaging 1303 eigencoefficients was nearly identical to averaging by spectral power. We first performed MTM 1304 on a single site and retained the five spectral eigencoefficients for each site that correspond to the 1305 five data tapers. We then averaged the five eigencoefficients across all sites by binning by 1306 frequency, as described in the Spectral Analysis section. We then calculated spectral power at each frequency using the averaged eigencoefficients and Equation 1, where $\hat{S}_k(f)$ is spectral 1307 power and $y_k(f)$ is the eigencoefficient for the kth data taper. Since we use five data tapers, this 1308 produces five estimates of $\hat{S}_k(f)$ which we average to estimate total spectral power (22). 1309

- 1310
- 1311

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

1312 1313 These estimates of total spectral power were used to estimate β . The eigencoefficient averaging 1314 provides an important complementary view to the MTM adaptive spectral power approaches 1315 noted above, as it explicitly considers signal phase at each site. That is, strong signals that are 1316 antiphased at different locations will cancel, instead of being amplified as the case for the MTM 1317 adaptive spectral power approaches. Eigencoefficient averaging is expected to reduce the overall 1318 power at a given frequency in the reconstructed spectrum and to diminish periodic signals that 1319 are not in phase globally since it allows for destructive interference across sites.

1320

1321 Lastly, we estimated the global continuum of vegetation turnover by directly averaging β at each 1322 site. Here, we performed MTM at each site as described in the *Spectral Analysis* section and then 1323 estimated β using an ordinary least squares regression in log-log space, retaining β at each site, 1324 not spectral power. Estimates of β were then averaged across sites resulting in a global estimate 1325 of the spectral continuum of fossil pollen turnover. These sensitivity tests were performed within 1326 the same Monte Carlo framework that we use to quantify uncertainty for the fossil pollen 1327 assemblages and TraCE-21ka climate parameters.

1328

1329 Our conclusions are robust to the method used to aggregate individual site-level power spectra of 1330 vegetation turnover into a global estimate. All three approaches reveal four characteristic 1331 timescales in global vegetation turnover each with distinct β s: high β at the highest frequencies,

1331 timescales in global vegetation turnover each with distinct ps: high p at the highest frequencies, 1332 low β in the high-intermediate frequency band, high β in the low-intermediate frequency band,

1332 now β in the low frequency band (Figure S3). Across much of the frequency space,

- 1334 uncertainties for these approaches overlap, particularly at high and low frequencies where
- 1335 spectral power estimates diverge.
- 1336

1337 This divergence is most prominent in two areas: the high and low frequencies. At low

1338 frequencies, global estimates that use the mean of site-level power spectra have greater spectral

1339 power than estimates that use the median of site-level power spectra and the mean of site-level

eigencoefficient estimates (Figure S3). At high frequencies, global estimates that use the median
of site-level power spectra and the mean of site-level eigencoefficient estimates have a bandlimited increase in the globally estimated spectral power, not present when in the global estimate

- 1343 that uses the mean of site-level power spectra (Figure S3). These discrepancies may stem from
- 1344 the different underlying distributions of site-level spectral power and eigencoefficient estimates,
- and the phase relationships that are preserved in the eigencoefficient estimates.
- 1346

1347 The spectral power estimates from MTM of a Gaussian process follow a chi-square distribution 1348 with two degrees of freedom, while the distribution of eigencoefficients approximately follows a 1349 normal distribution (22, 114). This suggests that the estimated global power spectra of vegetation 1350 turnover using the mean of site-level spectral power should be systematically higher than median 1351 estimates and mean of eigencoefficient estimates, while the latter two should be similar. Our 1352 sensitivity tests capture this systematic offset (Figure S3) and explain higher spectral power at 1353 low frequencies when using the mean of site-level spectral power. At low frequencies, individual 1354 sites with high spectral power pull the global estimate to higher values. While this offset should also exist at high frequencies, we observe a counterintuitive result: individual sites with low 1355 1356 spectral power pull the global estimate that uses the mean of site-level spectral power lower than 1357 the median and eigencoefficient global estimates (Figure S3). In light of this unexpected 1358 observation, and considering that each approach produces identical conclusions, we present 1359 results using the mean of spectral power to maintain consistency with prior studies (9, 10, 23).

