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

Authors:

1. **Christine R. Rollinson***, crollinson@mortonarb.org
    a. Center for Tree Science, The Morton Arboretum, 4100 Illinois Route 53, Lisle, IL, 60532
2. **Andria Dawson,** andria.dawson@gmail.com
    a. Department of General Education, Mount Royal University, Calgary, Alberta, T3E 6K6, Canada
3. **Ann M. Raiho**, ann.raiho@gmail.com
    a. Department of Biological Sciences, University of Notre Dame, 100 Galvin Life Science Center, Notre Dame, IN, 46556,
4. **John W. Williams**, jwwilliams1@wisc.edu, jww@geography.wisc.edu
    a. Department of Geography and Center for Climatic Research, University of Wisconsin-Madison, Madison, WI 53704
5. **Michael C. Dietze**, dietze@bu.edu orcid:0000-0002-2324-2518
    a. Department of Earth and Environment, Boston University, 685 Commonwealth Ave, Boston, MA 02215
6. **Thomas Hickler**, thomas.hickler@senckenberg.de
    a. Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Senckenberganlage 25, 60325 Frankfurt/Main, Germany
    b. Department of Physical Geography, Goethe University, Frankfurt/Main, Germany
7. **Stephen T. Jackson**, jackson@uwyo.edu; stjackson@usgs.gov
    a. Southwest Climate Adaptation Science Center, US Geological Survey,
    b. Department of Geosciences, University of Arizona, Tucson, AZ 85721
8. **Jason McLachlan,** Jason.S.McLachlan.2@nd.edu, jmclachl@nd.edu
    a. Department of Biological Sciences, University of Notre Dame, 100 Galvin Life Science Center, Notre Dame, IN, 46556
9. **David JP Moore**, davidjpmoore@email.arizona.edu
    a. School of Natural Resources, University of Arizona, Tucson, AZ, 85721
10. **Benjamin Poulter**, benjamin.poulter@nasa.gov
    a. NASA GSFC, Biospheric Sciences Lab., Greenbelt, MD 20771
11. **Tristan Quaife**, t.l.quaife@reading.ac.uk
    a. Department of Meteorology, University of Reading, Reading, RG6 6BB UK
12. **Jörg Steinkamp**, steinkamp.joerg@gmail.com
    a. Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Frankfurt/Main, Germany
    b. Johannes Gutenberg University, Mainz, Germany
13. **Mathias Trachsel**, mtrachs@gmail.com
    a. Department of Geography, University of Wisconsin-Madison, Madison, WI 53704

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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 and output are in the process of being archived on the ORNL DAAC. 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 best-suited to archiving 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/PalEON-Project/EcosystemVariability

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Corresponding Author: Christine R. Rollinson, Center for Tree Science, The Morton Arboretum, 4100 Illinois Route 53, Lisle, IL 60532; phone: 630-719-2422; email: crollinson@mortonarb.org

Abstract

Forecasts of forest responses to climate variability are governed by climate exposure and ecosystem sensitivity, but ecosystem model projections and process representations are under-constrained by data at multidecadal and longer timescales. Here, we assess ecosystem sensitivity to centennial-scale hydroclimate variability, by comparing dendroclimatic and pollen-inferred reconstructions of drought, forest composition and biomass for the last millennium with five ecosystem model simulations. In both observations and models, spatial patterns in ecosystem responses to hydroclimate variability are strongly governed by ecosystem sensitivity rather than climate exposure. Ecosystem sensitivity was highest in simpler models and higher than observations, suggesting that interactions among biodiversity, demography, and ecophysiology processes dampen the sensitivity of forest composition and biomass to climate variability and change. By integrating ecosystem models with observations from timescales extending beyond the instrumental record, we can better understand and forecast the mechanisms regulating forest sensitivity to climate variability in a complex and changing world.

Introduction

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

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

125 change, various simplifying assumptions, and tradeoffs between computational tractability and
126 process complexity (De Kauwe *et al.* 2013; Walker *et al.* 2014; Medlyn *et al.* 2015). Previous
127 data-model comparisons have returned mixed evidence about whether models underestimate or
128 overestimate the sensitivity of forest processes such as net primary productivity (NPP) and
129 mortality to climate change (Schimel *et al.* 2015; Walker *et al.* 2015; Rollinson *et al.* 2017). As a
130 result, projections of forest compositional and structural responses to climate change have high
131 uncertainty, limiting their utility for ecological forecasting and science-based adaptation
132 (Friedlingstein *et al.* 2014).
133 Several challenges have traditionally hindered the joint analysis and integration of
134 terrestrial ecosystem models and paleoecological data to better constrain modeled responses to
135 climate variations at multi-decadal and longer timescales. First, the raw observations collected
136 from fossil pollen records (counts of individual pollen taxa) have no direct counterparts in
137 ecosystem models. Bayesian hierarchical models are providing new process-based
138 approaches to infer emergent ecosystem properties from fossil pollen records, such as forest
139 composition, diversity, percent cover, and biomass (Raiho *et al.* in prep; Blarquez & Aleman
140 2016; Dawson *et al.* 2016), but the number of state variables that can be estimated from
141 paleoecological data remains small relative to the number of latent (i.e. unobservable) variables
142 simulated by ecosystem models (Fig. 1). Second, pre-instrumental model-data comparisons
143 are complicated by reliance on driver datasets derived from general circulation models (GCMs).
144 GCMs generally capture macroscale spatial patterns and low-frequency trends in climate but
145 are unable to fully capture the complexity and stochasticity of local to regional-scale weather
146 phenomena at the subdaily resolution needed to drive ecosystem models, resulting in
147 systematic spatial and temporal biases in model simulations (Anav *et al.* 2013; Matthes *et al.*
148 2016; Dietze *et al.* 2018). Third, the native temporal resolution varies between paleodata and
149 models and requires a temporal standardization. Due to these challenges, the predicted
150 sensitivity of ecosystem model state variables such as forest composition and biomass to

151 climate change is largely unvalidated by observations at multidecadal and longer timescales,
152 resulting in wide divergence among terrestrial ecosystem models in their 21st-century
153 projections (Friedlingstein *et al.* 2006, 2014). Fourth, terrestrial ecosystem models vary widely in
154 represented processes, which can challenge intermodel comparisons but also provide insight
155 into key governing ecological processes when data-model discrepancies emerge.
156 Here, we seek to establish the patterns of forest ecosystem and climate variability in the
157 north-central and northeastern US for the last millennium (850-1850 C.E.) and identify the
158 mechanisms underpinning both forest ecosystem sensitivity and observed data-model
159 discrepancies. In these analyses, we test hypotheses about the relative importance of
160 hydroclimate exposure and climate sensitivity as determinants of ecosystem variability. We also
161 hypothesize that ecosystem models will be overly sensitive to hydroclimate variability due to
162 insufficient representation of ecophysiological and demographic processes that can dampen
163 climate responses. To this end, we present a novel series of data-model and model-model
164 comparisons that are designed to overcome traditional barriers to data-model intercomparison
165 for pre-instrumental times. Our analyses combine dendroclimatic indices of drought, recently
166 published Bayesian spatiotemporal estimates of forest composition and biomass derived from
167 pollen that provide independent checks on last-millennium simulations from five terrestrial
168 ecosystem models for the northeastern and upper midwestern United States. The data-model
169 comparisons discriminate among differing representations of forest processes, while the model-
170 model comparisons help diagnose causal relationships among ecological processes, changes in
171 forest states, and climate variability (Fig. 1). To test hypotheses while also overcoming known
172 geographic biases in the model simulations of ecosystem state such as forest composition that
173 source back to biases in the climate model drivers (Matthes *et al.* 2016), we develop a new
174 variability metric that we apply to the data and model-derived products that focuses on
175 comparisons among variability of hydroclimate, composition, and biomass (Fig. 1). Our results
176 indicate that at centennial timescales, spatial patterns in the variability of forest composition and

