

Forest responses to last-millennium hydroclimate variability are governed by spatial variations in ecosystem sensitivity

Article

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3 **1 Forest responses to last-millennium hydroclimate variability are governed by spatial variations in**
4 **2 ecosystem sensitivity**
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CRR, AD, AMR, and JWW designed the study. AD, AMR, JWW, STJ, JM, and MT created pollen reconstructions and aided in interpretation (STEPPS, ReFAB). AD and AMR wrote the pollen methods. CRR, AMR, MCD, JM, DJPM, BP, TQ, and JS performed ecosystem model simulations and aided in interpretation. CRR and JWW wrote the manuscript with additional input from AD, AMR, and all authors.

Data Accessibility Statement:

Should the manuscript be accepted, the data supporting the results will be archived in two public repositories and the DOIs will be included at the end of this article. Pollen data is already available or will be made available upon acceptance on the EDI data portal as an msb-paleon product. The [Environmental Data Initiative](#) is an NSF-funded program tailored towards environmental data and works closely with the US Long-Term Ecological Research (LTER) Network, NSF Macrosystems Biology program (which funded our work), and DataONE. Terrestrial ecosystem model drivers are being archived on the ORNL DAAC and will be available at the following DOI:

<https://doi.org/10.3334/ORN LDAAC/1779>. The [Oak Ridge National Laboratory Distributed Active Archive Center \(ORNL DAAC\)](#) is managed by NASA's Earth Science Data and Information Systems program and is well suited to archive ecosystem model output, which is often large and has converged on netcdf as a standard file format. These repositories have been approved by *Ecology Letters* editorial staff. All code for analyses is publicly available on Github: <https://github.com/PaleEON-Project/EcosystemVariability>

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2
3 **83 Abstract**
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5 84 Forecasts of future forest change are governed by ecosystem sensitivity to climate change, but
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7 85 ecosystem model projections are under-constrained by data at multidecadal and longer
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9 86 timescales. Here, we quantify ecosystem sensitivity to centennial-scale hydroclimate variability,
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11 87 by comparing dendroclimatic and pollen-inferred reconstructions of drought, forest composition
12
13 88 and biomass for the last millennium with five ecosystem model simulations. In both
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15 89 observations and models, spatial patterns in ecosystem responses to hydroclimate variability are
16
17 90 strongly governed by ecosystem sensitivity rather than climate exposure. Ecosystem sensitivity
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19 91 was higher in models than observations and highest in simpler models. Model-data comparisons
20
21 92 suggest that interactions among biodiversity, demography, and ecophysiology processes dampen
22
23 93 the sensitivity of forest composition and biomass to climate variability and change. Integrating
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25 94 ecosystem models with observations from timescales extending beyond the instrumental record
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27 95 can better understand and forecast the mechanisms regulating forest sensitivity to climate
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29 96 variability in a complex and changing world.
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98 **Introduction**

99 Exposure to 21st-century climate change is expected to profoundly impact global forest
100 composition, diversity, and structure (Dawson *et al.* 2011; Keeley *et al.* 2019), but the sensitivity
101 of ecosystems to climate variability at multi-decadal to centennial time scales is poorly
102 constrained by instrumental observations. Multiple observational studies that employ
103 subcontinental- to continental-scale data networks across a broad range of timescales have
104 sought to empirically estimate the sensitivity of forest ecosystems to climate variability. The
105 sensitivity of tree growth rates, biomass accumulation, and ecophysiological processes to
106 interannual climate variability is well-documented by dendroecological data, with compelling
107 evidence that forest sensitivity to climate depends on forest age and is non-stationary across
108 space and time (Charney *et al.* 2016; Klesse *et al.* 2018; Thom *et al.* 2019; Peltier & Ogle
109 2020). On glacial-interglacial timescales, networks of fossil pollen records show that
110 temperature variations are the primary driver of forest composition and species distributions
111 (Shuman *et al.* 2004; Nolan *et al.* 2018), while over the last several thousand years, hydroclimate
112 variability has strongly affected forest composition and structure in temperate forests of the
113 northeastern and upper midwestern United States (Booth *et al.* 2012; Shuman *et al.* 2019).

114 Terrestrial ecosystem models used to forecast responses to climate change often have
115 difficulty reproducing broad-scale and long-term responses to environmental variability, despite
116 being well-grounded in empirical evidence and ecological theory (Friedlingstein *et al.* 2006,
117 2014; Matthes *et al.* 2016). These models mechanistically connect ecophysiological processes
118 and climate variability to past and present changes in forest composition and structure but are
119 subject to uncertainty in external forcings (e.g., drivers), process representation, and
120 parametrization that complicates data-model comparisons (Figure 1) (LeBauer *et al.* 2013;
121 Matthes *et al.* 2016; Dietze 2017; McLachlan & PaleON Project 2018). Each model includes

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3 122 hypotheses about the primary processes and ecosystem characteristics governing forest change,
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5 123 various simplifying assumptions, and tradeoffs between computational tractability and process
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7 124 complexity (De Kauwe *et al.* 2013; Walker *et al.* 2014; Medlyn *et al.* 2015). Previous data-
8
9 125 model comparisons have returned mixed evidence about whether models underestimate or
10
11 126 overestimate the sensitivity of forest processes such as net primary productivity (NPP) and
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13 127 mortality to climate change (Schimel *et al.* 2015; Walker *et al.* 2015; Rollinson *et al.* 2017). As
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15 128 a result, projections of forest compositional and structural responses to climate change have high
16
17 129 uncertainty, which propagates to increased uncertainty in science-based adaptation planning
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19 130 (Friedlingstein *et al.* 2014).

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24 131 Several challenges have traditionally hindered the joint analysis and integration of
25
26 132 terrestrial ecosystem models and paleoecological data to better constrain modeled responses to
27
28 133 climate variations at multi-decadal and longer timescales. First, the raw observations collected
29
30 134 from fossil pollen records (counts of individual pollen taxa) have no direct counterparts in
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32 135 ecosystem models. Bayesian hierarchical models are providing new process-based approaches to
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34 136 infer emergent ecosystem properties from fossil pollen records, such as forest composition,
35
36 137 diversity, percent cover, and biomass (Raiho *et al.* in prep; Blarquez & Aleman 2016; Dawson *et*
37
38 138 *al.* 2016), but the number of state variables that can be estimated from paleoecological data
39
40 139 remains small relative to the number of latent (i.e., unobservable) variables simulated by
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42 140 ecosystem models (Fig. 1). Second, pre-instrumental model-data comparisons are complicated
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44 141 by reliance on driver datasets derived from general circulation models (GCMs). GCMs generally
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46 142 capture macroscale spatial patterns and low-frequency trends in climate but are unable to fully
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48 143 capture the complexity and stochasticity of local to regional-scale weather phenomena at the
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50 144 subdaily resolution needed to drive ecosystem models, resulting in systematic spatial and
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3 145 temporal biases in model simulations (Anav *et al.* 2013; Matthes *et al.* 2016; Dietze *et al.* 2018).
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5 146 Third, the native temporal resolution varies between paleodata and models and requires a
6
7 147 temporal standardization. Due to these challenges, the predicted sensitivity of ecosystem model
8
9 148 state variables such as forest composition and biomass to climate change is largely unvalidated
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11 149 by observations at multidecadal and longer timescales, resulting in wide divergence among
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13 150 terrestrial ecosystem models in their 21st-century projections (Friedlingstein *et al.* 2006,
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15 151 2014). Fourth, terrestrial ecosystem models vary widely in represented processes, which can
16
17 152 challenge intermodel comparisons but also provide insight into key governing ecological
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19 153 processes when data-model discrepancies emerge.
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24 154 Here, we seek to establish the patterns of forest ecosystem and climate variability in the
25
26 155 north-central and northeastern US for the last millennium (850-1850 C.E.) and identify the
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28 156 mechanisms underpinning both forest ecosystem sensitivity and observed data-model
29
30 157 discrepancies. In these analyses, we test hypotheses about the relative importance of
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32 158 hydroclimate exposure, defined as the magnitude of drought variability, and ecosystem
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34 159 sensitivity as determinants of the variability seen in forest ecosystems. We also hypothesize that
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36 160 ecosystem models will be overly sensitive to hydroclimate variability due to insufficient
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38 161 representation of ecophysiological and demographic processes that can dampen climate
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40 162 responses. To this end, we present a novel series of data-model and model-model comparisons
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42 163 that are designed to overcome traditional barriers to data-model intercomparison for pre-
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44 164 instrumental times. Our analyses combine dendroclimatic indices of drought, recently published
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46 165 Bayesian spatiotemporal estimates of forest composition and biomass derived from pollen that
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48 166 provide independent checks on last-millennium simulations from five terrestrial ecosystem
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50 167 models for the northeastern and upper midwestern United States. The data-model comparisons
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3 168 discriminate among differing representations of forest processes such as productivity and
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5 169 demography, while the model-model comparisons help diagnose causal relationships among
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8 170 ecological processes, changes in forest states, and climate variability (Fig. 1). To test hypotheses
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10 171 while also overcoming known geographic biases in the model simulations of ecosystem state
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12 172 such as forest composition that source back to biases in the climate model drivers (Matthes *et al.*
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14 173 2016), we develop a new variability metric that we apply to the data and model-derived products
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17 174 that focuses on comparisons among variability of hydroclimate, composition, and biomass (Fig.
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19 175 1). Our results indicate that at centennial timescales, spatial patterns in the variability of forest
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21 176 composition and biomass are regulated by ecological factors such as ecotonal position and
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23 177 complexity rather than climate exposure as defined by the local magnitude of climate variability.
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27 28 179 **Materials & Methods**