1360

1361 In contrast to the robust conclusions when estimating the globally averaged power spectra of 1362 vegetation turnover using the mean, median, and mean of eigencoefficients we find that results 1363 were highly sensitive to averaging by β . This is a product of our piecewise regression procedure 1364 to determine the location of breaks in the log-log fit between spectral power and frequency in the 1365 high and intermediate frequency bands. Accurately identifying the location of breaks in β between the high and high-intermediate frequency bands requires high-resolution sampling 1366 1367 which is present in a subset of fossil pollen assemblages (Figure S3, Figure S10). Performing breakpoint identification on spectral power at a site level increases the weight of the more 1368 1369 abundant lower-resolution sites and reduces the weight of the less abundant high-resolution sites, reducing frequency resolution and biasing estimates of globally averaged β . 1370

1371

1372 Lastly, we assessed the sensitivity of our conclusions to the influence of anthropogenic land-use 1373 change. We performed all analyses after first removing any samples from the last 2,000 years 1374 (56), when anthropogenic influences in fossil pollen records are strongly expressed (61). 1375 Removing any samples within the last 2,000 years produces nearly identical power spectra at frequencies lower than 100⁻¹ years⁻¹ and suggests that climate tracking at millennial to multi-1376 1377 centennial scales persists (Figure 2, Figure S14). However, the detected breakpoints and β 1378 change if samples from the last 2,000 years are removed. The high frequency breakpoint (Figure 2, 146⁻¹ years⁻¹) decreases to 539⁻¹ years⁻¹ and β decreases from 4.58 to 0.39; the breakpoint at 1379 759⁻¹ years⁻¹ decreases to 3,673⁻¹ years⁻¹ and β increases from -0.1 to 2.02; the breakpoint at 1380 17,505⁻¹ years⁻¹ decreases to 21,717⁻¹ years⁻¹ and β decreases from 1.84 to 0.90; and β for the 1381 1382 lowest frequencies increases from -0.28 to 0.09. Our sampling density increases as age decreases (Figure S6) and sites with the highest temporal resolution span the last 2,000 years (Table S2), 1383 1384 therefore these changes in breakpoints and β may be a result of reduced sampling density. 1385 Despite statistically different β s at the highest frequencies, globally averaged power spectra still

1386	demonstrate a decrease in spectral power in the high frequency band which is particularly well
1387	demonstrated in the confidence intervals, matching results from the main manuscript (Figure 2,
1388	Figure S14) and results from similar analyses at a continental scale that also remove fossil pollen
1389	observations from the last 2,000 years (56). This suggests that climate decoupling at the highest
1390	frequencies may contain some influence of anthropogenic land use change (62, 115) but this is
1391	not the only control on high frequency vegetation turnover.
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1401	Supplemental Tables and Figures
1402	
1403	

Vegetation

				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	4.58*†	-0.10†	$1.84^{*\dagger}$	-0.28*†	146*	759*	17,505*
	(4.02, 5.12)	(-0.21,	(1.76,	(-0.47,	(150,	(802,	(18,162,
		0.09)	1.90)	-0.10)	141)	768)	16,831)
Extra-	4.51*†	-0.46*†	2.21*†	-0.15†	143*	696*	14,289*
tropics	(3.99,	(-0.54,	(2.17,	(-0.35,	(148,	(722,	(15,017,
(>23.5°)	4.96)	-0.38)	2.26)	0.07)	140)	680)	13,797)
Tropics	1.20*†			-0.50*†			7,609*
(< 23.5°)	(1.14, 1.29)			(-0.55,			(7,921,
				-0.43)			6,997)
1404					1		

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

β

Breakpoint

	(Weather Regime)	Low Frequency Band (Climate Regime)	High Frequency Band - Low Frequency Band. (⁻¹ years ⁻¹)
Global	-0.28*†	3.11*†	664*
	(-0.33,	(3.08,	(689,
	-0.21)	3.14)	645)
Extra-	-0.29*†	3.15*†	665*
tropics (>	(-0.34,	(3.12,	(668,
23.5°)	-0.24)	3.19)	647)
Tropics (< 23.5°)	0.99*†	3.08* [†]	910*
	(0.95,	(3.06,	(922,
	1.03)	3.11)	890)

TraCE-21ka Annual Precipitation Rate

		В	Breakpoint
	High Frequency Band	Low Frequency Band	High Frequency Band - Low
	(Weather Regime)	(Climate Regime)	Frequency Band (⁻¹ years ⁻¹)
Global	-0.52*†	2.69* [†]	675*
	(-0.59,	(2.68,	(691,
	-0.47)	2.71)	663)
Extra-	-0.99*†	2.52*†	629*
tropics (>	(-1.03,	(2.51,	(633,
23.5°)	-0.95)	2.43)	620)
Tropics (< 23.5°)	0.49* [†]	2.46* [†]	807*
	(0.40,	(2.45,	(829,
	0.61)	2.49)	779)

1406 Table S1. Parameter estimates and corresponding 95% confidence intervals (in parentheses) for 1407 Figures 2 and 3. * indicates that the estimated parameter is statistically distinct from 0 based on the bootstrapped confidence interval. For estimates of β , [†] indicates that β is statistically distinct 1408 from 2 (i.e. red noise) based on the bootstrapped confidence interval (for methods, see section 1409 Statistical Comparisons between Estimated Parameters from Spectral Analyses).

