

LETTER • **OPEN ACCESS**

Global forests are influenced by the legacies of past inter-annual temperature variability

To cite this article: Winslow D Hansen *et al* 2022 *Environ. Res.: Ecology* 1 011001

View the [article online](#) for updates and enhancements.

ENVIRONMENTAL RESEARCH ECOLOGY



LETTER

Global forests are influenced by the legacies of past inter-annual temperature variability

OPEN ACCESS

RECEIVED
20 January 2022

REVISED
2 March 2022

ACCEPTED FOR PUBLICATION
10 May 2022

PUBLISHED
30 August 2022

Original content from this work may be used under the terms of the [Creative Commons Attribution 4.0 licence](#).

Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.



Winslow D Hansen^{1,*}, Naomi B Schwartz², A Park Williams^{3,4}, Katharina Albrich^{5,10}, Lara M Kueppers^{6,7}, Anja Rammig⁵, Christopher P O Reyer⁸, A Carla Staver⁹ and Rupert Seidl^{5,10,11}

¹ Cary Institute of Ecosystem Studies, Millbrook, NY 12545, United States of America

² Department of Geography, The University of British Columbia, Vancouver, BC V6T1Z2, Canada

³ Department of Geography, University of California, Los Angeles, CA 90095, United States of America

⁴ Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY 10964, United States of America

⁵ Technical University of Munich, TUM School of Life Sciences Weihenstephan, Freising, Germany

⁶ Energy and Resources Group, University of California Berkeley, Berkeley, CA, United States of America

⁷ Lawrence Berkeley National Laboratory, Berkeley, CA, United States of America

⁸ Potsdam Institute for Climate Impact Research, Member of the Leibniz Association, PO Box 601203, D-14412 Potsdam, Germany

⁹ Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511, United States of America

¹⁰ University of Natural Resources and Life Sciences (BOKU) Vienna, Institute of Silviculture, Wien, Austria

¹¹ Berchtesgaden National Park, Doktorberg 6, 83471 Berchtesgaden, Germany

* Author to whom any correspondence should be addressed.

E-mail: hansenw@caryinstitute.org

Keywords: acclimation, climate change, drought, heatwave, ecosystem sensitivity, EVI, forest resilience

Supplementary material for this article is available [online](#)

Abstract

Inter-annual climate variability (hereafter climate variability) is increasing in many forested regions due to climate change. This variability could have larger near-term impacts on forests than decadal shifts in mean climate, but how forests will respond remains poorly resolved, particularly at broad scales. Individual trees, and even forest communities, often have traits and ecological strategies—the legacies of exposure to past variable conditions—that confer tolerance to subsequent climate variability. However, whether local legacies also shape global forest responses is unknown. Our objective was to assess how past and current climate variability influences global forest productivity. We hypothesized that forests exposed to large climate variability in the past would better tolerate current climate variability than forests for which past climate was relatively stable. We used historical (1950–1969) and contemporary (2000–2019) temperature, precipitation, and vapor pressure deficit (VPD) and the remotely sensed enhanced vegetation index (EVI) to quantify how historical and contemporary climate variability relate to patterns of contemporary forest productivity. Consistent with our hypothesis, forests exposed to large temperature variability in the past were more tolerant of contemporary temperature variability than forests where past temperatures were less variable. Forests were 19-fold times less sensitive to contemporary temperature variability where historical inter-annual temperature variability was 0.66 °C (two standard deviations) greater than the global average historical temperature variability. We also found that larger increases in temperature variability between the two study periods often eroded the tolerance conferred by the legacy effects of historical temperature variability. However, the hypothesis was not supported in the case of precipitation and VPD variability, potentially due to physiological tradeoffs inherent in how trees cope with dry conditions. We conclude that the sensitivity of forest productivity to imminent increases in temperature variability may be partially predictable based on the legacies of past conditions.

1. Introduction

Forests are central to biogeochemical cycling (Sitch *et al* 2008), land–atmosphere interactions (Bonan 2008, Swann *et al* 2010, Zemp *et al* 2017) and the provision of ecosystem services (Seidl *et al* 2016). Climate is a powerful determinant of forest cover, structure, and functions (McDowell *et al* 2020, Anderegg *et al* 2020a). Thus, human-caused multi-decadal shifts in mean climate could fundamentally alter 21st-century forests with profound consequences for our planet (Swann *et al* 2010, Trumbore *et al* 2015, Ghazoul and Chazdon 2017). Yet, the climate system is dynamic across multiple temporal scales, and interannual climate variability (hereafter referred to as climate variability), or the year-to-year fluctuations in key climate variables around long-term mean trends, is also increasing in many places (Jackson *et al* 2009, Pendergrass *et al* 2017). Growing climate variability may have larger near-term consequences for Earth's forests than long-term trends in mean climate conditions because it has the potential to generate climate extremes that exceed the physiological tolerances of the trees (Pederson *et al* 2014, Uriarte *et al* 2016), particularly if two or three extreme years occur consecutively, as was the case in central Europe in 2018–2020 (Senf and Seidl 2021).

Being long-lived sessile organisms, trees are uniquely exposed to their local environment (Canham *et al* 2018, Brodribb *et al* 2020). Thus, their survival depends on traits and ecological strategies that help individuals tolerate variable conditions (Johnstone *et al* 2016, Isaac-Renton *et al* 2018). For instance, many trees have leaf-level thermal tolerances that far exceed the temperatures they regularly experience, helping maintain photosynthesis under variable conditions (Sullivan *et al* 2020). Some trees can even adjust thermal limits within a growing season to cope with extreme heat waves (Gunderson *et al* 2010). Furthermore, the diversity of traits and strategies in populations and communities can buffer forest structure and functions, including productivity, from climate variability, even if individual trees or species are negatively affected (Warner and Chesson 1985, Sakschewski *et al* 2016, Anderegg *et al* 2018). For example, forests in the western United States recently experienced the driest 20-year period in at least 1200 years (Williams *et al* 2022), and in response, community-weighted hydraulic traits shifted toward greater drought tolerance (Trugman *et al* 2020), helping to maintain forest cover and function during a millennial-scale drought. The traits and strategies that confer individual- to community-level tolerance to contemporary conditions are often legacies of exposure to past environmental conditions (Ogle *et al* 2015, Johnstone *et al* 2016, Peltier and Ogle 2020). However, whether local traits and strategies aggregate to shape forest responses to changing climate variability at global scales remains unknown.