29 30 180 *Overview*

31
32 181 We employ a combination of data-model and model-model comparisons (Fig. 1) in which
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34 182 we combine paleoclimatic and paleoecological datasets to draw inferences about past variations
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36 183 in hydroclimate and forest composition and biomass. The temporal domain of this study is 850-
37
38 184 1850 AD and is bounded by the temporal extent of the climate drivers available for our model
39
40 185 simulations (850 AD) and time of EuroAmerican settlement-era tree surveys (ca. 1850 AD). In
41
42 186 our study, 'data' refers to observation-based statistical models of past drought, forest
43
44 187 composition, and biomass, reconstructed from tree rings, historical tree surveys, and networks of
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46 188 fossil pollen records. These data-based inferences are fully independent of the ecosystem model
47
48 189 simulations. Model-based comparisons are from the PaleON Ecosystem Model Intercomparison
49
50 190 Project (PEMIP) (Rollinson *et al.* 2017), which used spatially and temporally downscaled past
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52 191 climate simulations from the Fifth Coupled Model Intercomparison Project (CMIP5) as drivers.
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3 192 Comparisons among ecosystem model simulations and empirical data rely on normalized values
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5 193 compared in environmental space, rather than geographic space, in order to reduce the effects of
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8 194 any bias in the climate drivers in our analyses and to focus on sensitivity of ecosystems to
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10 195 climate variability (Supplemental Figure 1).

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12 19613
14 197 *Observational Datasets*

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16 198 The empirically inferred datasets leverage recent advances in pollen-vegetation modeling
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18 199 (Dawson *et al.* 2016), a form of proxy system modeling (Evans *et al.* 2013) in which ecosystem
19
20 200 state variables such as composition and biomass are estimated along with associated
21
22 201 observational uncertainties. Of the three inferred datasets used here, two were derived from
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24 202 networks of fossil pollen records provided by individual data contributors and the Neotoma
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26 203 Paleoecology Database and were calibrated against historical surveys of forest composition and
27
28 204 structure from the early stages of EuroAmerican settlement (Liu *et al.* 2011; Dawson *et al.* 2016;
29
30 205 Goring *et al.* 2016; Kujawa *et al.* 2016; Paciorek *et al.* 2016). Pollen-based inferences are based
31
32 206 on statistical pollen-vegetation models (PVMs) called STEPPS and ReFAB, and represent
33
34 207 fractional vegetation composition and total woody biomass, respectively, for 12 tree genera that
35
36 208 are common elements of upper Midwest forests. STEPPS is a Bayesian hierarchical spatio-
37
38 209 temporal model that infers fractional forest composition from networks of fossil pollen records
39
40 210 (Paciorek & McLachlan 2009; Dawson *et al.* 2016, 2019b; Trachsel *et al.* 2020). STEPPS
41
42 211 employs a process-based representation of pollen dispersal and production, with taxon-specific
43
44 212 parameterizations. STEPPS is calibrated using spatial datasets of pollen samples and forest
45
46 213 composition data, here from the settlement era (Paciorek & McLachlan 2009; Dawson *et al.*
47
48 214 2016), then run for fossil pollen assemblages for other time intervals to produce posterior
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50 215 estimates of past forest composition. Using this framework, STEPPS: (i) explicitly characterizes
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3 216 uncertainty in data and processes, with posterior distributions of process parameters and state
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5 217 variables such as forest composition, and (ii) borrows information across space and time,
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7 218 allowing for spatially comprehensive estimates of composition. For both the upper Midwestern
8
9 219 USA (UMW; Minnesota, Wisconsin, Michigan) (Dawson *et al.* 2019a) and the northeastern
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11 220 USA (NEUS) (Trachsel *et al.* 2020), STEPPS has been used to estimate centennially resolved
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13 221 forest composition for the late Holocene (250 B.C. to 1750 A.D) at a 24 km grid; here we use the
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15 222 results from 850 to 1750 AD.
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19 223 ReFAB also employs a similar approach to STEPPS but focuses specifically on
20
21 224 estimating total aboveground woody biomass (Raiho *et al.* in prep). ReFAB is calibrated using
22
23 225 the relationship between settlement-era multivariate pollen counts and biomass from PLS
24
25 226 surveys (Paciorek *et al.* 2019). Parameter estimates from calibration are then used to reconstruct
26
27 227 centennially resolved biomass for 77 sites in the UMW for the last 10,000 years (Raiho *et al.* in
28
29 228 prep). ReFAB can characterize the uncertainty in sediment pollen age estimates, calibration
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31 229 parameters, the relationship between species composition and total aboveground woody biomass,
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33 230 and species-level allometries.
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38 231 The Living Blended Drought Atlas (LBDA) provides yearly estimates of summer (mean
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40 232 June, July, August) Palmer Severity Drought Index (PDSI) for North America, based on
41
42 233 networks of tree-growth chronologies (Cook *et al.* 2010; Woodhouse *et al.* 2010). We used PDSI
43
44 234 as our measure of hydroclimate variability because it is an important predictor of forest dynamics
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46 235 in this domain and can also be calculated directly from the meteorological forcings used for the
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48 236 ecosystem model simulations (Clifford & Booth 2015; Cook *et al.* 2015). LBDA PDSIs are
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50 237 provided at 0.5-degree spatial grid resolution. Due to varying temporal extent of tree-growth
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3 238 chronologies, the temporal extent of the LBDA varies. The earliest years in this spatial domain
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5 239 ranged from 0 to 1671 AD, while the latest year was 2005 (Supplemental Figure 1).
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10 241 *Modeling Datasets*

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12 242 PEMIP model simulations here are composed of five ecosystem models with dynamic
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14 243 vegetation (ED2; LINKAGES; LPG-WSL; LPJ-GUESS; and JULES-TRIFFID) run at 254
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16 244 locations across the eastern and midwestern US at 0.5-degree spatial resolution (Rollinson *et al.*
17
18 245 2020). These models vary in how they characterize forest composition and carbon dynamics and
19
20 246 range from species-based with little ecophysiological process representation (e.g., LINKAGES)
21
22 247 to detailed ecophysiology and cohort representation, but reliance on plant functional types
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24 248 (PFTs; e.g. ED2, Table 1). LPJ-GUESS and LPJ-WSL both included stochastic fire disturbances
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26 249 in their simulations, while other models such as ED and LINKAGES include processes of tree
27
28 250 mortality that assume landscape-scale equilibrium (Rollinson *et al.* 2017).
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33 251 PEMIP climate drivers were temporally downscaled and bias-corrected from existing past
34
35 252 climate simulations to meet the external forcing needs of the ecosystem model ensemble
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37 253 (Supplemental Figure 1) (Kumar *et al.* 2012; Rollinson *et al.* 2017). CCSM4 output from the
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39 254 Paleoclimate Modeling Intercomparison Project, Phase III (PMIP3) past millennium simulations
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41 255 and the Coupled Model Intercomparison Project, Phase 5 (CMIP5) historical simulations were
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43 256 downscaled to 0.5-degree spatial resolution and 6-hourly temporal resolution using standard
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45 257 protocols (Kumar *et al.* 2012; Rollinson *et al.* 2017). After the 6-hourly PEMIP climate driver
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47 258 datasets were created, they were then temporally averaged to meet the specific driver
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49 259 requirements of individual ecosystem models, which vary in temporal resolution. ED2 and
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51 260 JULES-TRIFFID use the full suite of 6-hourly drivers for temperature, precipitation, shortwave
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54 261 radiation, longwave radiation, surface pressure, specific humidity, wind speed, and carbon
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3 262 dioxide concentration. Meteorological drivers for the two LPJ variants include daily
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5 263 temperature, precipitation, and shortwave radiation plus longwave radiation for LPJ-WSL.
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8 264 LINKAGES only requires monthly average temperature and precipitation. Soil texture used to
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10 265 parameterize locations in model simulations was extracted from the Harmonized World Soil
11
12 266 Database (Wei *et al.* 2014). Monthly temperature and precipitation were combined with soil
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14 267 water holding capacity computed from model driver soil texture and depth to calculate PDSI,
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17 268 following (Cook *et al.* 2015), but using the Thornthwaite equation for evapotranspiration
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19 269 (Thornthwaite & Mather 1957; Pelton *et al.* 1960). We used the Thornthwaite equation so that
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21 270 the calculation of PDSI was independent of internal model dynamics, including
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24 271 evapotranspiration, which can vary widely among ecosystem models, even when given the same
25
26 272 temperature and precipitation drivers, due to differences in model structure and parameterization.
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28 273 From the ecosystem models, we extracted fractional forest composition and total aboveground
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30 274 biomass, which can be directly compared to paleoecological observations, and four variables that
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32 275 are latent, i.e., unobservable in the paleoecological record (Fig. 1): gross primary productivity
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34 276 (GPP), net primary productivity (NPP), net ecosystem exchange (NEE), and leaf area index
35
36 277 (LAI).
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41 42 279 *Analyses*