177 biomass are regulated by ecological factors such as ecotonal position and complexity rather
178 than climate exposure as defined by the local magnitude of climate variability.
179
180 **Materials & Methods**
181 *Overview*
182 We employ a combination of data-model and model-model comparisons (Fig. 1) in which
183 we combine paleoclimatic and paleoecological datasets to draw inferences about past variations
184 in hydroclimate and forest composition and biomass. The temporal domain of this study is 850-
185 1850 AD and is bounded by the temporal extent of the climate drivers (850 AD) and time of
186 settlement-era tree surveys (ca. 1850 AD). In our study, 'data' refers to observation-based
187 statistical models of past drought, forest composition, and biomass, reconstructed from tree
188 rings, historical tree surveys, and networks of fossil pollen records. These data-based
189 inferences are fully independent of the ecosystem model simulations. Model-based
190 comparisons are from the PalEON Ecosystem Model Intercomparison Project (PEMIP)
191 (Rollinson *et al.* 2017), which used spatially and temporally downscaled past climate simulations
192 from the Fifth Coupled Model Intercomparison Project (CMIP5) as drivers. Comparisons among
193 ecosystem model simulations and empirical data rely on normalized values compared in
194 environmental space, rather than geographic space, in order to reduce the effects of any bias in
195 the climate drivers in our analyses and to focus on sensitivity of ecosystems to climate variability
196 (Supplemental Figure 1).
197
198 *Observational Datasets*
199 The inferred datasets leverage recent advances in pollen-vegetation modeling (Dawson
200 *et al.* 2016), a form of proxy system modeling (Evans *et al.* 2013) in which ecosystem state
201 variables such as composition and biomass are estimated along with associated observational
202 uncertainties. Of the three inferred datasets used here, two were derived from networks of

fossil pollen records provided by individual data contributors and the Neotoma Paleoecology Database and were calibrated against historical surveys of forest composition and structure from the early stages of EuroAmerican settlement (Liu *et al.* 2011; Dawson *et al.* 2016; Goring *et al.* 2016; Kujawa *et al.* 2016; Paciorek *et al.* 2016). Pollen-based inferences are based on statistical pollen-vegetation models (PVMs) called STEPPS and ReFAB, and represent fractional vegetation composition and total woody biomass, respectively, for 12 tree genera that are common elements of upper Midwest forests. STEPPS is a Bayesian hierarchical spatio-temporal model that infers fractional forest composition from networks of fossil pollen records (Paciorek & McLachlan 2009; Dawson *et al.* 2016, 2019b; Trachsel *et al.* 2020). STEPPS employs a process-based representation of pollen dispersal and production, with taxon-specific parameterizations. STEPPS is calibrated using spatial datasets of pollen samples and forest composition data, here from the settlement era ((Paciorek & McLachlan 2009; Dawson *et al.* 2016), then run for fossil pollen assemblages for other time intervals to produce posterior estimates of past forest composition. Using this framework, STEPPS: (i) explicitly characterizes uncertainty in data and processes, with posterior distributions of process parameters and state variables such as forest composition, and (ii) borrows information across space and time, allowing for spatially comprehensive estimates of composition. For both the upper Midwestern USA (UMW; Minnesota, Wisconsin, Michigan) (Dawson *et al.* 2019a) and the northeastern USA (NEUS) (Trachsel *et al.* 2020), STEPPS has been used to estimate centennially-resolved forest composition for the late Holocene (250 B.C. to 1750 A.D) at a 24 km grid; here we use the results from 850 to 1750 AD.

ReFAB also employs a similar approach to STEPPS, but focuses specifically on estimating total aboveground woody biomass (Raiho *et al.* in prep). ReFAB is calibrated using the relationship between settlement-era multivariate pollen counts and biomass from PLS surveys (Paciorek *et al.* 2019). Parameter estimates from calibration are then used to reconstruct centennially resolved biomass for 77 sites in the UMW for the last 10,000 years

(Raiho *et al.* in prep). ReFAB can characterize the uncertainty in sediment pollen age estimates, calibration parameters, the relationship between species composition and total aboveground woody biomass, and species-level allometries.

The Living Blended Drought Atlas (LBDA) provides yearly estimates of summer (mean June, July, August) Palmer Severity Drought Index (PDSI) for North America, based on networks of tree-growth chronologies (Cook *et al.* 2010; Woodhouse *et al.* 2010). We used PDSI as our measure of climate variability, because PDSI is an important predictor of forest dynamics in this domain and can also be calculated directly from the meteorological forcings used for the ecosystem model simulations (Clifford & Booth 2015; Cook *et al.* 2015). LBDA PDSIs are provided at 0.5-degree spatial grid resolution. Due to varying temporal extent of tree-growth chronologies, the temporal extent of the LBDA varies. The earliest years in this spatial domain ranged from 0 to 1671 AD, while the latest year was 2005 (Supplemental Figure 1).

Modeling Datasets

PEMIP model simulations here comprised five ecosystem models (ED2; LINKAGES; LPG-WSL; LPJ-GUESS; and JULES-TRIFFID) with dynamic vegetation run at 254 locations across the eastern and midwestern US at 0.5-degree spatial resolution. These models vary in how they characterize forest composition and carbon dynamics and range from species-based with little ecophysiological process representation (e.g. LINKAGES) to detailed ecophysiology and cohort representation, but reliance on plant functional types (PFTs; e.g. ED2, Table 1). LPJ-GUESS and LPJ-WSL both included stochastic fire disturbances in their simulations, while other models such as ED and LINKAGES include processes of tree mortality that assume landscape-scale equilibrium (Rollinson *et al.* 2017).

The PEMIP climate drivers were developed following a standard protocol (Rollinson *et al.* 2017, Supplemental Figure 1). CCSM4 output from the Paleoclimate Modeling Intercomparison Project, Phase III (PMIP3) past millennium simulations and the Coupled Model

Intercomparison Project, Phase 5 (CMIP5) historical simulations were downscaled to 0.5-degree spatial resolution and 6-hourly temporal resolution using standard protocols (Kumar *et al.* 2012; Rollinson *et al.* 2017). Soil texture is from the Harmonized World Soil Database (Wei *et al.* 2014). After the 6-hourly PEMIP climate driver datasets were created, they were then temporally averaged to meet the specific driver requirements of individual ecosystem models, which vary in temporal resolution. ED2 and JULES-TRIFFID use the full suite of 6-hourly drivers for temperature, precipitation, shortwave radiation, longwave radiation, surface pressure, specific humidity, wind speed, and carbon dioxide concentration. Meteorological drivers for the two LPJ variants include daily temperature, precipitation, and shortwave radiation plus longwave radiation for LPJ-WSL. LINKAGES only requires monthly average temperature and precipitation. Monthly temperature and precipitation were combined with soil water holding capacity computed from model driver soil texture and depth to calculate PDSI, following (Cook *et al.* 2015), but using the Thornthwaite equation for evapotranspiration (Thornthwaite & Mather 1957; Pelton *et al.* 1960) due to evapotranspiration varying among ecosystem models given the same temperature and precipitation drivers as a results of differences in model structure and parameterization. From the ecosystem models we extracted two variables that can be compared to paleoecological observations (fractional forest composition and biomass) and four latent variables (Fig. 1): gross primary productivity (GPP), net primary productivity (NPP), net ecosystem exchange (NEE), and leaf area index (LAI).

Analyses

Analyses focused on the comparison of empirical data and ecosystem model outputs of centennial-scale variability in forest composition and biomass driven by drought variability over the last 1,000 years. We first ensured temporal comparability by transforming or aggregating variables to a common centennial resolution. Second, we developed common metrics of

ecosystem and drought variability to support data-model and model-model intercomparisons and to minimize the potential effects of climate model driver bias.

With respect to temporal compatibility, STEPPS and ReFAB datasets are natively at 100-year resolution and variability was calculated as the mean of the absolute first differences between adjacent time points, using all posterior draws from these datasets and then calculating the mean variability value across posterior draws. For the annually resolved datasets (all model output, drivers, and LBDA), a generalized additive model (GAM) was used to smooth these time series to a centennial-scale resolution. For the GAM, we predicted the response variable (e.g. drought, biomass, GPP) as a function of time (year) as a thin-plate regression spline with one knot per 100 years using the *gam* function in the *mgcv* package in R (Wood 2017; Simpson 2018). From the GAM, we generated a 1000-member posterior distribution of each predicted variable through time using the error and covariance of the intercept and spline parameters. We then extracted the predicted values at 100-year intervals and calculated variability as described for STEPPS and ReFAB.