While increased climate variability is expected during the twenty-first century, the magnitude of projected change by 2100 within any one forest biome is modest compared to the geographic differences in climate variability among forest biomes. For example, boreal forests experience 2.5 times greater inter-annual temperature variability than tropical forests (Harris *et al* 2020). Many of the factors that determine global geographic gradients of climate variability, like solar angle, distance to coast, and large-scale climate teleconnections, are relatively stable over time. Thus, large geographic variations exist across the planet in the magnitude of climate variability that forests have experienced in the past and experience today. If local legacies shape broader forest responses to contemporary conditions, then the signal should be detectable across global geographic gradients of climate variability.

Here, our objective is to assess how past and current inter-annual climate variability influences global patterns of forest productivity. We hypothesized that forests exposed to large climate variability in the past will better tolerate current climate variability than forests where past climate was relatively stable. To test this hypothesis, we used the remotely-sensed enhanced vegetation index (EVI), a relatively robust proxy of forest gross primary production (hereafter forest productivity) (e.g. Shi *et al* 2017, Huang *et al* 2019), and global climate records to quantify whether and how historical and contemporary climate variability relates to patterns of contemporary forest productivity.

2. Materials and methods

2.1. Climate variables

Monthly mean, minimum, and maximum temperature ($^{\circ}\text{C}$), mean vapor pressure (hPa), and total precipitation (mm) (record length 1950–2019; product Climate Research Unit gridded Time Series (CRU TS) v. 4.04) gridded at a 0.5° spatial resolution were retrieved from the CRU, University of East Anglia (Harris *et al* 2020). The CRU TS 4.04 dataset is interpolated based on a global network of weather stations. We used monthly minimum and maximum temperature to calculate vapor pressure at saturation and then subtracted the actual vapor pressure to derive the monthly mean vapor pressure deficit (VPD). CRU TS is the only interpolated weather station-based product that provides global measurements of temperature, precipitation, and vapor pressure at a relatively fine spatial resolution for the last several decades. This was essential for our analysis, as we were interested in the concurrent influence of multiple climate variables on forest productivity.

We used climate records for two study periods; a historical period (1950–1969) and a contemporary period (2000–2019). The contemporary period was selected to correspond with the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite record. Two criteria determined the selection of the historical period. Because trees are long-lived, we wanted to maximize time between the two study periods to ensure that potential legacies of historical climate variability (e.g. trait plasticity and shifts in community composition) would have time to manifest. However, the global density of weather stations was much lower in the first half of the twentieth century than in the second half, which leads to large uncertainty regarding spatial and temporal patterns of interannual climate variability prior to 1950 in the CRU data (Harris *et al* 2014, 2020).

We aggregated temperature and VPD climate records from monthly to annual values by selecting the month of each year with the warmest mean temperature and with the highest mean VPD to capture the growing conditions without prescribing changes in growing season across latitude. For precipitation, which can be stored in snow and the subsurface for months, we quantified each year's annual total. We then expressed each annual precipitation total as a relative anomaly (a percentage) of the respective 20-year mean annual total for the two study periods. This was done because precipitation variance tends to scale with mean precipitation, where wetter places also inherently have more interannual variability in precipitation totals. As we were interested in the effects of climate variability separate from long-term mean trends, the climate records were linearly detrended for each grid cell and time period. We then quantified the interannual variability of temperature, VPD, and relative precipitation anomalies during each period using the standard deviation (SD) (figure S1 (available online at stacks.iop.org/ERE/1/011001/mmedia)). We also calculated the change in interannual temperature, precipitation, and VPD variability between the two periods (hereafter referred to as the late twentieth century change in climate variability).

Even after selecting the historical period to maximize weather station density, CRU-derived variability of temperature, precipitation, and VPD could still be biased in regions where weather station density is low. To minimize the effects of this bias, we excluded 0.17% of grid cells where climate records had an SD of zero during one or both study periods (CRU assigns long-term monthly mean values when insufficient nearby station data are available).

2.2. Forest variables

Monthly mean EVI (record length 2000–2019; product MOD13C2 V006) and the University of Maryland annual gridded land cover classification for the year 2019 (Product MOD12C1 V006) were retrieved from the United States Geological Survey Land Processes Distributed Active Archive Center (Didan 2015, Friedl and Sulla-Menashe 2015). In global comparisons with eddy-covariance flux towers, EVI is a relatively robust proxy for monthly (Huang *et al* 2019) and annual (Shi *et al* 2017) gross primary productivity. The EVI and land cover were gridded at a 0.05° spatial resolution, derived from 1 km² MODIS pixels. Off-nadir viewing angles have been shown to bias patterns of seasonal and interannual EVI (Sims *et al* 2011, Morton *et al* 2014). The MOD13C2 EVI product minimizes the effects of viewing angle in the compositing algorithm by selecting the highest quality constituent 1 km² MODIS pixels with the lowest viewing angle for each 0.05° grid cell (Didan *et al* 2015). To ensure the results were not an artifact of sensor viewing angle, we took a conservative approach by including only the 0.05° grid cells where most (≥50%) of the constituent 1 km² pixels had nadir viewing angles (<30°). Grid cells are also assigned the historical mean EVI when the satellite observations are of insufficient quality (missing data, cloudy, etc.). Thus, we only retained 0.05° grid cells which were assigned the top-quality flag of 'good: use with confidence.'

We masked monthly EVI to include only forested grid cells, which we defined as any cell where the forest types in the land cover classification (evergreen needleleaf, evergreen broadleaf, deciduous needleleaf, deciduous broadleaf, mixed forest) summed to 80%. In the land cover product, forests were delineated based on a canopy height >2 m and >60% tree cover in 2019. We chose 2019 to ensure we did not include grid cells that experienced a severe natural disturbance (e.g. stand-replacing wildfire) or deforestation during the contemporary period. We categorized forest grid cells as boreal, temperate, Mediterranean, or tropical using The World Wildlife Federation's Terrestrial Ecoregions of the World (Olson *et al* 2001).

For each grid cell that had six or more months of EVI observations in ten or more years, we aggregated from monthly to annual values by selecting the month with the highest mean EVI, following the treatment of the climate data. All grid cells that did not meet six months of observations in ten or more years were excluded from analysis. We linearly detrended the annual EVI in each grid cell and quantified interannual variability in EVI as the SD. We aggregated the EVI grid from 0.05° to the 0.5° resolution of the climate data. This final dataset of interannual variability in EVI included 7477 0.5° grid cells (figure S2). We also calculated the mean percent cover of evergreen, deciduous, broadleaf, and needleleaf in each 0.5° grid cell and converted these to categorical variables of leaf shape (one when % needleleaf exceeded % broadleaf, else

zero) and leaf habit (one when % evergreen exceeded % deciduous, else zero) to avoid zero inflation of using the continuous percent vegetation-type variables in regressions.