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44 280 Analyses focused on the comparison of empirical data and ecosystem model outputs of
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46 281 centennial-scale variability in forest composition and biomass driven by drought variability over
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48 282 the last 1,000 years. Our analytical approach involved three key stages to maximize
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50 283 commensurability between observations and model output: 1) temporal homogenization of all
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52 284 variables to a common centennial resolution; 2) development of a common normalized
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55 285 variability metric for ecosystem and drought variability to facilitate comparison across different
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286 variables, and 3) use of hydroclimate sensitivity as the basis for all model-data and model-model
 287 comparisons to minimize the potential effects of biases in the climate model drivers.

288

289 *i. Temporal Homogenization*

290 For annually resolved datasets in our study, including the LBDA and all model output
 291 and drivers, a generalized additive model (GAM) was used to generate time series with the
 292 similar centennial-scale smoothing as the pollen inferred observational datasets. In this process,
 293 the response variable for analysis (e.g. drought, biomass, GPP) was modeled as a function of
 294 time (year) using a thin-plate regression spline with one knot per 100 years (e.g. 10 knots for a
 295 1,000 year window) using the *gam* function in the *mgcv* package in R (Wood 2017; Simpson
 296 2018). To capture the temporal uncertainty similar to that generated in the PVMs, we generated
 297 a 1000-member posterior distribution of each predicted variable through time using the error and
 298 covariance of the intercept and spline parameters. We then extracted the predicted values at 100-
 299 year intervals corresponding to the windows captured by the STEPPS and ReFAB output.

300

301 *ii. Variability Metric*

302 To facilitate comparisons among variables with different units such as composition and
 303 biomass, we developed a base metric for all analyses, consisting of the normalized mean
 304 temporal variability of each dataset (eq. 1).

305 **equation 1:** $variability_i = \ln \frac{\bar{d}_i}{\bar{x}}$

306 **equation 2:** $d_{i,t} = |x_{i,t} - x_{i,t-1}|$

307 Mean temporal variability at each location (\bar{d}_i) for each variable (e.g., composition, biomass,
 308 PDSI) was calculated as the mean of the absolute first differences between adjacent time points

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3 309 $(t, t - 1)$ extracted from centennially resolved time series for each location (i) (eq. 2). The use
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5 310 of first differences is a discretization of the first derivative and describes the rate of change at
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7 311 each timestep. Each first-difference calculation was based on the mean of the posterior draws
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9 312 from the STEPPS or ReFAB PVM or to the GAMs fitted to the LBDA data and ecosystem
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11 313 model variables. We normalized variability by dividing the mean first differences for each
12
13 314 location (\overline{d}_i) by the variable mean for that dataset across the entire spatiotemporal domain (\overline{x}).
14
15 315 For forest compositional data, the variability metric was calculated using the taxon or plant
16
17 316 functional type (PFT) with the highest fractional composition at each location, with the choice of
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19 317 taxon or PFT allowed to vary among sites. For all analyses and presented results, normalized
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21 318 variability is log-transformed to meet standard statistical assumptions of Gaussian distributions
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23 319 and homoscedasticity (eq. 1).
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31 321 *iii. Hydroclimate Sensitivity*

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33 322 After the normalized temporal variability was calculated for PDSI and all ecosystem
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35 323 variables, sensitivity to hydroclimate variability was defined as the slope of a linear regression
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37 324 between variability as the independent variable and variability of the ecosystem response
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39 325 variable such as composition or biomass. These analyses always used the appropriate
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41 326 observational or modeled PDSI variability (i.e., LBDA for the pollen-inferred compositional
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43 327 variability; calculated PEMIP driver PDSI variability for the model-simulated compositional
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45 328 variability) to ensure internal consistency between climatic forcing and ecosystem response.
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51 330 **Results**

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53 331 In the observational data, variability in forest composition or biomass in the northeastern
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55 332 US (NEUS) and upper midwestern US (UMW), did not correlate to drought variability (Table 1,
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3 333 Figs. 2, 3) in contrast with the hypothesis that high exposure to climate variability should lead to
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5 334 increased compositional variability. Neither the full spatiotemporal domain (Table 1) nor the
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7 335 UMW (Fig. 3, sensitivity slope = 0.010 SE 0.018) showed a significant relationship between
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9 336 reconstructed drought and composition variability, although the NEUS showed weak sensitivity
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11 337 (Fig. 3, sensitivity slope = 0.065 SE 0.027). Reconstructed biomass variability (Fig 2., biomass
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13 338 reconstructions not available for the NEUS, (Paciorek *et al.* 2019)) also was uncorrelated to
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15 339 drought variability (Table 1) and instead showed the highest variability at the historic prairie-
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17 340 forest ecotone (Fig. 2) (Goring & Williams 2017). In pollen-based reconstructions, composition
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19 341 and biomass variability were weakly but positively related (Fig. 3c, $R^2=0.09$, slope=0.479 SE
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21 342 0.187) and locations with higher taxonomic richness tended to have higher variability
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23 343 (Supplemental Fig. 2).

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26 344 Modeled ecosystem sensitivity to drought variability was generally similar to or higher
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28 345 than observations, with less-complex models tending to have a too-high predicted sensitivity
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30 346 relative to the empirical reconstructions (Fig. 3). Composition variability was more sensitive to
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32 347 drought variability than in reconstructions for three of five ecosystem models (ED2, LPJ-WSL,
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34 348 and TRIFFID), with the data-model discrepancy most pronounced in models with fewer plant
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36 349 types or taxa (Fig. 3a, Table 1). JULES-TRIFFID, which had only two tree PFTs (deciduous and
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38 350 evergreen), had the highest drought sensitivity (composition slope = -8.633 SE = 1.075,
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40 351 composition sensitivity slope 0.411 SE = 0.022). LPJ-WSL and ED2, with respectively six and
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42 352 five PFTs, had similar mean compositional variability (LPJ-WSL slope = -7.829 SE = 0.943,
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44 353 ED2 slope = -7.156 SE = 0.514), although LPJ-WSL was approximately twice as sensitive to
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46 354 hydroclimate variability as ED2 (Fig. 3a, Table 1, LPJ-WSL slope = 0.252 SE =0.018, ED2
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48 slope = 0.118 SE = 0.018). LINKAGES, which simulated 15 individual species, had among the
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3 356 lowest sensitivity to drought variability (Fig. 3a, Table 1, composition slope = -6.598 SE =
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5 357 0.478, composition sensitivity slope 0.074 SE = 0.018).