1410

1411

Table S2. (Not within the Supplementary text but available as a Supplementary File) The list of 1412

1413 sites considered in this study including those that were filtered out for issues with taxonomy

1414 harmonization, data quality (negative abundances), or chronological controls that prevented

- developing age models. 1415
- 1416

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	Mq5F6F6nmLYKNIACGome	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 S3. Temperature12k sites that failed spectral analyses and the corresponding reason.

	Vegetation	Vegetati	Vegetati	Vegetat	TraCE-	TraCE-	TraCE-	TraCE-
	Turnover β	on	on	ion	21ka	21ka	21ka	21ka
	High	Turnove	Turnove	Turnov	Tempera	Tempera	Annual	Annual
	Frequency	rβ	rβLow-	er ß	ture β	ture β	Precipita	Precipita
	Band	High-	Interme	Low	High	Low	tion	tion
		Interme	diate	Freque	Frequen	Frequen	Rate ß	Rate ß
		diate	Frequen	ncv	cy Band	cy Band	High	Low
		Frequen	cy Band	Band	ey zana	ey zana	Frequen	Frequen
		cv Band	-)				cv Band	cv Band
Vegetation								
Turnover B High								
Frequency Band								
Vegetation	< 0.001***							
Turnover β								
High-								
Intermediate								
Frequency Band								
Vegetation	< 0.001***	<						
Turnover β		0.001**						
Low-		*						
Intermediate								
Frequency Band								
Vegetation	< 0.001***	0.0543	<					
Turnover β Low			0.001**					
Frequency Band			*					
TraCE-21ka	< 0.001***	0.0069*	<	0.882				
Temperature β		*	0.001**					
High Frequency			*					
Band								
TraCE-21ka	< 0.001***	<	<	<	<			
Temperature β		0.001**	0.001**	0.001*	0.001**			
Low Frequency		*	*	**	*			
Band								
TraCE-21ka	< 0.001***	<	<	0.33	<	<		
Annual		0.001**	0.001**		0.001**	0.001**		
Precipitation		*	*		*	*		

Rate β High Frequency Band								
TraCE-21ka	< 0.001***	<	<	<	<	<	<	
Annual		0.001**	0.001**	0.001*	0.001**	0.001**	0.001**	
Precipitation		*	*	**	*	*	*	
Rate β Low								
Frequency Band								

Table S4. P-values of permutation tests comparing β from Figure 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 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-Intermediate					
Frequency Band Break					
Location Vegetation Turnessen	< 0.001***				
Vegetation Tumover High-Intermediate	< 0.001				
Frequency Band - Low-					
Intermediate Frequency					
Band Break Location					
Vegetation Turnover	< 0.001***	< 0.001***			
Erequency Band - Low					
Frequency Band Break					
Location					
TraCE-21ka	< 0.001***	0.0083**	< 0.001***		
Temperature High					
Frequency Band Break					
Location					
TraCE-21ka Annual	< 0.001***	< 0.001***	< 0.001***	0.323	
Precipitation Rate High					
Frequency Band - Low					
Location					
Location	I	I	I	I	I

Table S5. P-values of permutation tests comparing break locations from Figure 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° | >23.5° | >23.5° | >23.5° | >23.5° | >23.5° | >23.5° | >23.5° |