2.3. Analysis

We first assessed how contemporary climate variability influenced forest productivity globally and within biomes. We fit a linear regression that predicted the $SD(EVI_{2000-2019})$ as a function of $SD(temperature_{2000-2019})$, $SD(precipitation_{2000-2019})$, and $SD(VPD_{2000-2019})$, leaf shape, leaf habit, and biome. Based on visual inspection of univariate scatter plots, we included a quadratic form of the climate variables to allow for nonlinear relationships. To ensure normality and homoscedasticity, the response variable was transformed using a box-cox transformation. We also evaluated collinearity among predictor variables using a variance inflation factor cutoff of seven. Response and non-categorical predictor variables were centered and scaled (converted to z-scores). We used exhaustive model selection with a maximum of four terms and selected the best fitting model based on Akaike information criterion (AIC). Regression residuals were spatially autocorrelated (Moran's $I < 0.05$). Thus, we also ran spatial error and spatial auto-regressive linear models to confirm the direction and statistical significance of relationships when spatial autocorrelation was accounted for (see appendix S1 for more details and table S1 for results of spatial models).

We also wanted to assess how historical climate variability contributed to patterns of contemporary forest productivity, but historical and contemporary climate variability could not be included in the same model due to collinearity. However, model residuals (differences between observed values of the dependent variable and the values predicted by regression) can contain ecologically relevant information (see Anderegg *et al* 2020b for an example), and thus, we used the model residuals from the contemporary climate variability regression described previously as a metric of the remaining sensitivity of forest productivity for subsequent analysis (hereafter forest sensitivity). This metric identifies forest grid cells where forest productivity was unusually stable (large negative residuals) and unusually variable (larger positive residuals) relative to grid cells of similar forest types that experienced similar contemporary climate variability.

We fit a linear regression to evaluate whether and how this remaining forest sensitivity was explained by historical climate variability; $SD(temperature_{1950-1969})$, $SD(precipitation_{1950-1969})$, $SD(VPD_{1950-1969})$, the late twentieth-century change in climate variability; $\Delta SD(temperature)$, $\Delta SD(precipitation)$, $\Delta SD(VPD)$ and interactions between historical climate variability and the late twentieth-century change in climate variability; $SD(temperature; 1950-1969) * \Delta SD(temperature)$, $SD(precipitation; 1950-1969) * \Delta SD(precipitation)$, $SD(VPD; 1950-1969) * \Delta SD(VPD)$. Again, normality, homoscedasticity, and collinearity were assessed, continuous variables were centered and scaled, quadratic terms were included, model selection was conducted, and the most parsimonious model was selected based on AIC. Spatial error and autoregressive models were also run.

We repeated analyses where interannual variability of EVI was quantified as the coefficient of variation (CV), instead of the SD. The CV is a relative rather than absolute measure of variability, allowing us to explore whether our results were sensitive to the property that cells with high mean EVI may inherently have more variable EVI. We also repeated analyses with the normalized difference vegetation index (NDVI) instead of EVI. However, EVI is preferable over NDVI because it is less likely to saturate in forests with high biomass (Huete *et al* 2002), and our analyses confirmed saturation of NDVI in tropical forests. Finally, because the historical period is relatively short for characterizing climate variability, we repeated analyses with a longer historical window of 1950–1989.

Analyses were conducted in R version 4.0.5 (R Core Team 2021), using the packages `ncdf4` (Pierce 2017), `gdalUtils` (Greenberg and Mattiuzzi 2018), `raster` (Hijmans 2020), `tidyverse` (Wickham *et al* 2019), `rgdal` (Bivand *et al* 2018), `sf` (Pebesma 2018), `broom` (Robinson and Hayes 2019), `spdep` (Bivand and Wong 2018), `spatialreg` (Bivand and Piras 2015), `MASS` (Venables and Ripley 2002), `car` (Fox and Weisberg 2019), `MuMIn` (Barton 2020), and `RStoolbox` (Leutner *et al* 2022).

3. Results

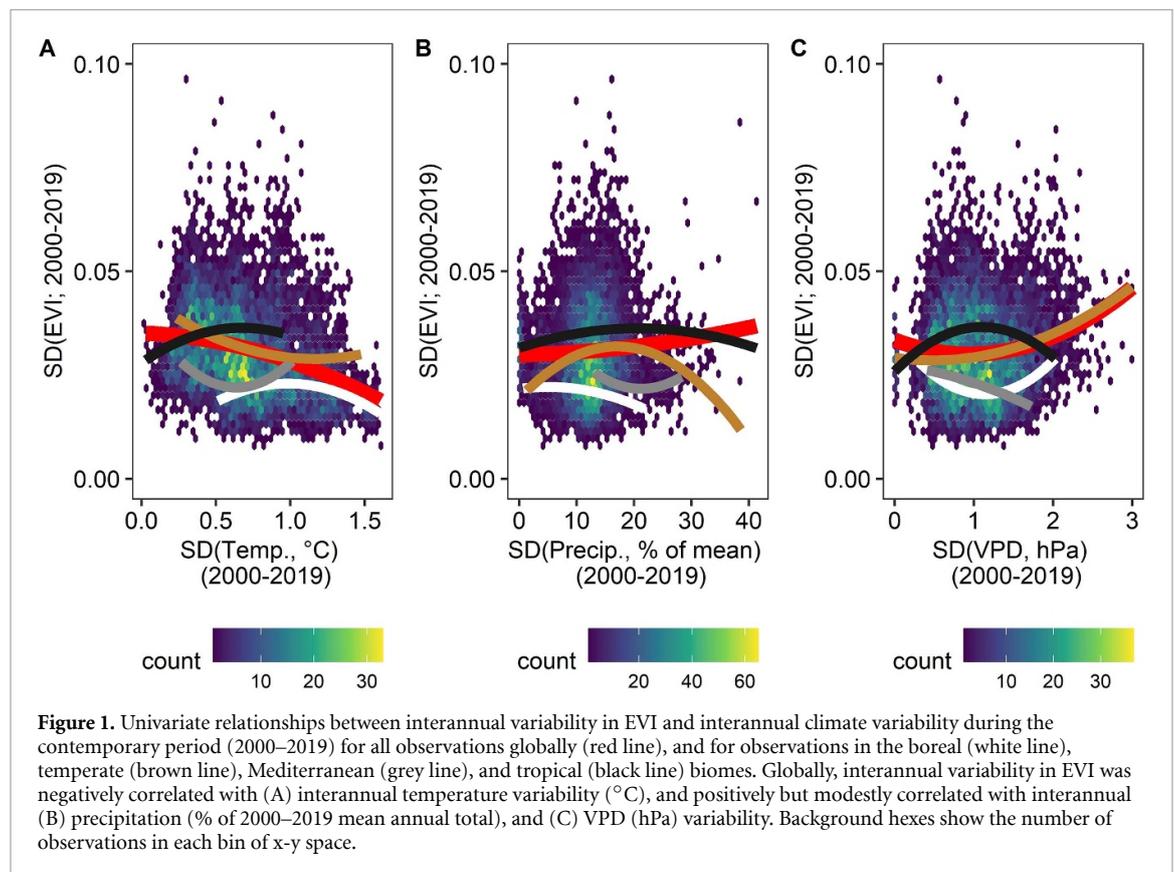
3.1. Relationship between forest productivity and contemporary interannual climate variability