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7 358 Ecosystem models with simpler representation of vegetation ecophysiology
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9 359 (LINKAGES, JULES-TRIFFID) also had a too-high sensitivity of biomass to drought variability
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11 360 relative to empirical reconstructions (Table 1, Fig. 3b). Both LINKAGES and JULES-TRIFFID
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13 361 showed a tight positive coupling of biomass sensitivity to drought variability, which
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15 362 corresponded to strong correlations between biomass and composition variability (Fig. 3c).
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17 363 LINKAGES showed a one-to-one relationship between composition and biomass variability,
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19 364 which is much stronger than reconstructions (Fig. 3c). Of all the models, only LPJ-WSL was
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21 365 consistent with the data in showing a weakly negative relationship between biomass and PDSI
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23 366 variability (Fig. 3b) while also showing a positive correlation between biomass and composition
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25 367 variability (Fig. 3c).

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27 368 Further analysis of latent variables in the ecosystem models confirmed that variations in
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29 369 modeled ecosystem sensitivity to hydroclimate variability is linked to model complexity of
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31 370 ecosystem composition and processes (Fig. 4). There is a cascading series of linkages in
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33 371 physiological variables within and among taxa (Figs. 1, 4), in which gross primary productivity
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35 372 (GPP) is directly influenced by temperature and moisture availability, while other state variables
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37 373 such as net primary productivity (NPP), leaf area index (LAI), and aboveground biomass (AGB)
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39 374 are regulated by additional downstream processes that may decouple their variability from
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41 375 climate variability (Fig. 1). Hence, in most models, GPP variability is the most sensitive to
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43 376 drought variability (Fig. 4, Supplemental Table 1). In all models, sensitivity of forest
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45 377 composition to drought variability seems to be most closely linked to sensitivity of NPP. NPP
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47 378 sensitivity tended to be higher in low-diversity models such as JULES-TRIFFID (Figure 4,
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3 379 Supplemental Table 1). Higher diversity through more tree types or taxa was associated with
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5 380 higher compositional variability and reduced sensitivity to drought (Figure 3, Table 1,
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7 381 Supplemental Figure 2).

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10 382 Models with more detailed representation of plant ecophysiology and either demography
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12 383 or disturbance (e.g., ED2, LPJ-GUESS, LPJ-WSL) also tended to have lower biomass sensitivity
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14 384 to hydroclimate variability (Fig. 4) and agree more closely with observations (Fig. 3). Biomass
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16 385 sensitivity to drought variability in our model ensemble was similar to NEE sensitivity in all
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18 386 models except LPJ-GUESS (Fig. 4, Supplemental Table 1). LINKAGES and JULES-TRIFFID
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20 387 may be overly sensitive to hydroclimate variability for entirely different reasons. LINKAGES
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22 388 has a fairly simple representation of ecophysiological processes while being able to represent
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24 389 species-level demographic dynamics (Table 1). In contrast, JULES-TRIFFID contains a
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26 390 sophisticated representation of ecophysiology but for only two tree PFTs and five PFTs total
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28 391 (Table 1). The other models tend to be more intermediate cases, with intermediate to more
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30 392 sophisticated representations of both ecophysiology and vegetation dynamics.
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394 Discussion

395 Over the last millennium (850-1850 A.D.), both paleodata networks and model
396 simulations suggest that spatial patterns in forest composition and biomass variability in
397 northeastern and upper midwestern United States are governed more by spatial variations in
398 ecosystem sensitivity and less by spatial variations in exposure to climate variability. Ecotonal
399 regions such as the prairie-forest border have higher variability in composition and structure than
400 areas of high PDSI variability (Fig. 2). The intermodel comparisons suggest that added
401 complexity allows slow-to-change variables such as composition and biomass to be insensitive to
402 climate variability at centennial scales despite sensitivity of fast-changing ecophysiological

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3 403 processes such as gross and net primary productivity (Fig. 4). Incorporation of ecological
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5 404 processes and characteristics such as diversity and demography all tend to reduce simulated
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8 405 climate sensitivity and better align simulations with observations (Figs. 3, 4).
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10 406 These analyses represent a milestone towards the goal of more comprehensive and
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12 407 rigorous data-model comparisons for timescales and time periods extending beyond the
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14 408 instrumental record. Common challenges for multi-centennial data-model comparisons include
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17 409 1) a need for process-informed statistical models of inference for paleoecological data, 2)
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19 410 generally lower temporal resolution in paleoecological data than in model simulations and with
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21 411 more latent variables than for the instrumental period, 3) biases in paleoclimatic simulations
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23 412 leading to biases in ecosystem model simulations, and 4) differences among models in driver
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25 413 datasets and represented processes. The pollen-vegetation models used in our study include
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27 414 processes for pollen productivity and dispersal that translates relative pollen abundances into
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29 415 metrics of forest composition and biomass that can be directly compared to those produced by
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31 416 ecosystem models (Paciorek & McLachlan 2009; Dawson *et al.* 2016). We further increased the
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33 417 commensurability between centennially resolved pollen-based quantifications of forest change
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35 418 and higher-frequency information from tree rings and ecosystem models by using GAMs to
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37 419 achieve time series with similarly temporally smoothed properties (Simpson 2018). By focusing
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39 420 on time series variability rather than directly comparing magnitude and timing of change in
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41 421 specific geographic locations or taxonomic groupings we were able to overcome documented
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43 422 ecosystem model biases arising from driver, process, and parameter limitations (Matthes *et al.*
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45 423 2016; Dietze 2017). Finally, we leveraged differences in process representation among models
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47 424 as a means of evaluating the importance of specific ecosystem processes for producing emergent
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3 425 patterns of climate sensitivity that are consistent with paleoecological data (Medlyn *et al.* 2015;
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5 426 McLachlan & PaleON Project 2018).

7 427 Prior studies have indicated that forest composition and growth is sensitive to climate
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9 428 variability at annual to centennial scales (Shuman *et al.* 2004; Allen *et al.* 2010; Thom *et al.*
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11 429 2019), yet there is also increasingly strong evidence that tree-climate relationships are non-
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13 430 stationary and subject to multiple interacting factors, leading to spatially complex forest
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15 431 responses to climate change (Girardin *et al.* 2016) and variations in climatic sensitivity across
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17 432 space and time (Rollinson *et al.* in press; Thom *et al.* 2019; Peltier & Ogle 2020; Wilmking *et al.*
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19 433 2020). Several possible explanations exist for the reporting here of generally low sensitivity of
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21 434 forest composition and biomass to hydroclimate in reconstructions (Fig. 2). First, this apparent
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23 435 insensitivity may be due to the temporal grain of this study. The centennially resolved temporal
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25 436 grain of our analyses limits detection of annual-scale growth variations, the effects of stochastic
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27 437 or short-lived extreme events such as sub-decadal to decadal drought (Breshears *et al.* 2005;
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29 438 Allen *et al.* 2010; Seidl *et al.* 2011), or disturbance events such as fire and pest outbreaks, unless
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31 439 these are large enough to cause stand-replacing mortality events. Disturbance processes are
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33 440 often unrepresented in ecosystem models or treated as purely stochastic and with implicit
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35 441 assumptions of landscape-scale equilibria (Seidl *et al.* 2011; Fisher *et al.* 2018; McCabe &
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37 442 Dietze 2019). Of the ecosystem models used here, LPJ-WSL and LPJ-GUESS included fire in
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39 443 their simulations as a semi-mechanistic process following GLOBFIRM (Thonicke *et al.* 2001),
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41 444 which estimates burned area as a function of daily fire probabilities that are a function of fuel
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43 445 moisture and fuel load threshold. These models showed dampened biomass sensitivity to
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45 446 hydroclimate variability that was more closely aligned with observations (Fig. 4), but so did
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47 447 ED2, which lacked fire. Hence, process representation of fire or similar semi-stochastic
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3 448 disturbances is not a clear differentiator among modelled estimates of ecosystem climate
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5 449 sensitivity.

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8 450 Second, apparent climate sensitivity might increase if the temporal extent was increased
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10 451 to include larger climate variations during the Holocene and last deglaciation. Although the last
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12 452 millennium includes climatic events such as the Medieval Climate Anomaly and Little Ice Age
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14 453 (PAGES 2k Consortium 2013), these climate variations appear to have been muted relative to
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16 454 earlier hydroclimate and temperature variations (Fischer *et al.* 2018). During the Holocene,
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18 455 hydroclimatic variability around the North Atlantic appears to have been an important driver of
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20 456 forest compositional changes and the collapses of individual tree species (Shuman *et al.* 2019).
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22 457 Large vegetation changes associated with the abrupt temperature variations of the Younger
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24 458 Dryas and last deglaciation are well documented (Williams *et al.* 2011), but the temporal extent
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26 459 of this study was constrained by the temporal extent of the last-millennium PMIP3/CMIP5
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28 460 simulations used to drive ecosystem models (Braconnot *et al.* 2011; Taylor *et al.* 2012). As the
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30 461 next generation of transient Holocene simulations become available, the conclusions reached
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32 462 here about low apparent sensitivity can be revisited.