For the second step, we developed two common metrics for our comparisons: mean relative variability and sensitivity to hydroclimate variability. Mean relative variability was calculated by normalizing all variability values by dividing by the mean for the variable across the dataset (i.e. across all spatiotemporal loci for a given combination of variable and model or observational dataset). This normalization is intended to facilitate comparison among variables with different units and scales. Because each grid cell had multiple taxa, for the compositional response variable we used the variability of the taxon or plant functional type with the highest fractional composition at each location. Sensitivity to hydroclimate variability was quantified as the slope of a linear regression between variability as the independent variable and variability of the ecosystem response variable such as composition or biomass. These analyses always used the appropriate observational or modeled PDSI variability (i.e. LBDA for the pollen-inferred compositional variability; calculated PEMIP driver PDSI variability for the model-simulated

306 compositional variability) to ensure internal consistency between climatic forcing and ecosystem
307 response. For all analyses and presented results, normalized variability is log-transformed to
308 meet standard statistical assumptions of Gaussian distributions and homoscedasticity.
309
310 **Results**
311 In the observational data, variability in forest composition or biomass in the northeastern
312 US (NEUS) and upper midwestern US (UMW), did not correlate to drought variability (Table 1,
313 Figs. 2, 3) in contrast with the hypothesis that high exposure to climate variability should lead to
314 increased compositional variability. Neither the full spatiotemporal domain (Table 1) nor the
315 UMW (Fig. 3, sensitivity slope = 0.010 SE 0.018) showed a significant relationship between
316 reconstructed drought and composition variability, although the NEUS showed weak sensitivity
317 (Fig. 3, sensitivity slope = 0.065 SE 0.027). Reconstructed biomass variability (Fig 2., biomass
318 reconstructions not available for the NEUS, (Paciorek *et al.* 2019)) also was uncorrelated to
319 drought variability (Table 1) and instead showed the highest variability at the historic prairie-
320 forest ecotone (Fig. 2) (Goring & Williams 2017). In pollen-based reconstructions, composition
321 and biomass variability were weakly but positively related (Fig. 3c, R^2=0.09, slope=0.479 SE
322 0.187) and locations with higher taxonomic richness tended to have higher variability
323 (Supplemental Fig. 2).
324 Modeled ecosystem sensitivity to drought variability was generally similar to or higher
325 than observations, with less-complex models tending to have a too-high predicted sensitivity
326 relative to the empirical reconstructions (Fig. 3). Composition variability was more sensitive to
327 drought variability than in reconstructions for three of five ecosystem models (ED2, LPJ-WSL,
328 and TRIFFID), with the data-model discrepancy most pronounced in models with fewer plant
329 types or taxa (Fig. 3a, Table 1). JULES-TRIFFID, which had only two tree PFTs (deciduous and
330 evergreen), had the highest drought sensitivity (composition slope = -8.633 SE = 1.075,
331 composition sensitivity slope 0.411 SE = 0.022). LPJ-WSL and ED2, with respectively six and

five PFTs, had similar mean compositional variability (LPJ-WSL slope = -7.829 SE = 0.943, ED2 slope = -7.156 SE = 0.514), although LPJ-WSL was approximately twice as sensitive to hydroclimate variability as ED2 (Fig. 3a, Table 1, LPJ-WSL slope = 0.252 SE =0.018, ED2 slope = 0.118 SE = 0.018). LINKAGES, which simulated 15 individual species, had among the lowest sensitivity to drought variability (Fig. 3a, Table 1, composition slope = -6.598 SE = 0.478, composition sensitivity slope 0.074 SE = 0.018).

Ecosystem models with simpler representation of vegetation ecophysiology (LINKAGES, JULES-TRIFFID) also had a too-high sensitivity of biomass to drought variability relative to empirical reconstructions (Table 1, Fig. 3b). Both LINKAGES and JULES-TRIFFID showed a tight positive coupling of biomass sensitivity to drought variability, which corresponded to strong correlations between biomass and composition variability (Fig. 3c). LINKAGES showed a one-to-one relationship between composition and biomass variability, which is much stronger than reconstructions (Fig. 3c). Of all the models, only LPJ-WSL was consistent with the data in showing a weakly negative relationship between biomass and PDSI variability (Fig. 3b) while also showing a positive correlation between biomass and composition variability (Fig. 3c).

Further analysis of latent variables in the ecosystem models confirmed that variations in modeled ecosystem sensitivity to hydroclimate variability is linked to model complexity of ecosystem composition and processes (Fig. 4). There is a cascading series of linkages in physiological variables within and among taxa (Figs. 1, 4), in which gross primary productivity (GPP) is directly influenced by temperature and moisture availability, while other state variables such as net primary productivity (NPP), leaf area index (LAI), and aboveground biomass (AGB) are regulated by additional downstream processes that may decouple their variability from climate variability (Fig. 1). Hence, in most models, GPP variability is the most sensitive to drought variability (Fig. 4, Supplemental Table 1). In all models, sensitivity of forest composition to drought variability seems to be most closely linked to sensitivity of NPP. NPP sensitivity tended to be higher in low-diversity models such as JULES-TRIFFID (Figure 4, Supplemental

Table 1). Higher diversity through more tree types or taxa was associated with higher compositional variability and reduced sensitivity to drought (Figure 3, Table 1, Supplemental Figure 2).

Models with more detailed representation of plant ecophysiology and demography (e.g. ED2, the two LPJ variants) also tended to have lower biomass sensitivity to hydroclimate variability (Fig. 4) and agree more closely with observations (Fig. 3). Biomass sensitivity to drought variability in our model ensemble was similar to NEE sensitivity in all models except LPJ-GUESS (Fig. 4, Supplemental Table 1). LINKAGES and JULES-TRIFFID may be overly sensitive to hydroclimate variability for entirely different reasons. LINKAGES has a fairly simple representation of ecophysiological processes while being able to represent species-level demographic dynamics (Table 1). In contrast, JULES-TRIFFID contains a sophisticated representation of ecophysiology but for only two tree PFTs and five PFTs total (Table 1). The other models tend to be more intermediate cases, with intermediate to more sophisticated representations of both ecophysiology and vegetation dynamics.

Discussion

Over the last millennium (850-1850 A.D.), both paleodata networks and model simulations suggest that spatial patterns in forest composition and biomass variability in northeastern and upper midwestern United States are governed more by spatial variations in ecosystem sensitivity and less by spatial variations in exposure to climate variability. Ecotonal regions such as the prairie-forest border have higher variability in composition and structure than areas of high PDSI variability (Fig. 2). The intermodel comparisons suggest that added complexity allows slow-to-change variables such as composition and biomass to be insensitive to climate variability at centennial scales despite sensitivity of fast-changing ecophysiological processes such as gross and net primary productivity (Fig. 4). Incorporation of ecological

processes and characteristics such as diversity and demography all tend to reduce simulated climate sensitivity and better align simulations with observations (Figs. 3, 4).

These analyses represent a milestone towards the goal of more comprehensive and rigorous data-model comparisons for timescales and time periods extending beyond the instrumental record. Common challenges for multi-centennial data-model comparisons include 1) a need for process-informed statistical models of inference for paleoecological data, 2) generally lower temporal resolution in paleoecological data than in model simulations and with more latent variables than for the instrumental period, 3) biases in paleoclimatic simulations leading to biases in ecosystem model simulations, and 4) differences among models in driver datasets and represented processes. The pollen-vegetation models used in our study include processes for pollen productivity and dispersal that translates relative pollen abundances into metrics of forest composition and biomass that can be directly compared to those produced by ecosystem models (Paciorek & McLachlan 2009; Dawson *et al.* 2016). We further increased the commensurability between centennially resolved pollen-based quantifications of forest change and higher-frequency information from tree rings and ecosystem models by using GAMs to achieve time series with similarly temporally smoothed properties (Simpson 2018). By focusing on time series variability rather than directly comparing magnitude and timing of change in specific geographic locations or taxonomic groupings we were able to overcome document ecosystem model biases arising from driver, process, and parameter limitations (Matthes *et al.* 2016; Dietze 2017). Finally, we leveraged differences in process representation among models as a means of evaluating the importance of specific ecosystem processes for producing emergent patterns of climate sensitivity that are consistent with paleoecological data (Medlyn *et al.* 2015; McLachlan & PalEON Project 2018).

Given widespread evidence that forest composition and growth is sensitive to climate variability (Shuman *et al.* 2004; Allen *et al.* 2010; Thom *et al.* 2019), the reporting here of generally low sensitivity of forest composition and biomass to hydroclimate in reconstructions

409 may seem surprising (Fig. 2). Several possible explanations exist. First, this apparent
410 insensitivity may be due to the temporal grain of this study: the centennially resolved temporal
411 grain of our analyses limits detection of the effects of stochastic or short-lived extreme events
412 such as sub-decadal to decadal drought, which can cause massive mortality events that affect
413 centennial-scale forest composition (Breshears *et al.* 2005; Allen *et al.* 2010; Seidl *et al.* 2011).
414 At centennial scales, the effects of extreme weather may be confounded by additional
415 punctuated disturbances such as fire and pest outbreaks that are often unrepresented in
416 ecosystem models or purely stochastic and with implicit assumptions of landscape-scale
417 equilibria (Seidl *et al.* 2011; Fisher *et al.* 2018; McCabe & Dietze 2019). Second, apparent
418 climate sensitivity might increase if the temporal extent was increased to include larger climate
419 variations during the Holocene and last deglaciation. During the Holocene, hydroclimatic
420 variability around the North Atlantic appears to have been an important driver of forest
421 compositional changes and the collapses of individual tree species (Shuman *et al.* 2019). Large
422 vegetation changes associated with the abrupt temperature variations of the Younger Dryas and
423 last deglaciation are well documented (Williams *et al.* 2011), but the temporal extent of this
424 study was constrained by the temporal extent of the last-millennium PMIP3/CMIP5 simulations
425 used to drive ecosystem models (Braconnot *et al.* 2011; Taylor *et al.* 2012). As the next
426 generation of transient Holocene simulations become available, the conclusions reached here
427 about low apparent sensitivity can be revisited. Third, this paper focuses on spatial patterns of
428 climate and ecosystem variability, whereas most prior paleoecological studies have tended to
429 focus on temporal variations (Shuman *et al.* 2004; Booth *et al.* 2012). Dendroecological studies
430 of climate-driven rates of tree growth are quickly shifting from assumptions of stationary tree-
431 climate relationships to demonstrations that climatic sensitivity varies across space and time
432 (Rollinson *et al.* in press; Thom *et al.* 2019; Peltier & Ogle 2020; Wilmking *et al.* 2020). By
433 focusing on spatial variations in ecosystem variability over the last millennium, our analyses
434 suggest spatial variation in ecosystem properties are a more important regulator than spatial