Contemporary temperature variability was the most important climate predictor of interannual variability in EVI (table 1), and the two were negatively correlated (figure 1(A)). On average, the interannual variability in EVI was 24% lower in forested grid cells that experienced the most variable temperatures (≥ 75 th percentile) as compared to grid cells that experienced the least variable temperatures (≤ 25 th percentile). This matched our expectations because geographic patterns of climate variability are relatively stationary over time, and thus forests exposed to large climate variability during the historical period should better tolerate large contemporary climate variability if the legacies of past conditions shape current ecological responses. The relationship was nonlinear (figure 1(A), table 1) and varied markedly among biomes, however. In temperate

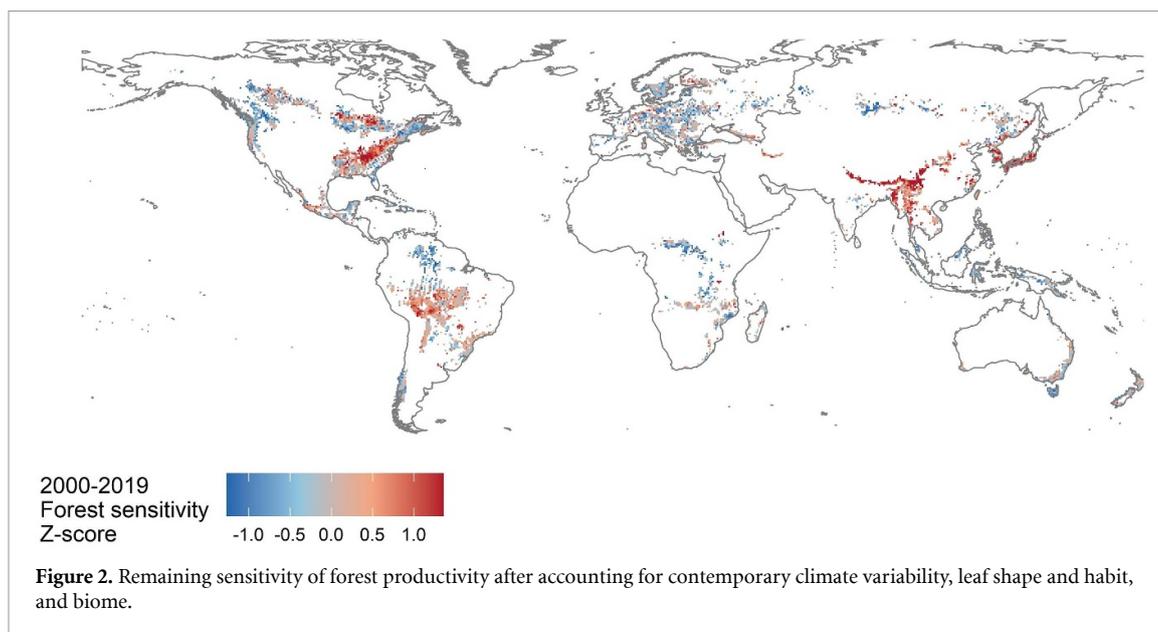
Table 1. Results of linear regression models explaining (A) contemporary forest productivity as a function of contemporary climate variability, leaf habit, shape, and biome, and (B) how historical climate variability relates to remaining sensitivity of forest productivity after accounting for effects of contemporary climate variability, leaf habit, shape, and biome. Note that the two historical models had an $AIC < 2$ (Model 1 and 2). $N = 7477$.

	Model 1	Model 2
<i>(A) Contemporary model</i>		
Intercept	−0.18***	
SD(temperature; 2000–2019)	−0.14***	
SD(temperature; 2000–2019) ²	−0.03***	
Evergreen	−0.51***	
Needleleaf	−0.45***	
Temperate biome	0.62***	
Mediterranean biome	0.006	
Tropical biome	0.86***	
Model R^2	0.35	
Moran's I	0.45***	
<i>(B) Historical model</i>		
Intercept	0.02**	0.02*
SD(temperature; 1950–1969)	−0.14***	−0.08***
SD(temperature; 1950–1969) ²	−0.04***	−0.04***
SD(VPD; 1950–1969)	0.10***	
SD(VPD; 1950–1969) ²	−0.024**	
Δ SD(temperature)	0.08***	0.08***
Δ SD(precipitation)		0.08***
SD(temperature; 1950–1969) * Δ SD(temp)	0.09***	0.08***
SD(temperature; 1950–1969) ² * Δ SD(temp)	−0.11***	−0.11***
Model R^2	0.05	0.05
Moran's I	0.41***	0.41***

* $p \leq 0.1$, ** $p \leq 0.05$, *** $p \leq 0.01$



forests, the correlation between variability in EVI and temperature variability largely agreed with the global trend, except where temperatures were most variable (figure 1(A)). Interannual variability in EVI increased with greater temperature variability in the tropical biome, was varied and inconsistent in the Mediterranean



biome, and declined in the boreal biome, particularly where temperature variability was highest (figure 1(A)). Interannual variability in EVI grew modestly with increasing precipitation and VPD variability (figures 1(B) and (C)), but neither variable was retained in the top model (table 1).

Biome, leaf habit and shape were also important predictors of interannual variability in EVI, irrespective of climate variability (table 1). EVI was more variable in temperate and tropical biomes than in the boreal biome, and was lower in evergreen and needleleaf forests than in deciduous and broad leaf forests (table 1). We repeated analyses using the CV(EVI) with qualitatively similar results (figure S3). Replacing EVI with NDVI confirmed that NDVI saturated in high-biomass forests obscuring relationships (figure S4).