	Vegetati on Turnove r β High Frequen cy Band	Vegetatio n Turnover β High- Intermedi ate Frequenc y Band	Vegetatio n Turnover β Low- Intermedi ate Frequenc y Band	Vegetati on Turnove r β Low Frequen cy Band	TraCE- 21ka Temperat ure β High Frequenc y Band	TraCE- 21ka Temperat ure β Low Frequenc y Band	TraCE- 21ka Annual Precipitat ion Rate β High Frequenc y Band	TraCE- 21ka Annual Precipitat ion Rate β Low Frequenc y Band
Latitude >								
23.5° Vagatation								
Turnover B								
High								
Frequency								
Band Latituda >								
23.5°	< 0.001**							
Vegetation	*							
Turnover β								
High-								
Frequency								
Band								
Latitude >	<	<						
23.5°	0.001**	0.001***						
Vegetation	*							
Low-								
Intermediate								
Frequency								
Band		0.0224*						
Latitude > 23.5°	<	0.0224*	<					
Vegetation	*		0.001					
Turnover β								
Low Frequency								
Band Latituda >	-			0.0224*				
23.5° TraCE-	0.001**	0.001***	0.001***	0.0224				
21ka	*	0.001	01001					
Temperature β								
High								
Band								
Latitude >	<	<	<	<	<			
23.5° TraCE-	0.001**	0.001***	0.001***	0.001**	0.001***			
21ka	*			*				
I emperature p								
Band								
Latitude >	<	<	<	<	<	<		
23.5° TraCE-	0.001**	0.001***	0.001***	0.001**	0.001***	0.001***		
21ka Annual Precipitation	*			*				
Rate β High								

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

- **Table S6.** P-values of permutation tests comparing β for the extra-tropics from Figure 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 - 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° Vegetation	< 0.001***	< 0.001***			
Turnover Low-Intermediate					
Frequency Band - Low					
Frequency Band Break Location					
Latitude > 23.5° TraCE-21ka	< 0.001***	0.0109*	< 0.001***		
Temperature High Frequency					
Band - Low Frequency Band					
Break Location					
Latitude $> 23.5^{\circ}$ TraCE-21ka	< 0.001***	< 0.001***	< 0.001***	< 0.001***	
Annual Precipitation Rate High					
Frequency Band - Low					
Frequency Band Break Location					

Table S7. P-values of permutation tests comparing break locations for the extra-tropics from Figure 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	Latitude < 23.5° TraCE-21ka Annual Precipitation Rate High Frequency Band - Low
	Band Break	Frequency
	Location	Band Break
		Location
< 0.001***		
< 0.001***	< 0.001***	
	Latitude < 23.5° Vegetation Turnover High Frequency Band – Low Frequency Band Break Location < 0.001***	Latitude < 23.5° Latitude <Vegetation Turnover High Frequency Band – Low Frequency Band Break LocationTraCE-21ka Temperature High Frequency Band - Low Frequency Band Break Location< 0.001***

Table S8. P-values of permutation tests comparing break locations for the tropics from Figure 3

where *** corresponds to values <0.001, ** indicates values between 0.001 and 0.01, and * indicates values between 0.01 and 0.05.

marcates values be	u u u u u u	nu 0.05.				
	Latitude <	Latitude <	Latitude <	Latitude <	Latitude <	Latitude <
	23.5°	23.5°	23.5°	23.5°	23.5°	23.5°
	Vegetation	Vegetation	TraCE-21ka	TraCE-21ka	TraCE-21ka	TraCE-21ka
	Turnover β	Turnover	Temperature	Temperature	Annual	Annual
	High	β Low	βHigh	βLow	Precipitation	Precipitation
	Frequency	Frequency	Frequency	Frequency	Rate $\hat{\beta}$ High	Rate $\hat{\beta}$ Low
	Band	Band	Band	Band	Frequency	Frequency
					Band	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***				
IIuon Tiku		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						

1446 **Table S9.** P-values of permutation tests comparing β for the tropics from Figure 3 where ***

1447 corresponds to values <0.001, ** indicates values between 0.001 and 0.01, and * indicates values 1448 between 0.01 and 0.05.





Figure S1. (A-C) Synthetic time series with arbitrary units with a β of (A) 0, (B) 1, and (C) 2. (D-F) The corresponding power spectra for the synthetic time series in (A-C).



1453 Figure S2. (A) Individual records of vegetation turnover from fossil pollen from the 1,321 site 1454 compilation that are selected to demonstrate characteristics of the global average power spectra that are presented in Figures 2 and 3. (B) The corresponding power spectra for the selected sites 1455 1456 in (A). (C) A map of selected sites in (A-B). The colors correspond to different spectral characteristics that are highlighted in the main text. Green corresponds to sites that demonstrate a 1457 constant power-law scaling relationship across all frequencies and fast tracking at intermediate 1458 1459 frequencies in the global average. Orange corresponds to sites that demonstrate a break in spectral power at low-intermediate frequencies (~1,000 years⁻¹) and a small β at high-1460 intermediate frequencies. Purple indicates sites that demonstrate an increase in β at the highest 1461 1462 frequencies. Note, that all sites demonstrate a decrease in β at multimillennial timescales present in the global average. Note, in (A) the PCO1 time series are scaled by the corresponding 1463 1464 eigenvalue, unlike in Figure S7.