variations in climate exposure. Finally, uncertainties in the proxy-based reconstructions may lower correlations as detrending techniques used to remove non-climatic signals such as age effects may dampen estimates of centennial-scale variability (Allen *et al.* 2018; Esper *et al.* 2018). Despite lower PDSI variability in the LBDA than model drivers, we do not think that spatial variability in hydroclimate variability in the empirical dataset is too low to detect effects on ecosystem variability. Hydroclimate data syntheses for the last 2000 years and accompanying EOF analyses suggest opposite loading patterns between MN/WI and New England, for both principal components 2 & 3, which together explain 30% of variance in the hydroclimate records (Shuman *et al.* 2019).

Process-based ecosystem models are the main vehicle for forecasting climate-driven ecosystem dynamics across a range of timescales and in principle are better able to accommodate past and future no-analog climates (Williams & Jackson 2007; Veloz *et al.* 2012). However, all ecosystem models face tradeoffs in their ability to represent taxonomic or functional diversity versus detailed ecophysiological processes that drive ecosystem change (Fisher *et al.* 2018). Process-based ecosystems models will never be able to capture the full complexity of ecosystems nor perfectly reproduce the patterns of climatological or ecological variability observed in the past due to observational uncertainties and incomplete constraints of many processes and parameterizations (Dietze 2017). This paper has shown how multiple paleoecological data streams can be combined with harmonized paleoclimatic simulations and multiple terrestrial ecosystem models to gain new insight into a) the patterns and controls on past ecosystem variability and b) aspects of models such as diversity and demography where complex representations are needed to achieve better agreement with the data. Nevertheless, these analyses followed a traditional approach in which past ecosystem reconstructions and simulations were run independently and compared at the final stage of analysis. The next major step forward is to move to a full data-assimilation framework, in which paleoecological observations and simulations are combined to provide joint estimates of state variables or better

constrain ecosystem model parameterizations (McLachlan & PalEON Project 2018). Through this iterative process that draws upon an ever-growing and diversifying suite of observational data streams (Farley *et al.* 2018), we can better understand the mechanisms regulating forest sensitivity to climate variability across a broad range of timescales and thereby better forecast future forest dynamics in a complex and rapidly changing world.

Acknowledgements

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References

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., *et al.* (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.*, 259, 660–684.

Allen, K.J., Villalba, R., Lavergne, A., Palmer, J.G., Cook, E.C., Fenwick, P., *et al.* (2018). A comparison of some simple methods used to detect unstable temperature responses in tree-ring chronologies. *Dendrochronologia*, 48, 52–73.

Anav, A., Friedlingstein, P., Kidston, M., Bopp, L., Ciais, P., Cox, P., *et al.* (2013). Evaluating the Land and Ocean Components of the Global Carbon Cycle in the CMIP5 Earth System Models. *J. Clim.*, 26, 6801–6843.

Blarquez, O. & Aleman, J.C. (2016). Tree biomass reconstruction shows no lag in postglacial afforestation of eastern Canada. *Can. J. For. Res.*, 46, 485–498.

Booth, R.K., Jackson, S.T., Sousa, V.A., Sullivan, M.E., Minckley, T.A. & Clifford, M.J. (2012). Multi-decadal drought and amplified moisture variability drove rapid forest community change in a humid region. *Ecology*, 93, 219–226.

Braconnot, P., Otto-Bliesner, B., Jungclaus, J. & Peterschmitt, J.-Y. (2011). The Paleoclimate Modeling Intercomparison Project contribution to CMIP5. *CLIVAR Exch.*, 16, 15–19.

494 Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., *et al.* (2005).
495 Regional vegetation die-off in response to global-change-type drought. *Proc. Natl. Acad.*
496 *Sci.*, 102, 15144–15148.
497 Charney, N.D., Babst, F., Poulter, B., Record, S., Trouet, V.M., Frank, D., *et al.* (2016).
498 Observed forest sensitivity to climate implies large changes in 21st century North
499 American forest growth. *Ecol. Lett.*, 19, 1119–1128.
500 Clifford, M.J. & Booth, R.K. (2015). Late-Holocene drought and fire drove a widespread change
501 in forest community composition in eastern North America. *The Holocene*, 25, 1102–
502 1110.
503 Cook, B.I., Ault, T.R. & Smerdon, J.E. (2015). Unprecedented 21st century drought risk in the
504 American Southwest and Central Plains. *Sci. Adv.*, 1, e1400082.
505 Cook, E.R., Seager, R., Heim, R.R., Vose, R.S., Herweijer, C. & Woodhouse, C. (2010).
506 Megadroughts in North America: placing IPCC projections of hydroclimatic change in a
507 long-term palaeoclimate context. *J. Quat. Sci.*, 25, 48–61.
508 Dawson, A., Goring, S., Paciorek, C.J., Jackson, S.T., McLachlan, J.S. & Williams, J.W.
509 (2019a). *STEPPS 2000 Year Forest Composition Estimates, Upper Midwest US, Level*
510 *2*. Environmental Data Initiative.
511 Dawson, A., Paciorek, C.J., Goring, S.J., Jackson, S.T., McLachlan, J.S. & Williams, J.W.
512 (2019b). Quantifying trends and uncertainty in prehistoric forest composition in the upper
513 Midwestern United States. *Ecology*, 100.
514 Dawson, A., Paciorek, C.J., McLachlan, J.S., Goring, S., Williams, J.W. & Jackson, S.T. (2016).
515 Quantifying pollen-vegetation relationships to reconstruct ancient forests using 19th-
516 century forest composition and pollen data. *Quat. Sci. Rev.*, 137, 156–175.
517 Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.M. (2011). Beyond
518 predictions: biodiversity conservation in a changing climate. *Science*, 332.
519 De Kauwe, M.G., Medlyn, B.E., Zaehle, S., Walker, A.P., Dietze, M.C., Hickler, T., *et al.* (2013).
520 Forest water use and water use efficiency at elevated CO_2: a model-data
521 intercomparison at two contrasting temperate forest FACE sites. *Glob. Change Biol.*, 19,
522 1759–1779.
523 Dietze, M.C. (2017). Prediction in ecology: a first-principles framework. *Ecol. Appl.*, 27, 2048–
524 2060.
525 Dietze, M.C., Fox, A., Beck-Johnson, L.M., Betancourt, J.L., Hooten, M.B., Jarnevich, C.S., *et*
526 *al.* (2018). Iterative near-term ecological forecasting: Needs, opportunities, and
527 challenges. *Proc. Natl. Acad. Sci.*, 115, 1424–1432.
528 Esper, J., George, S.St., Anchukaitis, K., D'Arrigo, R., Ljungqvist, F.C., Luterbacher, J., *et al.*
529 (2018). Large-scale, millennial-length temperature reconstructions from tree-rings.
530 *Dendrochronologia*, 50, 81–90.
531 Evans, M.N., Tolwinski-Ward, S.E., Thompson, D.M. & Anchukaitis, K.J. (2013). Applications of
532 proxy system modeling in high resolution paleoclimatology. *Quat. Sci. Rev.*, 76, 16–28.
533 Farley, S.S., Dawson, A., Goring, S.J. & Williams, J.W. (2018). Situating Ecology as a Big-Data
534 Science: Current Advances, Challenges, and Solutions. *BioScience*, 68, 563–576.
535 Fisher, R.A., Koven, C.D., Anderegg, W.R.L., Christoffersen, B.O., Dietze, M.C., Farrior, C.E., *et*
536 *al.* (2018). Vegetation demographics in Earth System Models: A review of progress and
537 priorities. *Glob. Change Biol.*, 24, 35–54.
538 Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., *et al.* (2006). Climate–
539 Carbon Cycle Feedback Analysis: Results from the C^4 MIP Model Intercomparison. *J.*
540 *Clim.*, 19, 3337–3353.
541 Friedlingstein, P., Meinshausen, M., Arora, V.K., Jones, C.D., Anav, A., Liddicoat, S.K., *et al.*
542 (2014). Uncertainties in CMIP5 Climate Projections due to Carbon Cycle Feedbacks. *J.*
543 *Clim.*, 27, 511–526.