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34 463 Third, this paper focuses on spatial patterns of climate and ecosystem variability, whereas
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36 464 most prior paleoecological studies have tended to focus on temporal variations (Shuman *et al.*
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38 465 2004; Booth *et al.* 2012). Our analyses of low sensitivity are consistent with recent
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40 466 dendroecological studies of climate-driven rates of tree growth, which are quickly shifting from
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42 467 assumptions of stationary tree-climate relationships to demonstrations of spatially complex forest
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44 468 responses (Girardin *et al.* 2016) and variations in climatic sensitivity varies across space and
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46 469 time (Rollinson *et al.* in press; Thom *et al.* 2019; Peltier & Ogle 2020; Wilmking *et al.* 2020).
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48 470 By focusing on spatial variations in ecosystem variability over the last millennium, our analyses
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3 471 suggest spatial variation in ecosystem properties are a more important regulator than spatial
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5 472 variations in climate exposure. Finally, uncertainties in the proxy-based reconstructions may
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7 473 lower correlations as detrending techniques used to remove non-climatic signals such as age
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9 474 effects may dampen estimates of centennial-scale variability (Allen *et al.* 2018; Esper *et al.*
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11 475 2018). Despite lower PDSI variability in the LBDA than model drivers, we do not think that
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13 476 spatial variability in hydroclimate variability in the empirical dataset is too low to detect effects
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15 477 on ecosystem variability. For example, hydroclimate data syntheses for the last 2000 years
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17 478 suggest opposite patterns of hydroclimate variations between Minnesota/Wisconsin and New
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19 479 England, which explain 30% of variance in the hydroclimate records (Shuman *et al.* 2019).

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24 480 Process-based ecosystem models are the main vehicle for forecasting climate-driven
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26 481 ecosystem dynamics across a range of timescales and in principle are better able to accommodate
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28 482 past and future no-analog climates (Williams & Jackson 2007; Veloz *et al.* 2012). However, all
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30 483 ecosystem models face tradeoffs in their ability to represent taxonomic or functional diversity
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32 484 versus detailed ecophysiological processes that drive ecosystem change (Fisher *et al.* 2018).
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34 485 Process-based ecosystem models will never be able to capture the full complexity of ecosystems
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36 486 nor perfectly reproduce the patterns of climatological or ecological variability observed in the
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38 487 past due to observational uncertainties and incomplete constraints of many processes and
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40 488 parameterizations (Dietze 2017). This paper has shown how multiple paleoecological data
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42 489 streams can be combined with harmonized paleoclimatic simulations and multiple terrestrial
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44 490 ecosystem models to gain new insight into a) how diversity and biological processes can dampen
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46 491 ecosystem sensitivity to drought variability at broad spatial scales and b) the importance of
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48 492 complex representations of these aspects of ecosystems to achieve better agreement with the
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50 493 data. Nevertheless, these analyses followed a traditional approach in which past ecosystem
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3 494 reconstructions and simulations were run independently and compared at the final stage of
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5 495 analysis. The next major step forward is to move to a full data-assimilation framework, in which
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7 496 paleoecological observations and simulations are combined to overcome systematic biases in
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9 497 model drivers, parameterization, and output to better evaluate paleoecological change using
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11 498 mechanistic process-based frameworks (McLachlan & PaleON Project 2018). Through this
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13 499 iterative process that draws upon an ever-growing and diversifying suite of observational data
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15 500 streams (Farley *et al.* 2018), we can better understand the mechanisms regulating forest
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17 501 sensitivity to climate variability across a broad range of timescales and thereby better forecast
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19 502 future forest dynamics in a complex and rapidly changing world.
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33
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35
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37
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39
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41
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44 513 descriptive purposes only and does not imply endorsement by the U.S. Government.
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49 514 50 515 **References**

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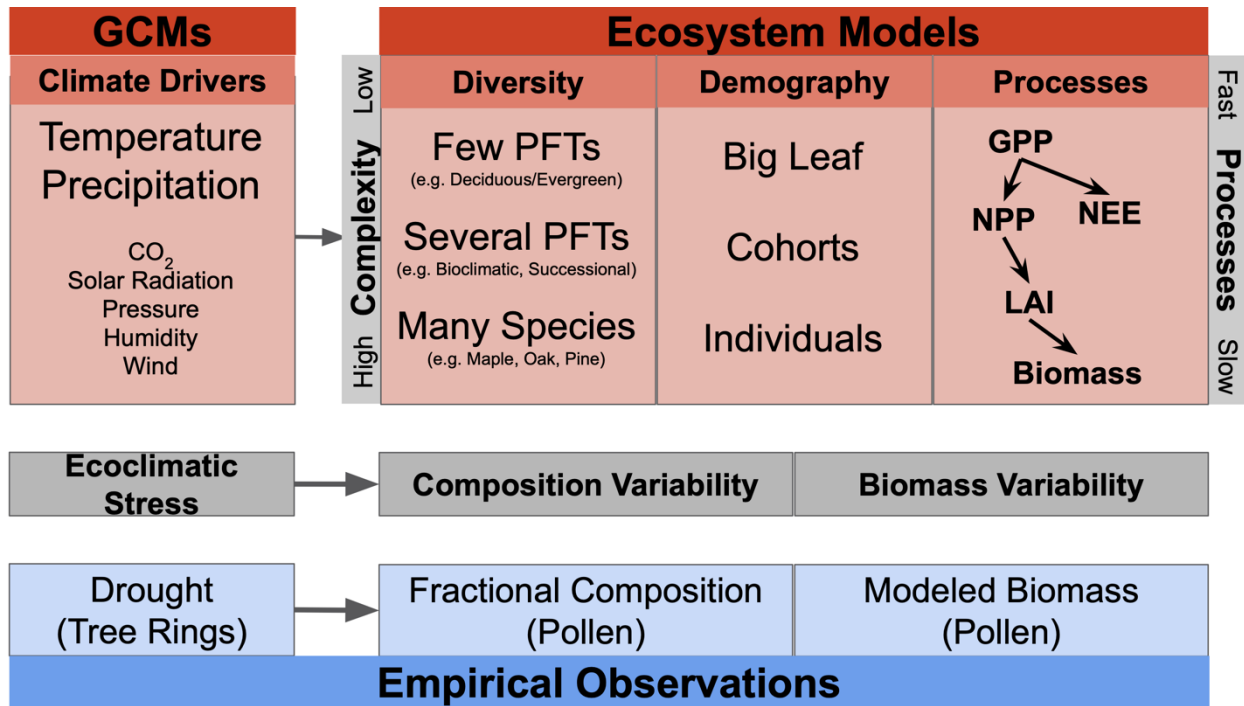
694 **Manuscript Tables**

695 **Table 1:** Comparison of 1) ecosystem model complexity, based on representation of diversity,
 696 demographic, and ecophysiological processes with 2) variability in forest composition (Comp) and
 697 biomass (Biom) and sensitivity to hydroclimate variability. Variability is a normalized metric of total
 698 change in the centennially resolved time series. Sensitivity is presented as the slope and standard error of
 699 linear regression between composition or biomass variability and hydroclimate variability. PFT = plant
 700 functional types. For sensitivity columns, * indicates slopes significantly different from zero ($p < 0.05$); †
 701 indicates model slope significantly different from pollen ($p < 0.05$).

| Data Source & Model Name | Tree Diversity Representation | Demographic Representation | Vegetation Processes | Comp. Var. (SD) | Comp. Sens. (SE) | Biom. Var. (SD) | Biom. Sens. (SE) |
|--------------------------|--------------------------------|----------------------------|---|-------------------|--------------------|-------------------|--------------------|
| Pollen: STEPPS, ReFAB | Genera: 12 trees | relative abundance | [implicit] | -2.032 (0.617) | 0.026 (0.019) | -7.798 (0.770) | -0.156 (0.119) |
| ED2 | PFTs: 5 tree | cohort | photosynthesis, allocation, cross-PFT competition, cross-cohort competition | -7.156 (0.514) | 0.118 (0.018)*† | -7.505 (0.446) | -0.079 (0.027)* |
| LINK-AGES | Species: 15 tree | individual | cross-PFT competition, cross-cohort competition | -6.598 (0.478) | 0.074 (0.018)* | -6.741 (0.999) | 0.230 (0.028)*† |
| LPJ-GUESS | PFTs: 6 tree, 1 grass | cohort | photosynthesis, allocation, cross-PFT competition, cross-cohort competition | -7.290 (0.452) | 0.056 (0.018)* | -7.379 (0.597) | -0.069 (0.027)* |
| LPJ-WSL | PFTs: 5 tree, 1 grass | PFT | photosynthesis, allocation, cross-PFT competition, cross-PFT competition | -7.829 (0.943) | 0.252 (0.018)*† | -7.106 (0.964) | -0.020 (0.027) |
| JULES-TRIFFID | PFTs: 2 Tree, 2 grass, 1 shrub | PFT | Photosynthesis, allocation, cross-PFT competition | -8.633 (1.075) | 0.411 (0.022)*† | -8.639 (0.952) | 0.203 (0.033)*† |