1467 Figure S3. Sensitivity tests for the continuum of ecological variability, in which the 1468 dimensionality-reduction methods and spectral-averaging methods are varied. Power spectra line 1469 opacity indicates the number of ensemble members that resolve each frequency. Results are presented for the primary dimension of variability from dimensionality reduction on fossil pollen 1470 1471 assemblages. For the power average approach, we bin by frequency and then average the spectral 1472 power values across sites. For the eigencoefficient average approach, we bin by frequency and average the five MTM eigencoefficients corresponding to each data taper. We calculate spectral 1473 1474 power following Equation 1. For the β average approach, we estimate β through an ordinary least 1475 squares regression between spectral power and frequency at a single site. We then average across 1476 sites to produce a global estimate of β . This procedure only retains β , not spectral power. 1477 Therefore, for the β average method only the resulting β fit is presented. The separate lines for β average correspond to β in four frequency bands. The breakpoint of these two lines indicates the 1478 1479 calculated average break location averaged across sites. All sensitivity analyses were performed 1480 with the Monte Carlo resampling procedure detailed in Uncertainty Estimation with the shaded 1481 area corresponding to the 95% confidence interval. Note, that all averaged power spectra based on PCO1 (the first axis of Principal Coordinates Analysis) of the site-level community 1482 dissimilarity matrix demonstrate a decrease in β after the common ~17,000⁻¹ years⁻¹ breakpoint 1483 1484 $(\beta = 0.45 \text{ for Bray-Curtis PCO1}, \beta = 0.67 \text{ for Bray-Curtis PCO1}, \beta = -0.28 \text{ for Squared Chord}$ 1485 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 1486 1487 ecosystems (i.e. is the most sensitive dissimilarity metric) (26, 88). In contrast, CA1 (the first axis 1488 of Correspondence Analysis), which cannot saturate like metric-based approaches, shows no 1489 such decrease in β . The averaged power spectra for CA1, which represents the primary 1490 dimension of variation in fossil pollen assemblages (not the dissimilarity matrix), has a higher β

1491 ($\beta = 0.83$ for frequencies lower than the 17,824⁻¹ years⁻¹ breakpoint) and more consistent β s 1492 across all frequencies, demonstrating that the decrease in β observed at low frequencies for PCO-1493 based approaches is caused by metric saturation.

- 1494
- 1495



1496 1497 Figure S4. (A) Probability density distributions and (B) empirical cumulative distributions for 1498 the ensemble of breakpoint estimated for globally averaged power spectra between the lowintermediate and high-intermediate frequency band for fossil pollen (green) from our Monte 1499 Carlo resampling approach compared to tree longevity estimates from the International Tree 1500 Ring Data Bank (brown). Break locations for TraCE-21ka near-surface temperature (blue) and 1501 TraCE-21ka precipitation (light blue) correspond to one break location, previously reported (9, 1502 10), at frequencies between 100^{-1} to 1,000 years⁻¹. Tree longevity from the International Tree 1503 1504 Ring Data Bank corresponds to the top horizontal axis. All pollen results presented are from 1505 PCO1 using the squared chord distance metric and averaged by spectral power. 1506





Figure S5. (A-C) Measured vegetation assemblage dissimilarity, for all sites in the global fossil pollen compilation. Dissimilarity was calculated only for assemblages from the same site and was not calculated for assemblages from different sites. Within each site, all possible pairs of fossil pollen assemblages were compared using the (A) Bray Curtis, (B) Jaccard, and (C)

1512 Squared Chord Distance metrics with the corresponding temporal span between the samples

1513 being compared retained. (D-F) The empirical cumulative distribution of all points shown in the

- 1514 top row of plots.
- 1515



1517 Figure S6. (A) All sites used in the spectral analyses, as in Figure 2A. The probability density of

1518 (B) temporal resolution and (C) temporal span for all sites analyzed and all corresponding

1519 posterior age estimates. Note, that the Northern Hemisphere is more well-represented than the 1520 Southern Hemisphere.