Goring, S.J., Mladenoff, D.J., Cogbill, C.V., Record, S., Paciorek, C.J., Jackson, S.T., *et al.* (2016). Novel and Lost Forests in the Upper Midwestern United States, from New Estimates of Settlement-Era Composition, Stem Density, and Biomass. *PLOS ONE*, 11, e0151935.

Keeley, J.E., van Mantgem, P. & Falk, D.A. (2019). Fire, climate and changing forests. *Nat. Plants*, 5, 774–775.

Klesse, S., Babst, F., Lienert, S., Spahni, R., Joos, F., Bouriaud, O., *et al.* (2018). A Combined Tree Ring and Vegetation Model Assessment of European Forest Growth Sensitivity to Interannual Climate Variability. *Glob. Biogeochem. Cycles*.

Kujawa, E.R., Goring, S., Dawson, A., Calcote, R., Grimm, E.C., Hotchkiss, S.C., *et al.* (2016). The effects of anthropogenic land cover change on pollen-vegetation relationships in the American Midwest. *Anthropocene*, 15, 60–71.

Kumar, J., Brooks, B.-G.J., Thornton, P.E. & Dietze, M.C. (2012). Sub-daily Statistical Downscaling of Meteorological Variables Using Neural Networks. *Procedia Comput. Sci.*, 9, 887–896.

LeBauer, D.S., Wang, D., Richter, K.T., Davidson, C.C. & Dietze, M.C. (2013). Facilitating feedbacks between field measurements and ecosystem models. *Ecol. Monogr.*, 83, 133–154.

Liu, F., Mladenoff, D.J., Keuler, N.S. & Moore, L.S. (2011). Broadscale variability in tree data of the historical Public Land Survey and its consequences for ecological studies. *Ecol. Monogr.*, 81, 259–275.

Matthes, J.H., Goring, S., Williams, J.W. & Dietze, M.C. (2016). Benchmarking historical CMIP5 plant functional types across the Upper Midwest and Northeastern United States. *J. Geophys. Res. Biogeosciences*, 121, 523–535.

McCabe, T.D. & Dietze, M.C. (2019). Scaling Contagious Disturbance: A Spatially-Implicit Dynamic Model. *Front. Ecol. Evol.*, 7.

McLachlan, J.S. & PalEON Project. (2018). Forecasting long-term ecological dynamics using open paleodata. *Past Glob. Change Mag.*, 26, 76–76.

Medlyn, B.E., Zaehle, S., De Kauwe, M.G., Walker, A.P., Dietze, M.C., Hanson, P.J., *et al.* (2015). Using ecosystem experiments to improve vegetation models. *Nat. Clim. Change*, 5, 528–534.

Nolan, C., Overpeck, J.T., Allen, J.R.M., Anderson, P.M., Betancourt, J.L., Binney, H.A., *et al.* (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Science*, 361, 920–923.

Paciorek, C.J., Cogbill, C.V., Peters, J.A., Goring, S.J., Williams, J.W., Mladenoff, D.J., *et al.* (2019). *Statistically-estimated tree biomass, stem density, and basal area for the upper Midwestern United States at the time of Euro-American settlement* (preprint). Ecology.

Paciorek, C.J., Goring, S.J., Thurman, A.L., Cogbill, C.V., Williams, J.W., Mladenoff, D.J., *et al.* (2016). Statistically-Estimated Tree Composition for the Northeastern United States at Euro-American Settlement. *PLOS ONE*, 11, e0150087.

Paciorek, C.J. & McLachlan, J.S. (2009). Mapping Ancient Forests: Bayesian Inference for Spatio-Temporal Trends in Forest Composition Using the Fossil Pollen Proxy Record. *J. Am. Stat. Assoc.*, 104, 608–622.

Peltier, D.M.P. & Ogle, K. (2020). Tree growth sensitivity to climate is temporally variable. *Ecol. Lett.*, 1–20.

Pelton, W.L., King, K.M. & Tanner, C.B. (1960). An evaluation of the Thornthwaite and mean temperature methods for determining potential evapotranspiration. *Agron. J.*, 52, 387–395.

Raiho, A.M., Paciorek, C.J. & McLachlan, J.S. (in prep). Species migrations created a 5,000 year regional carbon sink past.

Rollinson, C.R., Finley, A.O., Alexander, M.R., Banerjee, S., Dixon Hamil, K.-A., Koenig, L., *et al.* (in press). Working across space and time: nonstationarity in ecological research and application. *Front. Ecol. Environ.*

Rollinson, C.R., Liu, Y., Raiho, A., Moore, D.J.P., McLachlan, J., Bishop, D.A., *et al.* (2017). Emergent climate and CO_2 sensitivities of net primary productivity in ecosystem models do not agree with empirical data in temperate forests of eastern North America. *Glob. Change Biol.*, 23, 2755–2767.

Schimel, D., Stephens, B.B. & Fisher, J.B. (2015). Effect of increasing CO_2 on the terrestrial carbon cycle. *Proc. Natl. Acad. Sci.*, 112, 436–441.

Seidl, R., Fernandes, P.M., Fonseca, T.F., Gillet, F., Jönsson, A.M., Merganičová, K., *et al.* (2011). Modelling natural disturbances in forest ecosystems: a review. *Ecol. Model.*, 222, 903–924.

Shuman, B., Newby, P., Huang, Y. & Webb, T. (2004). Evidence for the close climatic control of New England vegetation history. *Ecology*, 85, 1297–1310.

Shuman, B.N., Marsicek, J., Oswald, W.W. & Foster, D.R. (2019). Predictable hydrological and ecological responses to Holocene North Atlantic variability. *Proc. Natl. Acad. Sci.*, 116, 5985–5990.

Simpson, G.L. (2018). Modelling Palaeoecological Time Series Using Generalised Additive Models. *Front. Ecol. Evol.*, 6.

Taylor, K.E., Stouffer, R.J. & Meehl, G.A. (2012). An Overview of CMIP5 and the Experiment Design. *Bull. Am. Meteorol. Soc.*, 93, 485–498.

Thom, D., Golivets, M., Edling, L., Meigs, G.W., Gourevitch, J.D., Sonter, L.J., *et al.* (2019). The climate sensitivity of carbon, timber, and species richness covaries with forest age in boreal–temperate North America. *Glob. Change Biol.*, 25, 1446–2458.

Thornthwaite, C.W. & Mather, J.R. (1957). Instructions and tables for computing potential evapotranspiration and the water balance. *Publ. Climatol.*, 10, 185–311.

Trachsel, M., Dawson, A., Paciorek, C.J., Williams, J.W., McLachlan, J.S., Cogbill, C.V., *et al.* (2020). Comparison of settlement-era vegetation reconstructions for STEPPS and REVEALS pollen–vegetation models in the northeastern United States. *Quat. Res.*, 95, 23–42.

Veloz, S.D., Williams, J.W., Blois, J.L., He, F., Otto-Bliesner, B. & Liu, Z. (2012). No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. *Glob. Change Biol.*, 18, 1698–1713.

Walker, A.P., Hanson, P.J., De Kauwe, M.G., Medlyn, B.E., Zaehle, S., Asao, S., *et al.* (2014). Comprehensive ecosystem model-data synthesis using multiple data sets at two temperate forest free-air CO_2 enrichment experiments: Model performance at ambient CO_2 concentration: FACE MODEL-DATA SYNTHESIS. *J. Geophys. Res. Biogeosciences*, 119, 937–964.

Walker, A.P., Zaehle, S., Medlyn, B.E., De Kauwe, M.G., Asao, S., Hickler, T., *et al.* (2015). Predicting long-term carbon sequestration in response to CO_2 enrichment: How and why do current ecosystem models differ? *Glob. Biogeochem. Cycles*, 29, 476–495.

Wei, Y., Liu, S., Huntzinger, D.N., Michalak, A.M., Viovy, N., Post, W.M., *et al.* (2014). The North American Carbon Program Multi-scale Synthesis and Terrestrial Model Intercomparison Project – Part 2: Environmental driver data. *Geosci. Model Dev.*, 7, 2875–2893.

Williams, J.W., Blois, J.L. & Shuman, B.N. (2011). Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary: Extrinsic and intrinsic abrupt ecological change. *J. Ecol.*, 99, 664–677.

Williams, J.W. & Jackson, S.T. (2007). Novel Climates, No-Analog Communities, and Ecological Surprises. *Front. Ecol. Environ.*, 5, 475–482.