702

703 Manuscript Figures



704 **Figure 1:** Overview of the unified conceptual framework (gray boxes) for parallel analysis of
 705 empirical data (blue boxes) and model output (red boxes). For ecosystem models, we describe
 706 the latent climatic and ecosystem processes that are unobservable in paleoecological data and
 707 differences among models in complexity. Complexity here is organized into three categories: 1)
 708 diversity, ranging from a few plant functional types (PFTs) to many species; 2) demography,
 709 ranging from ‘big leaf’ models with no explicit treatment of forest demography to models with
 710 individual trees; and 3) ecophysiological processes. Changes in forest biomass emerge from
 711 latent ecophysiological processes including gross primary productivity (GPP), net primary
 712 productivity (NPP), net ecosystem exchange (NEE), and leaf area index (LAI).
 713 Ecophysiological processes are controlled by model representation of higher-level vegetation
 714 processes (Table 1). Latent model drivers, processes, and states (red boxes) result in estimates
 715 of forest composition and biomass that can be compared to paleoecological data products (blue
 716 boxes). Models vary in complexity due to design philosophy and tradeoffs between model
 717 complexity and computational speed.

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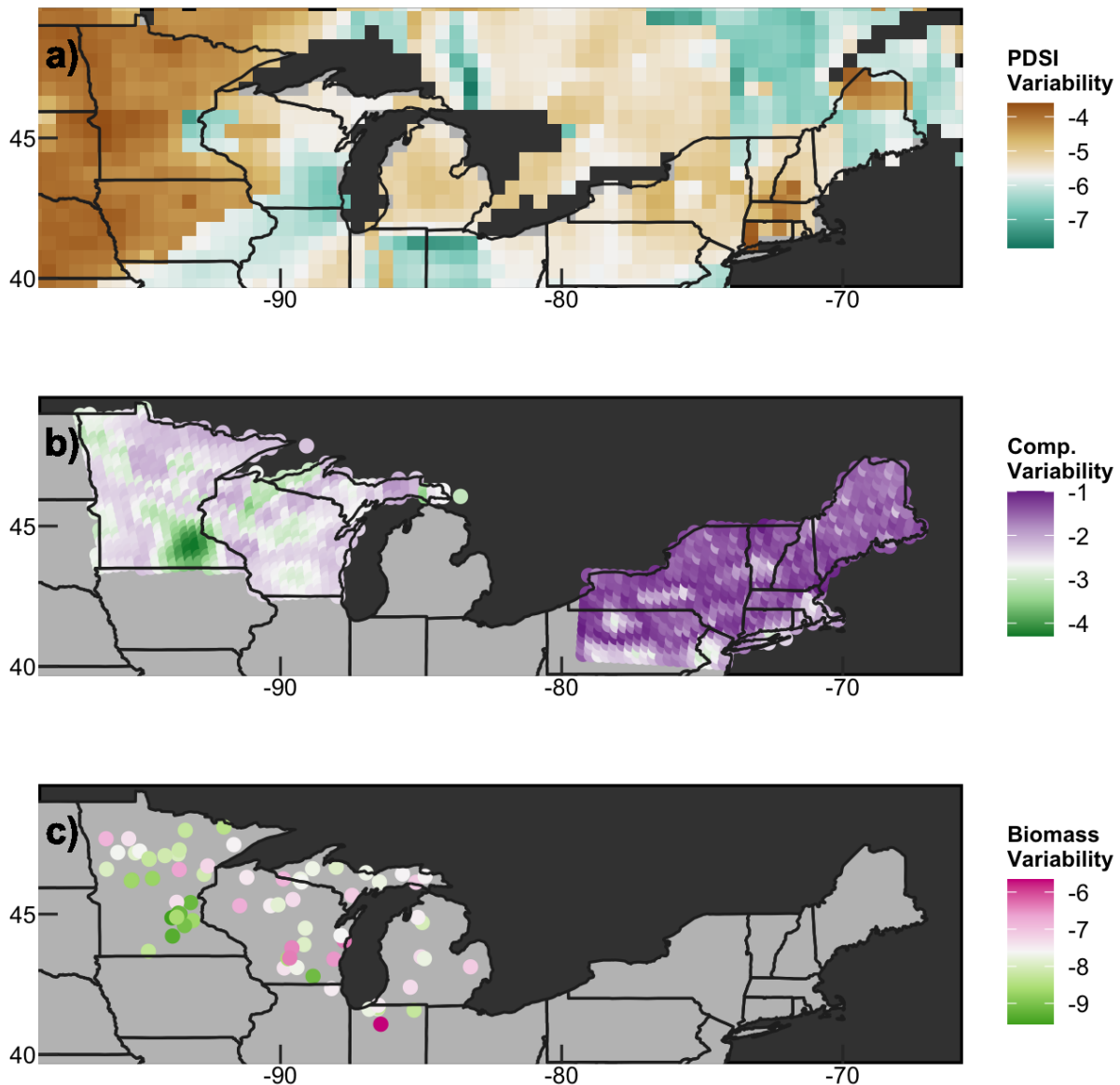
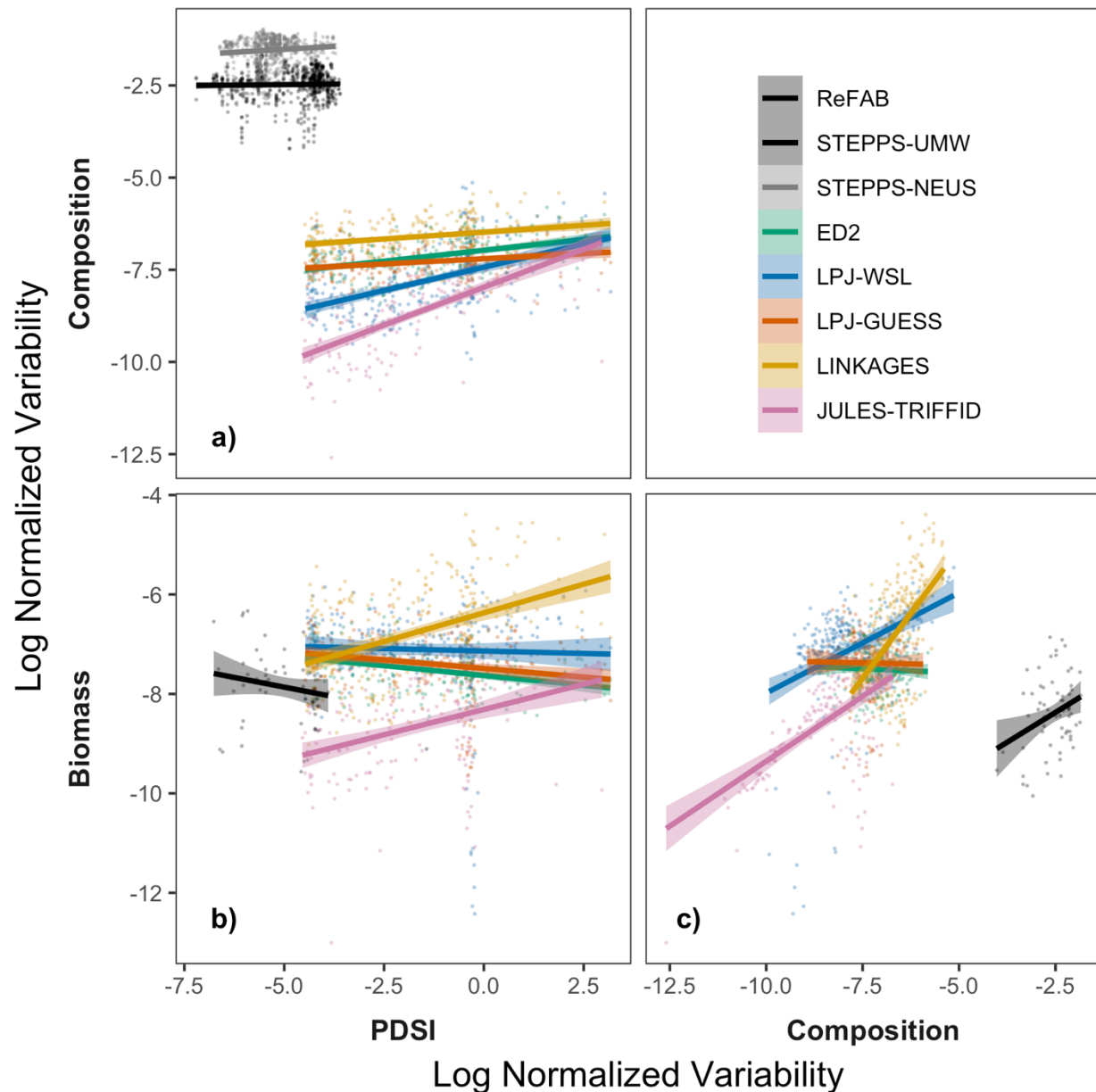