3.2. Relationship between forest productivity, historical interannual climate variability, and late twentieth-century change in climate variability

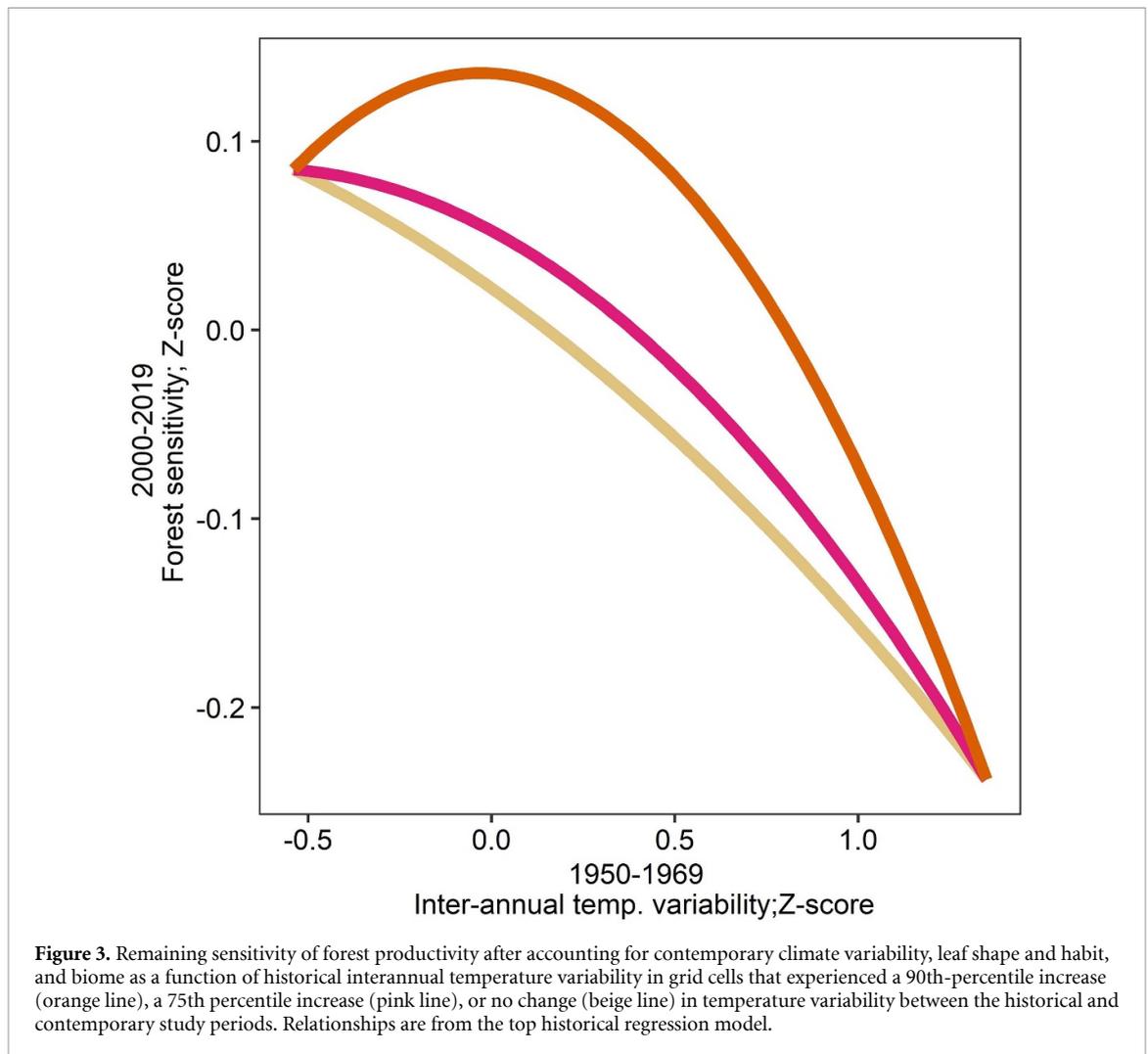
Hotspots of remaining forest sensitivity after accounting for contemporary climate variability, leaf habit and shape, and biome were prevalent in all biomes (figure 2). Boreal forests in eastern North America, temperate forests in the south-central and south-east United States, temperate forests in Asia, and tropical forests in the southern Amazon were all particularly sensitive.

Historical temperature variability is an important predictor of remaining forest sensitivity after accounting for the effects of contemporary climate variability, forest type, and biome, but the overall model R^2 was low (table 1). Given similar contemporary conditions, forest productivity was less variable in grid cells where historical temperatures were more variable (table 1). Forests were 19-fold times less sensitive to contemporary temperature variability where historical temperature variability was two SDs ($0.66\text{ }^\circ\text{C}$) greater than the global average historical temperature variability.

The strength of legacies from exposure to historical temperature variability was altered by late twentieth-century increases in temperature variability (table 1, figure 3). Where historical temperature variability was close to the global average ($\sim 50\%$ of observations), large increases in temperature variability between the two study periods eroded forest tolerance to contemporary climate variability (figure 3). Forest sensitivity also increased with historical VPD variability and the late twentieth-century change in precipitation variability (table 1). All relationships were consistent when we repeated analyses using the CV, instead of the SD of EVI (figure S5), and when we characterized historical climate variability using a 40 year window (1950–1989) (figure S6).

4. Discussion

Our results suggest that exposure to temperature variability in the past can foster legacies that shape how forests respond to contemporary temperature variability at broad scales. Boreal forests, which experienced large temperature variability historically, were more tolerant of contemporary temperature variability than tropical forests where historical temperatures were comparatively stable. We also found that larger increases in temperature variability between the two study periods often eroded the tolerance conferred by legacy



effects of historical temperature variability. Meanwhile, exposure to variable precipitation and VPD in the past did not confer tolerance to contemporary precipitation and VPD variability.

Our study provides useful insights regarding the likely relative impact of increasing future climate variability vs. projected multi-decadal shifts in mean climate. Climate models predict relatively modest twenty-first-century mean warming in the tropics compared to high latitudes, but temperature variability is expected to markedly increase (Bathiany *et al* 2018), and tropical forests are acutely sensitive to contemporary interannual temperature variability in our analysis. This is consistent with recent experimental studies that show temperatures in tropical forests now often approach and exceed thermal photosynthetic safety margins of several tree species (Doughty and Goulde 2008). Furthermore, precipitation variability (in addition to total amount) is a strong determinant of tropical forest cover (Staver *et al* 2011, Staal *et al* 2014, Ciemer *et al* 2019) and is increasing in the tropics (Pendergrass *et al* 2017). Thus, perhaps changes in variability rather than shifting mean conditions will be the dominant climate driver of twenty-first-century forest dynamics in the tropics. However, tropical forests also contain the highest tree-species diversity on Earth, and traits that are currently rare but present may confer some community-level tolerance (Anderegg *et al* 2018, Powell *et al* 2018).