644 Wilmking, M., Maaten-Theunissen, M., Maaten, E., Scharnweber, T., Buras, A., Biermann, C., *et*
645 *al.* (2020). Global assessment of relationships between climate and tree growth. *Glob.*
646 *Change Biol.*, 26, 3212–3220.
647 Wood, S.N. (2017). *Generalized Additive Models: An Introduction with R*. 2nd edn. Chapman
648 and Hall/CRC, New York.
649 Woodhouse, C.A., Meko, D.M., MacDonald, G.M., Stahle, D.W. & Cook, E.R. (2010). A 1,200-
650 year perspective of 21st century drought in southwestern North America. *Proc. Natl.*
651 *Acad. Sci.*, 107, 21283–21288.
652

Manuscript Tables

Table 1: Comparison of 1) ecosystem model complexity, based on representation of diversity, demographic, and ecophysiological processes with 2) variability in forest composition and biomass and sensitivity to hydroclimate variability. Compositional and biomass variability (Log Comp. Var.; Log Biom. Var) are represented by log-transformed mean and standard deviation across space of temporal variability, represented in turn as the sum of centennially-resolved first differences of fractional composition of the dominant plant type or aboveground biomass. Composition and biomass sensitivity are represented as the mean slope and standard error of log-log regression between composition or biomass variability and hydroclimate variability. PFT = plant functional types. For sensitivity columns, * indicates slopes significantly different from zero ($p<0.05$); † indicates model slope significantly different from pollen ($p<0.05$).

Data Source & Model Name	Tree Diversity Representation	Demographic Representation	Vegetation Processes	Comp. Var. (log)	Comp. Sens. (log-log)	Biom. Var. (log)	Biom. Sens. (log-log)
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	cohort	photosynthesis, allocation, cross-PFT competition, cross-cohort 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)*†

Manuscript Figures

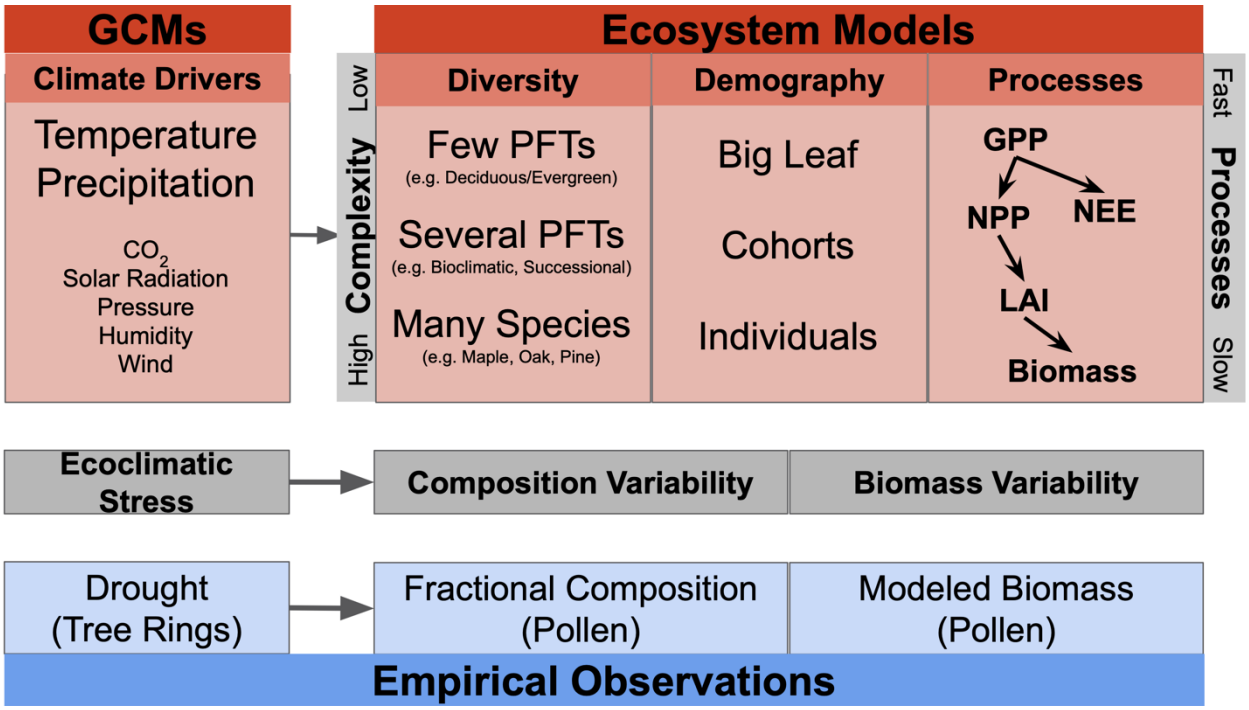
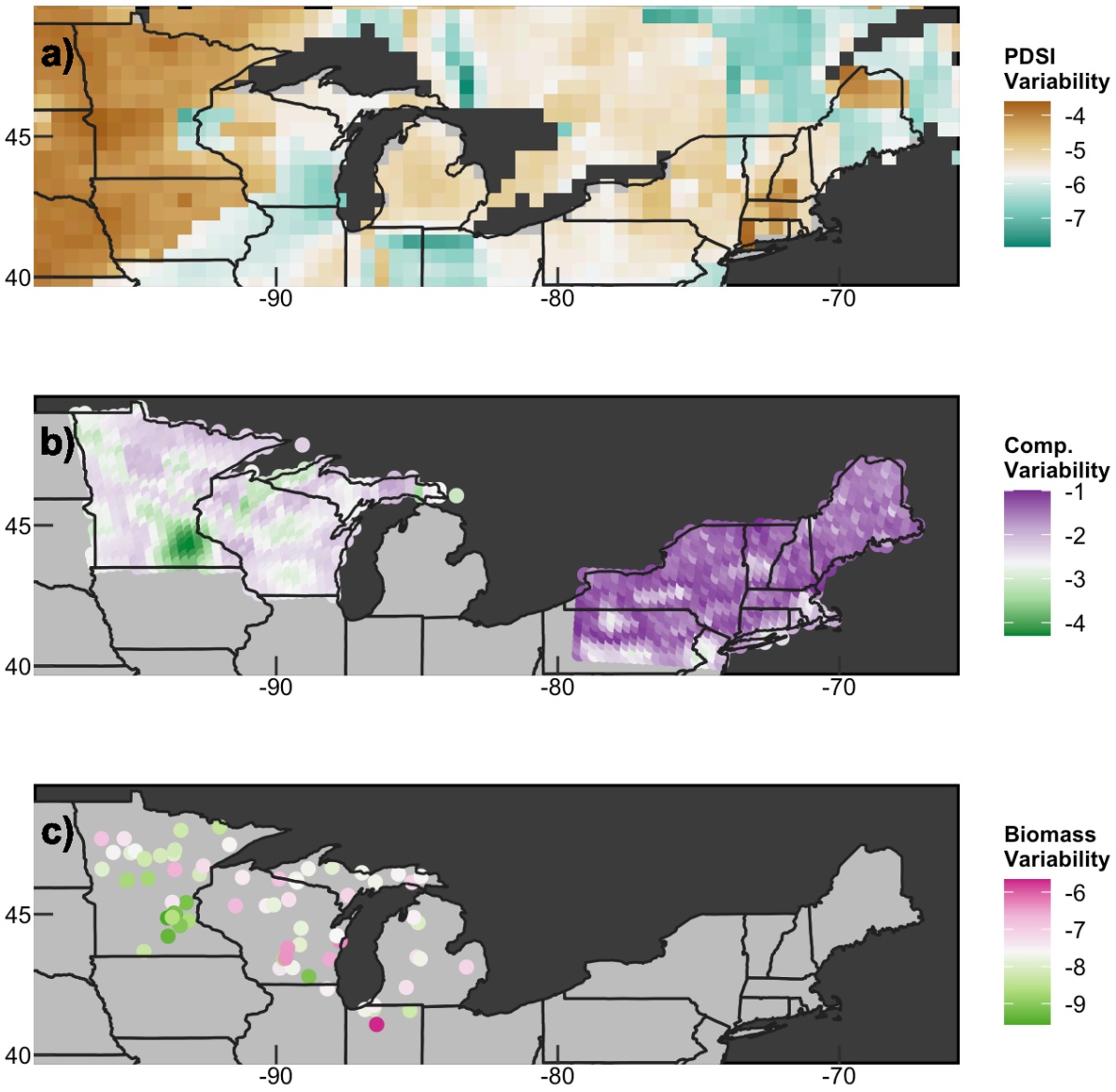


Figure 1: Overview of the unified conceptual framework (gray boxes) for parallel analysis of empirical data (blue boxes) and model output (red boxes). For ecosystem models, we describe the latent climatic and ecosystem processes that are unobservable in paleoecological data and differences among models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