- and 2) (G) correspondence analysis on fossil pollen assemblages for each site analyzed. We also
- 1525 performed correspondence analyses on fossil pollen assemblages after degrading the abundance
- observations to presence/absence (I). (B, D, F, H, J) Eigenvalues corresponding to PCO1 for
- each site plotted against the absolute value of the site latitude. For correspondence analyses,
- eigenvalues do not correspond to variance explained as they do for principal coordinate analyses.
- 1529 Rather, eigenvalues correspond to correlation coefficients between the coordinates for species in 1530 the fossil pollen assemblage (i.e. species score) and coordinates for time intervals (i.e. site score)
- 1530 in the ordination coordinate system. For visual simplicity, the PCO1 and CA1 results for each
- 1532 site are unscaled by the corresponding eigenvalue. Several scaled time series are presented in
- 1532 Figure S2. In addition, the right column (B, D, F, H, J) demonstrates that eigenvalues tend to be
- 1534 higher in the high latitudes, causing PCO1 for high-latitude sites to be upscaled, producing
- 1535 greater total spectral power in Figure 3, relative to the low latitudes. Also for visual simplicity,
- 1536 we only present sites here that span the last 50,000 years, we direct readers to our Zenodo
- 1537 repository (74) where all data are present.
- 1538



1539 1540 **Figure S8.** Each plot corresponds to the probability density function for all breakpoint and β 1541 parameter estimates in Figure 2 and Table S1. Colors correspond to parameter estimates for

1542 fossil pollen (green), TraCE-21ka annual precipitation rate (light blue), and TraCE-21ka near-1543 surface temperature (blue).



Figure S9. As in Figure S8 but for breakpoint and β estimates in Figure 3. Colors correspond to

- 1546 the spatial average with red indicating the tropics ($< 23.5^{\circ}$) and blue indicating the extra-tropics 1547 (>23.5°).
- 1548



1549

1550 Figure S10. As in Figure S3 but for the secondary dimension of variability from dimensionality reduction on fossil pollen assemblages. 1551

1552



1553

1554 Figure S11. Sensitivity tests for latitudinal averaged power spectra for PCO1 of fossil pollen

assemblages where the dimensionality reduction method is varied. All power spectra were 1555 1556 generated by averaging spectral power after binning by frequency. Power spectra line opacity indicates the number of ensemble members that resolve each frequency. 1557



Figure S13. A) The averaged power spectrum for non-pollen temperature estimates from Temperature 12k (yellow). The averaged power spectrum of temperature variability for TraCE-21ka (blue) is estimated after degrading TraCE-21ka to match the time-averaged and spatial characteristics of the Temperature12k sites. Power spectra line opacity indicates the number of sites that resolve each frequency. Note, the similar β at low frequencies and the similar break location between the high frequency and low frequency scaling regimes. B) The Temperature12k sites are colored by proxy.

1570





Figure S14. Sensitivity tests for the continuum of vegetation turnover and climate variability based on the median of an ensemble of spectral power estimates after removing any observations younger than 2,000 years to assess the influence of anthropogenic land use change. The blue line corresponds to results from Figure 2 and Figure S3 and the yellow line corresponds to the sensitivity test. Power spectra line opacity indicates the number of ensemble members that resolve each frequency. Note, that the confidence intervals for the power spectra overlap across all of frequency space suggesting a limited influence of anthropogenic land use change.



1580

Figure S15. 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 Páramo de Agua Blanca (21978). B) The effect of averaging spectral power across
these sites, each with a unique sampling resolution and temporal span. Here, the averaging is a
running 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 is the average of Ioannina (4112), Grays Lake (16113), and Lake

1588 Louise (1669). We use the median Bchron age model in these analyses and do not employ the

- 1589 resampling procedure of the main manuscript.
- 1590





Figure S16. Spectral power for near-surface temperature for TraCE-21ka at each fossil pollen

1593 site where the temperature time series is resolved annually (yellow) and degraded (blue) to match 1594 the temporal characteristics of the fossil pollen assemblage. For degradation, each annually-

- resolved 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
- 1597 smoothed using a low-pass filter with a timescale twice the mean resolution of the fossil pollen
- abundances (58). The frequency associated with a spurious drop in spectral power in the
- 1599 degraded power spectra, not present in the annually resolved power spectra, is defined as the
- highest resolvable frequency for (A) global, (B) extra-tropical, and (C) tropical spectral power estimates and marked with a dashed line. These frequencies are 58⁻¹ years⁻¹, 57⁻¹ years⁻¹, and 160⁻¹
- 1602 ¹ years⁻¹, respectively. Confidence intervals result from a Monte-Carlo resampling procedure
- 1603 outlined in *Uncertainty Estimation*.
- 1604
- 1605