In contrast, climate variability in the boreal forest is expected to modestly increase relative to past conditions, but mean temperature in the boreal biome is rising at a rate at least twice the global average (Wolken *et al* 2011). Disturbance agents that affect boreal forests (e.g. severe wildfires and bark beetle outbreaks) are also sensitive to warming (Abatzoglou *et al* 2018, Seidl *et al* 2020). Thus, future changes in mean climate and climate-sensitive disturbances will likely be more important than the direct effects of increasing climate variability in high-latitude forests.

A remaining challenge is to identify the traits and strategies that underpin forest tolerance to temperature variability at broad scales and to determine why there is little evidence of legacies that confer tolerance to

precipitation and VPD variability. Precipitation and VPD exert different physiological pressures on trees than temperature, which may explain the lack of legacies. When exposed to unusually dry conditions (low precipitation and/or high VPD), many tree species close stomata to avoid hydraulic failure. This comes at the cost of photosynthesis and can cause carbon starvation (Adams *et al* 2017). Tradeoffs between maintaining photosynthesis and avoiding cavitation/embolism may fundamentally constrain hydraulic safety margins (Choat *et al* 2018, Brodribb *et al* 2020), which would inhibit forest responses. Indeed, studies suggest that trees (particularly angiosperms) operate with surprisingly small hydraulic safety margins irrespective of prevailing hydro-climatic conditions, likely to maximize carbon gain (Choat *et al* 2012). Conversely, tradeoffs in physiological buffering against the direct effects of temperature variability are not as strong (Vico *et al* 2019).

Differential responses might also be explained by the climate drivers themselves. Patterns of precipitation and VPD variability are far more spatially heterogeneous than temperature variability, which changes more consistently across latitude (figure S1). Thus, legacy effects of precipitation and VPD variability may manifest at finer spatial resolutions than can be resolved in global analyses. Furthermore, the effects of precipitation and VPD are modulated by edaphic conditions (e.g. soil depth, soil texture, organic matter content), which also vary. In some areas, large variability in precipitation or VPD might not trigger forest responses because the soil-moisture storage capacity is high, and trees continue to access ample water supplies. We chose not to include edaphic conditions in this analysis because of the large uncertainties in global soil datasets (e.g. Hengl *et al* 2017, Tifafi *et al* 2018).

As climate varies across multiple temporal scales, forests may also be responding to precipitation and VPD variability at a different frequency than our analysis evaluated. For instance, the El Niño-Southern Oscillation is a strong determinant of rainfall variability across much of Earth's land surface and varies on a roughly three- to six year temporal scale (Holmgren *et al* 2006). While the CRU climate dataset is one of the best available for capturing geographic patterns of global climate during the last few decades, it is less reliable prior to 1950 when fewer weather stations were in operation (Harris *et al* 2014, 2020). This hinders our ability to evaluate forest responses to climate variability over longer temporal scales. However, an analysis using paleo reconstructions of climate and forest biomass and composition showed that processes consistent with what we found may have helped forests tolerate hydro-climate variability over the last millennium (Rollinson *et al* 2021).

It is worth noting that EVI and similar satellite-based vegetation indices are coarse indicators of forest responses to climate variability, integrating information on fractional cover, productivity, and myriad other factors that affect greenness. This likely introduces uncertainty into our analysis. Yet, these remotely sensed vegetation indices are the only ones currently available with simultaneously sufficient spatial resolution and record length. The next generation of space-based vegetation indices can characterize forest structure, photosynthesis, evapotranspiration, and canopy chemistry, and they will offer opportunities to evaluate previously intractable questions about how climate influences forest ecosystems (Stavros *et al* 2017). However, those records are still too short to enable the analysis we present here. In the near term, these next-generation indices could still be used for real-time monitoring of forest sensitivity to identify emerging hotspots of climate-change impacts and to help prioritize mitigation and adaptation strategies.

We focused on multi-decadal forest responses to increasing climate variability, but did not explicitly consider whether and how exposure to discrete extreme climate events, such as severe heat waves or droughts, might confer tolerance to subsequent events (Jentsch *et al* 2007, Harris *et al* 2018). This is important because extreme climate events occur more frequently with increasing climate variability (Cook *et al* 2020, Perkins-Kirkpatrick and Lewis 2020, Williams *et al* 2020). While it is plausible that exposure to past droughts and heat waves could make forests more tolerant of subsequent climate extremes, increased sensitivity is also possible, particularly if the period between recurring climate extremes is shorter than the time required for forests to recover and acclimate (Ratajczak *et al* 2018, Turner *et al* 2020). Indeed, broad-scale analyses of forests that experienced two or more droughts over a two-decade period suggest that deleterious effects often grow as events recur (Anderegg *et al* 2020b).

5. Conclusions

Twenty-first-century climate will diverge considerably from what forests have experienced over the last century. The impact on forest cover, structure, and function could be profound (Trumbore *et al* 2015) with important consequences for climate and life globally (Lenton *et al* 2008). Yet, the climate system is temporally dynamic, and fluctuations in climate variables will have differential impacts depending on the frequencies at which they occur. Interannual climate variability is expected to increase, which will likely have acute impacts across low-latitude forests. Our analysis offers a valuable framework for diagnosing where and

how the legacies of past climate variability might confer tolerance in forests to recent and imminent increases in climate variability, providing critical information to guide forest and climate policy.

Data availability statement

This study used publically available datasets, including the CRU TS v. 4.04 climate dataset (doi: [10.1038/s41597-020-0453-3](https://doi.org/10.1038/s41597-020-0453-3)), the MOD12C1 V006 MODIS land cover dataset (<https://lpdaac.usgs.gov/products/mcd12c1v006/>), and the MOD13C2 V006 EVI and NDVI datasets (<https://lpdaac.usgs.gov/products/mod13c2v006/>). The code for this analysis has been permanently archived at Cary Institute for Ecosystem Studies data repository (<https://doi.org/10.25390/caryinstitute.19527169>).

The data that support the findings of this study are openly available at the following URL/DOI: https://data.ceda.ac.uk/badc/cru/data/cru_ts/cru_ts_4.04, <https://lpdaac.usgs.gov/products/mod13c2v006/>.