683
684 **Figure 2:** Spatial distribution of inferred temporal variability for 850 to 1850 AD for a) drought
685 (PDSI) from the Living Blended Drought Atlas (44), b) forest composition from the STEPPS
686 pollen-vegetation model (8, 24), and c) forest aboveground biomass from the ReFab pollen-
687 biomass model (7). All variability estimates were divided by mean to facilitate inter-variable
688 comparison (*Methods*). Spatial extent of compositional and biomass reconstructions are
689 uneven across the study domain, as is the temporal extent of reconstructed drought variability
690 (Supplemental Figure 1). Empirical comparisons of composition or biomass variability with
691 drought variability are restricted to the common temporal extents for each location.
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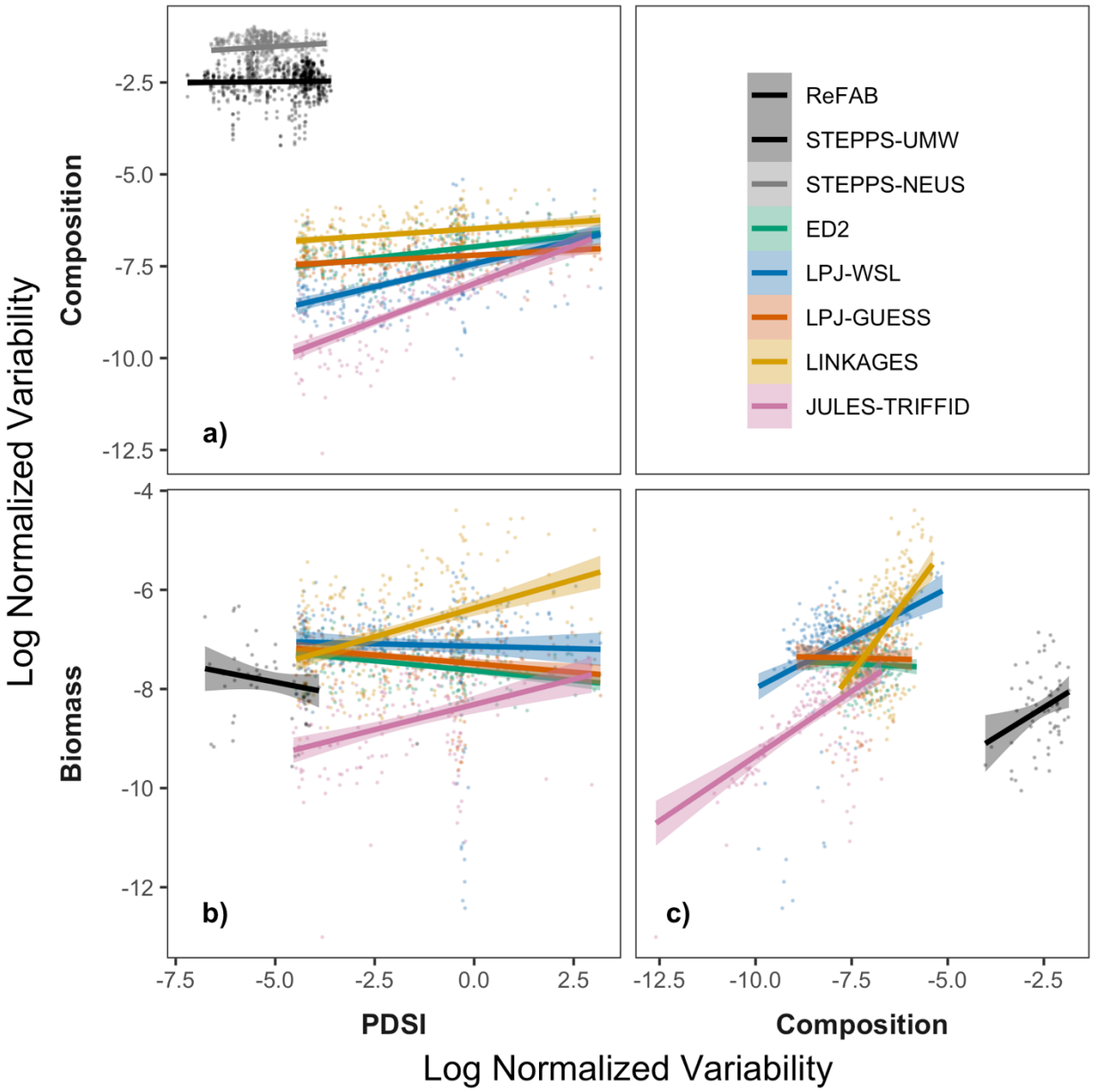


Figure 3: Inferred (black, gray) and simulated (colors) sensitivity of variability of forest composition and biomass to ecohydrological variability (PDSI) (a,b) and of biomass variability to compositional variability (c). Inferred variables suggest weak to no correlation (low sensitivity) between climate 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.