Figure 2: Spatial distribution of inferred temporal variability for 850 to 1850 AD for a) drought (PDSI) from the Living Blended Drought Atlas (44), b) forest composition from the STEPPS pollen-vegetation model (8, 24), and c) forest aboveground biomass from the ReFab pollen-biomass model (7). All variability estimates were divided by mean to facilitate inter-variable comparison (*Methods*). Spatial extents of compositional and biomass reconstructions are uneven across the study domain, as is the temporal extent of reconstructed drought variability (Supplemental Figure 1). Empirical comparisons of composition or biomass variability with drought variability are restricted to the common temporal extents for each location. In the log scale, negative values indicate locations with low variability whereas more positive values indicate high variability.

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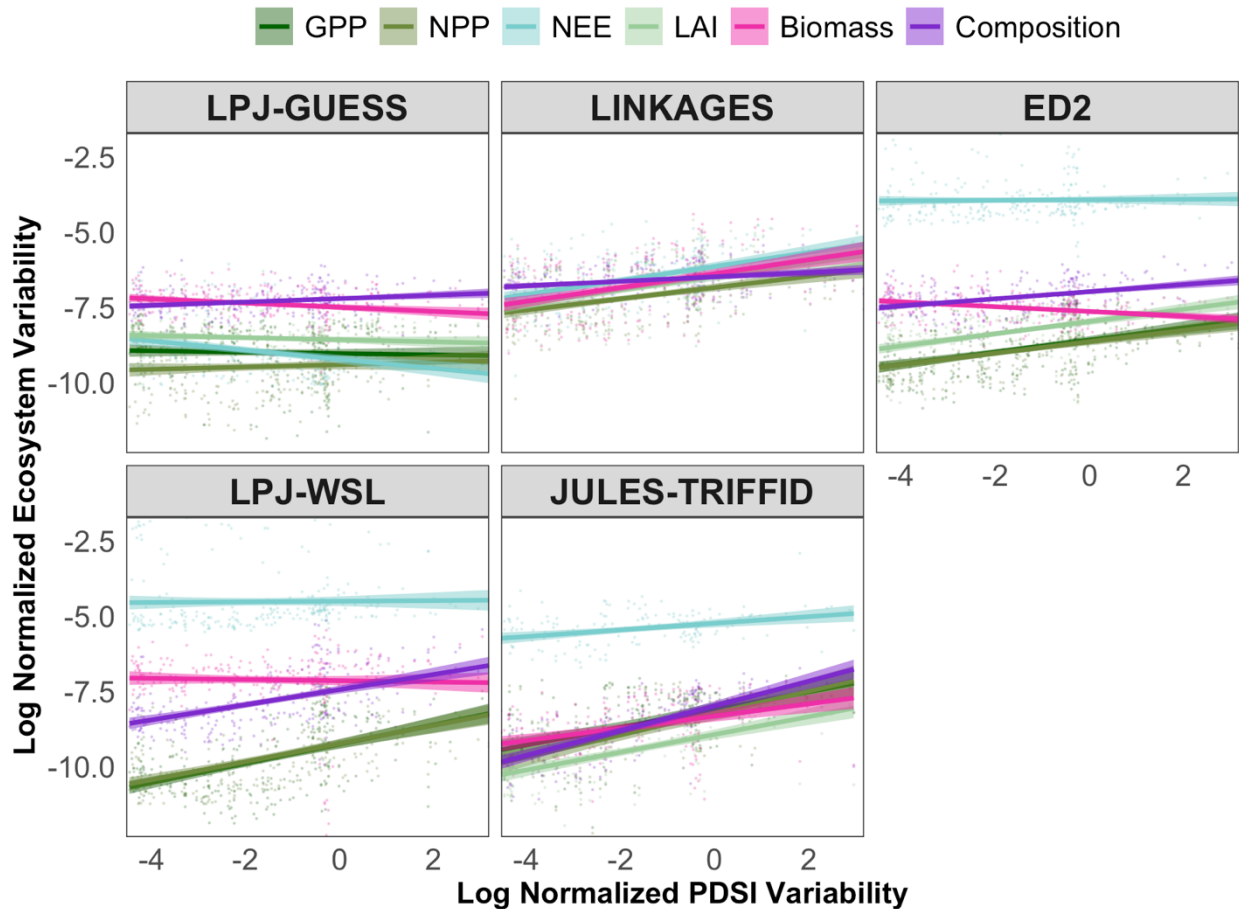
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Figure 3: Inferred (black, gray) and simulated (colors) sensitivity of variability of forest composition and biomass to ecohydrological variability (PDSI) (a,b) and of biomass variability to compositional variability (c). Inferred variables suggest weak to no correlation (low sensitivity) between climate variability and ecosystem variability (composition and biomass). In contrast, ecosystem models generally simulate higher sensitivity of ecosystems to climate variability. Inferred compositional (STEPPS) and biomass (ReFAB) variability are positively correlated, while this relationship varied among models. In the log scale, negative values indicate locations with low variability whereas more positive values indicate high variability.



746
747 **Figure 4:** Diagnosing the observed and latent relationships among ecohydrological variability
748 and variability in forest composition, structure, and function in five terrestrial ecosystem models.
749 Models in the top row (LPJ-GUESS, LINKAGES, ED2) have individual- or cohort-level
750 representation of demography whereas those in the bottom row (LPJ-WSL, JULES-TRIFFID) do
751 not simulate demography. All models showed positive correlations between composition and
752 drought variability, but some models showed positive biomass sensitivities (LINKAGES,
753 JULES-TRIFFID) while others were negative (ED2, LPJ-WSL, LPJ-GUESS). In all models,
754 composition sensitivity to hydroclimate variability was most similar to NPP whereas biomass
755 sensitivity tended to mirror NEE. In the log scale, negative values indicate locations with low
756 variability whereas more positive values indicate high variability.