Acknowledgments

This paper is the result of an organized session at the 2019 International Association for Landscape Ecology World Congress in Milan. I T. WDH acknowledges support from the Earth Institute at Columbia University, Columbia University's Center for Climate and Life, and NSF Award AGS-1243204. C P O R acknowledges funding from the German Federal Ministry of Education and Research (BMBF Grant No. 01LS1711A), the European Union's Horizon 2020 research and innovation program (Grant No. 821010), and from the Fachagentur nachwachsende Rohstoffe E V (Grant No. 773324). AR acknowledges funding from the Bavarian Ministry of Science and the Arts in the context of the Bavarian Climate Research Network (bayklif) and from the ERANet 'Sumforest' project 'Forests and extreme weather events: Solutions for risk resilient management in a changing climate' (FOREXCLIM). R S and K A acknowledge support from the Austrian Science Fund FWF through START Grant Y895-B25.

ORCID iDs

Winslow D Hansen  <https://orcid.org/0000-0003-3868-9416>

Naomi B Schwartz  <https://orcid.org/0000-0002-3439-2888>

A Park Williams  <https://orcid.org/0000-0001-8176-8166>

Katharina Albrich  <https://orcid.org/0000-0002-5157-523X>

Lara M Kueppers  <https://orcid.org/0000-0002-8134-3579>

Anja Rammig  <https://orcid.org/0000-0001-5425-8718>

Christopher P O Reyer  <https://orcid.org/0000-0003-1067-1492>

A Carla Staver  <https://orcid.org/0000-0002-2384-675X>

Rupert Seidl  <https://orcid.org/0000-0002-3338-3402>

References

- Abatzoglou J T, Williams A P, Boschetti L, Zubkova M and Kolden C A 2018 Global patterns of interannual climate-fire relationships *Glob. Change Biol.* **24** 5164–75
- Adams H D *et al* 2017 A multi-species synthesis of physiological mechanisms in drought-induced tree mortality *Nat. Ecol. Evol.* **1** 1285–91
- Anderregg W R L *et al* 2018 Hydraulic diversity of forests regulates ecosystem resilience during drought *Nature* **561** 538–41
- Anderregg W R L *et al* 2020a Climate-driven risks to the climate mitigation potential of forests *Science* **368** eaaz7005
- Anderregg W R L, Trugman A T, Badgley G, Konings A G and Shaw J 2020b Divergent forest sensitivity to repeated extreme droughts *Nat. Clim. Change* **10** 1091–5
- Barton K 2020 MuMIn: multi-model inference *R Package Version 1.43.17* (available at: <https://CRAN.R-project.org/package=MUMIn>)
- Bathiany S, Dakos V, Scheffer M and Lenton T M 2018 Climate models predict increasing temperature variability in poor countries *Sci. Adv.* **4** eaar5809
- Bivand R S and Wong D W S 2018 Comparing implementations of global and local indicators of spatial association *Test* **27** 716–48
- Bivand R, Keitt T and Rowlingson B 2018 rgdal: bindings for the “geospatial” data abstraction library *R Package Version 1.5-23* (available at: <https://CRAN.R-project.org/package=rgdal>)
- Bivand R and Piras G 2015 Comparing implementations of estimation methods for spatial econometrics *J. Stat. Softw.* **63** 1–36
- Bonan G B 2008 Forests and climate change: forcings, feedbacks, and the climate benefits of forests *Science* **320** 1444–9
- Brodribb T J, Powers J, Cochard H and Choat B 2020 Hanging by a thread? Forests and drought *Science* **368** 261–6
- Canham C D, Murphy L, Riemann R, McCullough R and Burrill E 2018 Local differentiation in tree growth responses to climate *Ecosphere* **9** e02368
- Choat B *et al* 2012 Global convergence in the vulnerability of forests to drought *Nature* **491** 752–5
- Choat B, Brodribb T J, Brodersen C R, Duursma R A, López R and Medlyn B E 2018 Triggers of tree mortality under drought *Nature* **558** 531–9
- Ciemer C, Boers N, Hirota M, Kurths J, Müller-Hansen F, Oliveira R S and Winkelmann R 2019 Higher resilience to climatic disturbances in tropical vegetation exposed to more variable rainfall *Nat. Geosci.* **12** 174–9