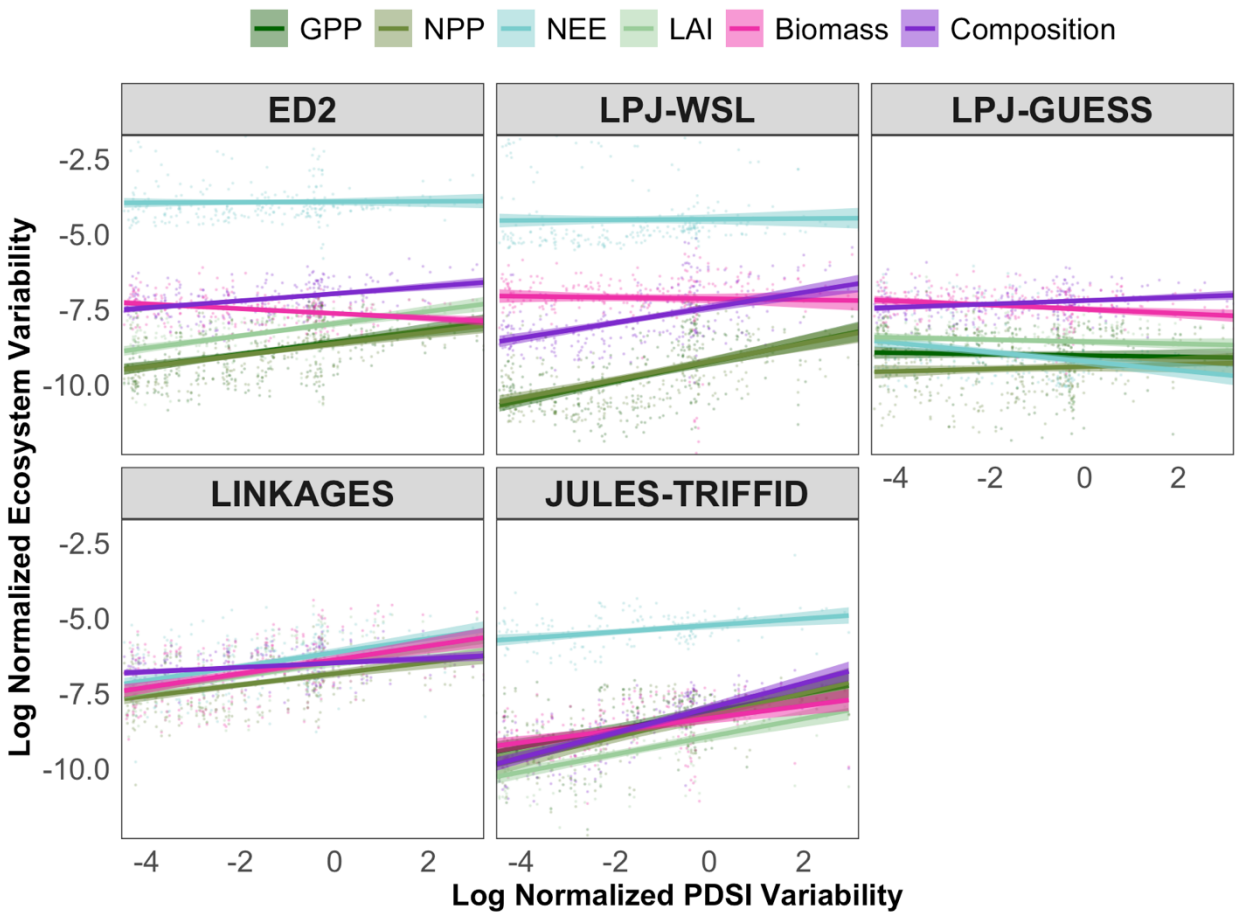


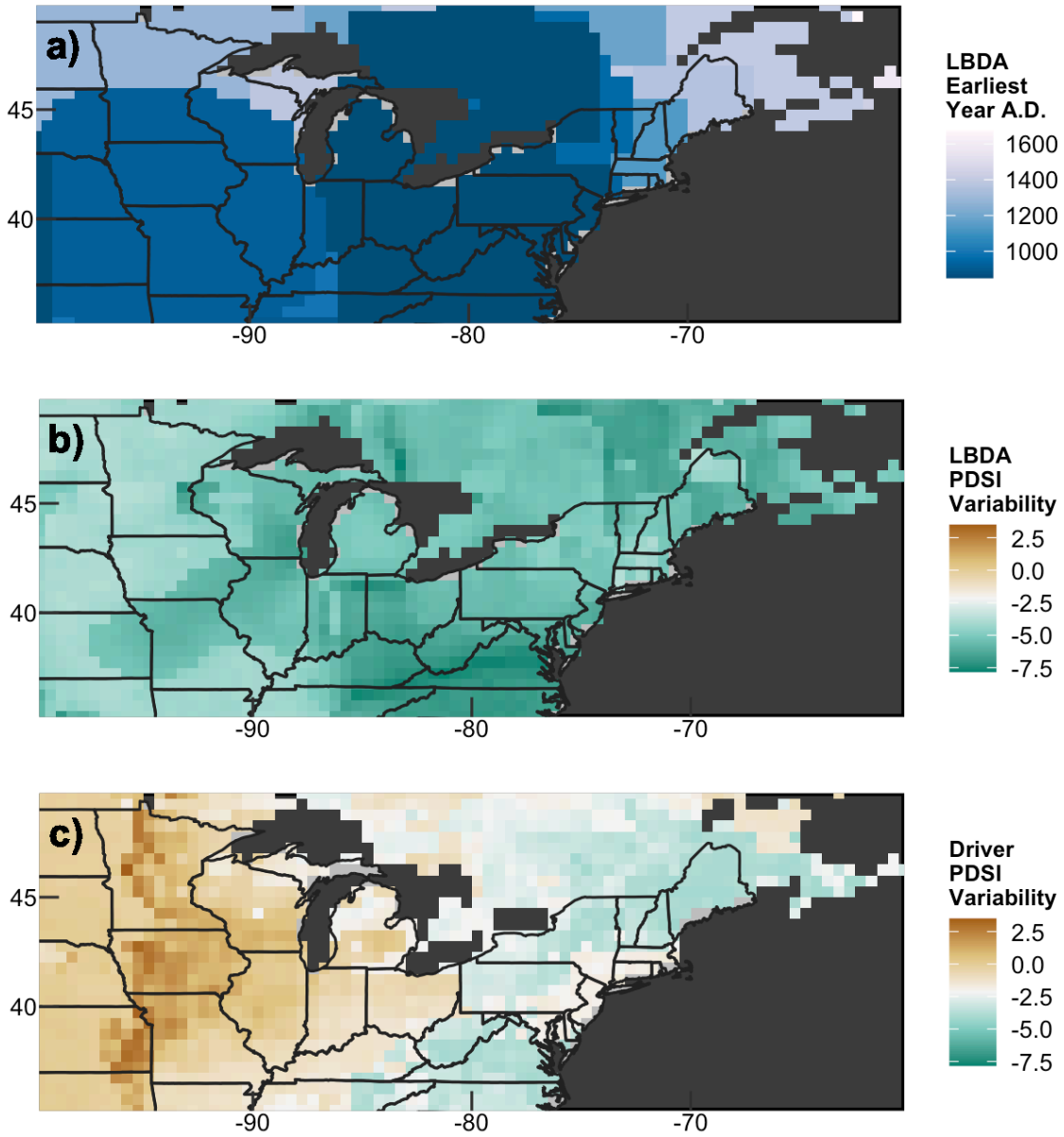
Figure 4: Diagnosing the observed and latent relationships among ecohydrological variability and variability in forest composition, structure, and function in five terrestrial ecosystem models (ED2, LPJ-WSL, LPJ-GUESS, LINKAGES, and JULES-TRIFFID). All models showed positive correlations between composition and drought variability, but some models showed positive biomass sensitivities (LINKAGES, JULES-TRIFFID) while others were negative (ED2, LPJ-WSL, LPJ-GUESS). In all models, composition sensitivity to hydroclimate variability was most similar to NPP whereas biomass sensitivity tended to mirror NEE.

Supplemental Tables

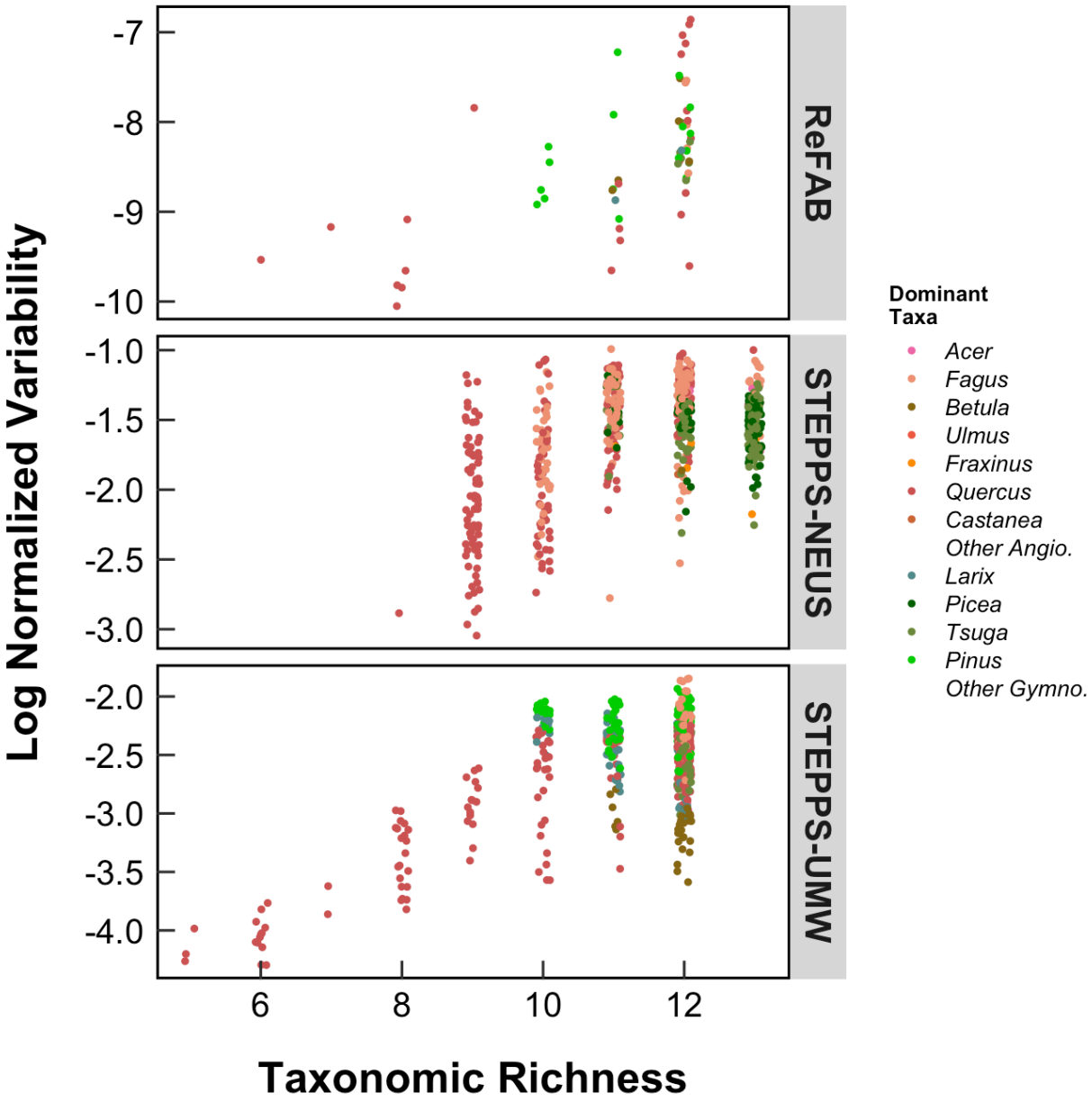
Supplemental Table 1: Sensitivity of latent state variability to hydroclimate (PDSI) variability in ecosystem models and pollen data products. Sensitivity is presented as the mean and standard error slope from log-log regression; * indicates slopes significantly different from zero ($p<0.05$). LINKAGES 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)*

Supplemental Figures



Supplemental Figure 1: Comparison of log normalized PDSI variability in empirically-inferred reconstructions from the Living Blended Drought Atlas (LBDA, 41, a, b) and model drivers (c). Due to the regional differences in the length of tree-ring chronologies available for PDSI reconstruction, the temporal extent of analyses involving LBDA drought is uneven across space. Overall, model drivers had greater PDSI variability than seen in the LBDA, but both datasets show greater variability in the western region of the study domain.



Supplemental Figure 2: Relationship between taxonomic richness and log normalized biomass (ReFAB) and composition (STEPPS) variability in pollen-inferred datasets.