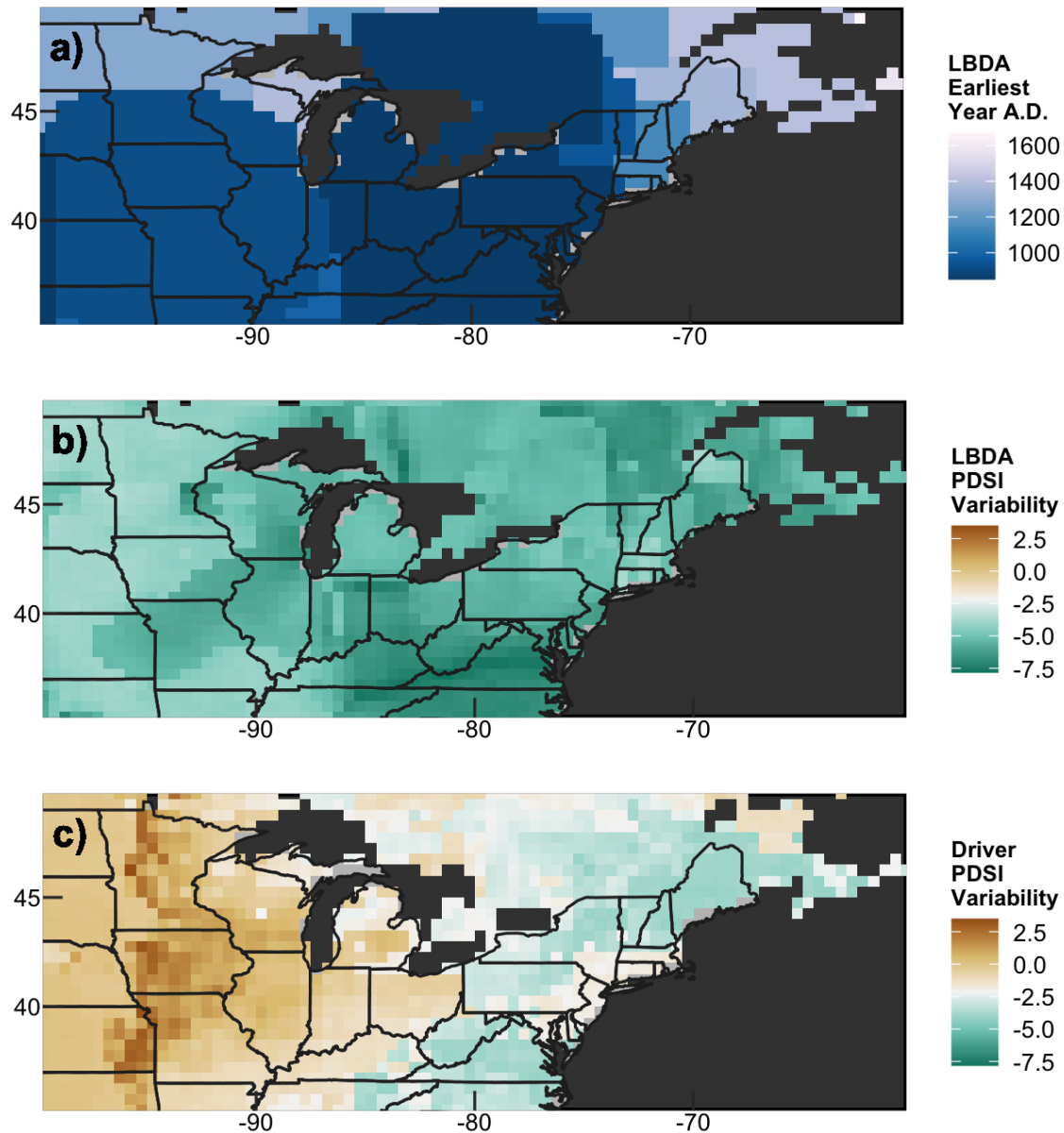
757 **Supplemental Tables**

758 **Supplemental Table 1:** Sensitivity of latent state variability to hydroclimate (PDSI) variability
 759 in ecosystem models and pollen data products. Sensitivity is presented as the mean and standard
 760 error slope from log-log regression; * indicates slopes significantly different from zero ($p < 0.05$).
 761 LINKAGES does not simulate GPP. LAI output was not available for LPJ-WSL.

| Model | GPP | NPP | NEE | LAI | Biomass | Composition |
|---------------|-------------------|-------------------|--------------------|-------------------|--------------------|----------------|
| Pollen | | | | | -0.156 (0.119) | 0.026 (0.019) |
| ED2 | 0.201 (0.028)* | 0.190 (0.025)* | 0.008 (0.024) | 0.203 (0.024)* | -0.079 (0.015)* | 0.118 (0.017)* |
| LPJ-WSL | 0.320 (0.033)* | 0.301 (0.033)* | 0.010 (0.034) | | -0.020 (0.034) | 0.252 (0.029)* |
| LPJ-GUESS | -0.022 (0.031) | 0.038 (0.034) | -0.152 (0.031)* | -0.034 (0.022) | -0.069 (0.020)* | 0.056 (0.015)* |
| LINKAGES | | 0.186 (0.027)* | 0.232 (0.030)* | 0.222 (0.031)* | 0.230 (0.033)* | 0.074 (0.016)* |
| JULES-TRIFFID | 0.294 (0.051)* | 0.365 (0.051)* | 0.110 (0.028)* | 0.295 (0.035)* | 0.203 (0.038)* | 0.411 (0.033)* |

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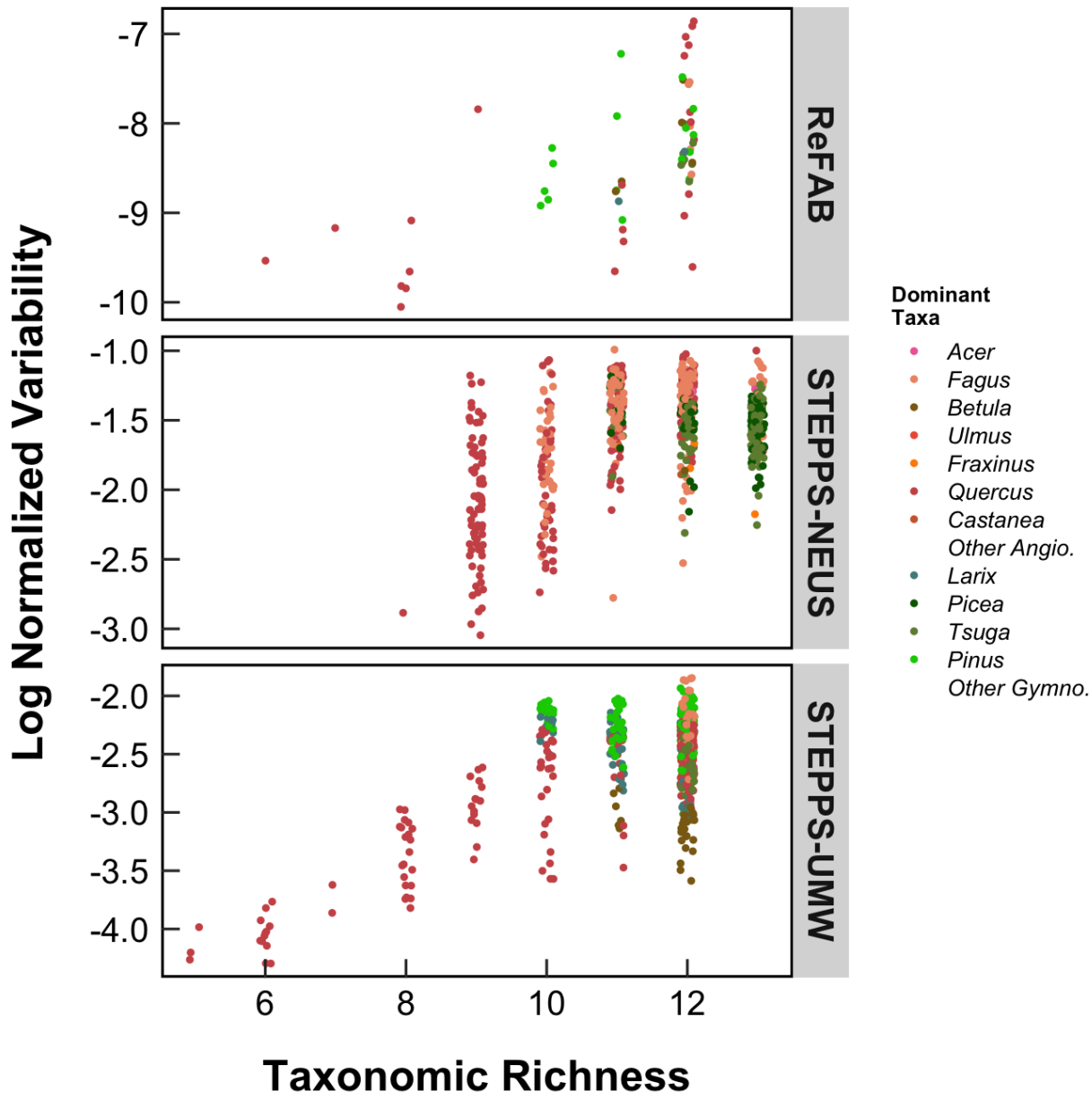
763 Supplemental Figures



764
 765 **Supplemental Figure 1:** Comparison of log normalized PDSI variability in empirically-inferred
 766 reconstructions from the Living Blended Drought Atlas (LBDA, 41, a, b) and model drivers (c).
 767 Due to the regional differences in the length of tree-ring chronologies available for PDSI
 768 reconstruction, the temporal extent of analyses involving LBDA drought is uneven across space.
 769 Overall, model drivers had greater PDSI variability than seen in the LBDA, but both datasets
 770 show greater variability in the western region of the study domain.
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Supplemental Figure 2: Relationship between taxonomic richness and log normalized biomass (ReFAB) and composition (STEPPS) variability in pollen-inferred datasets.

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