- Cook B I, Mankin J S, Marvel K, Williams A P, Smerdon J E and Anchukaitis K J 2020 Twenty-first century drought projections in the CMIP6 forcing scenarios *Earth's Future* **8** e2019EF001461
- Didan K 2015 MOD13C2 MODIS/Terra vegetation indices monthly L3 global 0.05Deg CMG V006 [data set]
- Didan K, Munoz A B, Solano R and Huete A 2015 MODIS vegetation index user's guide (MOD13 series) V. 3.00 collection 6
- Doughty C E and Goulden M L 2008 Are tropical forests near a high temperature threshold? *J. Geophys. Res.* **114** 1–12
- Fox J and Weisberg S 2019 *An R Companion to Applied Regression* 3rd edn (Thousand Oaks, CA: Sage)
- Friedl M and Sulla-Menashe D. 2015. MCD12C1 MODIS/Terra+aqua land cover type yearly L3 global 0.05Deg CMG V006 [data set]
- Ghazoul J and Chazdon R 2017 Degradation and recovery in changing forest landscapes: a multiscale conceptual framework *Ann. Rev. Environ. Resour.* **42** 1–28
- Greenberg J A and Mattiuzzi M. 2018. gdalUtils: wrappers for the geospatial data abstraction library (GDAL) utilities *R Package Version 2.0.1.14* (available at: <https://cran.r-project.org/src/contrib/Archive/gdalUtils/>)
- Gunderson C A, O'hara K H, Campion C M, Walker A V and Edwards N T 2010 Thermal plasticity of photosynthesis: the role of acclimation in forest responses to a warming climate *Glob. Change Biol.* **16** 2272–86
- Harris I, Jones P D, Osborn T J and Lister D H 2014 Updated high-resolution grids of monthly climatic observations—the CRU TS3.10 dataset *Int. J. Climatol.* **34** 623–42
- Harris I, Osborn T J, Jones P and Lister D 2020 Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset *Sci. Data* **7** 1–18
- Harris R *et al* 2018 Biological responses to the press and pulse of climate trends and extreme events *Nat. Clim. Change* **8** 579–87
- Hengl T *et al* 2017 SoilGrids250m: global gridded soil information based on machine learning *PLoS One* **12** e0169748
- Hijmans R J 2020 raster: geographic data analysis and modeling *R Package Version 3.4-5* (available at: <https://CRAN.R-project.org/package=raster>)
- Holmgren M *et al* 2006 Extreme climatic events shape arid and semiarid ecosystems *Front. Ecol. Environ.* **4** 87–95
- Huang X, Xiao J and Ma M 2019 Evaluating the performance of satellite-derived vegetation indices for estimating gross primary productivity using FLUXNET observations across the globe *Remote Sens.* **11** 1823
- Huete A, Didan K, Miura T, Rodriguez E P, Gao X and Ferreira L G 2002 Overview of the radiometric and biophysical performance of the MODIS vegetation indices *Remote Sens. Environ.* **83** 195–213
- Isaac-Renton M, Montwé D, Hamann A, Spiecker H, Cherubini P and Treydte K 2018 Northern forest tree populations are physiologically maladapted to drought *Nat. Commun.* **9** 5254
- Jackson S T, Betancourt J L, Booth R K and Gray S T 2009 Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions *Proc. Natl Acad. Sci.* **106** 19685–92
- Jentsch A, Kreyling J and Beierkuhnlein C 2007 A new generation of climate-change experiments: events, not trends *Front. Ecol. Environ.* **5** 365–74
- Johnstone J F *et al* 2016 Changing disturbance regimes, ecological memory, and forest resilience *Front. Ecol. Environ.* **14** 369–78
- Lenton T M, Held H, Kriegler E, Hall J W, Lucht W, Rahmstorf S and Schellnhuber H J 2008 Tipping elements in the Earth's climate system *Proc. Natl Acad. Sci.* **105** 1786–93
- Leutner B, Horning N and Schwalb-Willmann J 2022 RStoolbox: tools for remote sensing data analysis *R Package Version 0.3.0* (available at: <https://CRAN.R-project.org/package=RStoolbox>)
- McDowell N G *et al* 2020 Pervasive shifts in forest dynamics in a changing world *Science* **368** eaaz9463
- Morton D C, Nagol J, Carabajal C C, Rosette J, Palace M, Cook B D, Vermote E F, Harding D J and North P R J 2014 Amazon forests maintain consistent canopy structure and greenness during the dry season *Nature* **506** 221–4
- Ogle K, Barber J J, Barron-Gafford G A, Bentley L P, Young J M, Huxman T E, Loik M E and Tissue D T 2015 Quantifying ecological memory in plant and ecosystem processes *Ecol. Lett.* **18** 221–35
- Olson D M *et al* 2001 Terrestrial ecoregions of the world: a new map of life on Earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity *BioScience* **51** 933–8
- Pebesma E 2018 Simple features for R: standardized support for spatial vector data *R J.* **10** 439–46
- Pederson N, Dyer J M, McEwan R W, Hessler a.e., Mock C J, Orwig D A, Rieder H E and Cook B I 2014 The legacy of episodic climatic events in shaping temperate, broadleaf forests *Ecol. Monogr.* **84** 599–620
- Peltier D M P and Ogle K 2020 Tree growth sensitivity to climate is temporally variable *Ecol. Lett.* **23** 1561–72
- Pendergrass A G, Knutti R, Lehner F, Deser C and Sanderson B M 2017 Precipitation variability increases in a warmer climate *Sci. Rep.* **7** 1–9
- Perkins-Kirkpatrick S E and Lewis S C 2020 Increasing trends in regional heatwaves *Nat. Commun.* **11** 3357
- Pierce D 2017 ncd4: interface to unidata netcdf (version 4 or earlier) format data files
- Powell T L *et al* 2018 Variation in hydroclimate sustains tropical forest biomass and promotes functional diversity *New Phytol.* **219** 932–46
- R Core Team 2021 R: a language and environment for statistical computing (available at: <https://www.R-project.org/>)
- Ratajczak Z, Carpenter S R, Ives A R, Kucharik C J, Ramiadantsoa T, Stegner M A, Williams J W, Zhang J and Turner M G 2018 Abrupt change in ecological systems: inference and diagnosis *Trends Ecol. Evol.* **33** 513–26
- Robinson D and Hayes A 2019 broom: convert statistical analysis objects into tidy tibbles *R Package Version 0.7.5* (available at: <https://CRAN.R-project.org/package=broom>)
- Rollinson C R *et al* 2021 Forest responses to last-millennium hydroclimate variability are governed by spatial variations in ecosystem sensitivity *Ecol. Lett.* **24** 498–508
- Sakschewski B, Von Bloh W, Boit A, Poorter L, Peña-Claros M, Heinke J, Joshi J and Thonicke K 2016 Resilience of Amazon forests emerges from plant trait diversity *Nat. Clim. Change* **6** 1032–6
- Seidl R *et al* 2020 Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems *Ecography* **43** 967–78
- Seidl R, Spies T A, Peterson D L, Stephens S L and Hicke J A 2016 Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services *J. Appl. Ecol.* **53** 120–9
- Senf C and Seidl R 2021 Persistent impacts of the 2018 drought on forest disturbance regimes in Europe *Biogeosciences* **18** 5223–30
- Shi H *et al* 2017 Assessing the ability of MODIS EVI to estimate terrestrial ecosystem gross primary production of multiple land cover types *Ecol. Indic.* **72** 153–64
- Sims D A, Rahman A F, Vermote E F and Jiang Z 2011 Seasonal and inter-annual variation in view angle effects on MODIS vegetation indices at three forest sites *Remote Sens. Environ.* **115** 3112–20

- Sitch S *et al* 2008 Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five dynamic global vegetation models (DGVMs) *Glob. Change Biol.* **14** 2015–39
- Staal A, Dekker S C, Hirota M and Van Nes E H 2014 Synergistic effects of drought and deforestation on the resilience of the south-eastern Amazon rainforest *Ecol. Complexity* **22** 65–75
- Staver A C, Archibald S and Levin S A 2011 The global extent and determinants of savanna and forest as alternative biome states *Science* **334** 230–2
- Stavros E N *et al* 2017 ISS observations offer insights into plant function *Nat. Ecol. Evol.* **1** 0194
- Sullivan M J P *et al* 2020 Long-term thermal sensitivity of Earth's tropical forests *Science* **368** 869–74
- Swann A L, Fung I Y, Levis S, Bonan G B and Doney S C 2010 Changes in arctic vegetation amplify high-latitude warming through the greenhouse effect *Proc. Natl Acad. Sci.* **107** 1295–300
- Tifafi M, Guenet B and Hatté C 2018 Large differences in global and regional total soil carbon stock estimates based on SoilGrids, HWSD, and NCSCD: intercomparison and evaluation based on field data From USA, England, Wales, and France *Glob. Biogeochem. Cycles* **32** 42–56
- Trugman A T, Anderegg L D L, Shaw J D and Anderegg W R L 2020 Trait velocities reveal that mortality has driven widespread coordinated shifts in forest hydraulic trait composition *Proc. Natl Acad. Sci.* **117** 8532–8
- Trumbore S, Brando P and Hartmann H 2015 Forest health and global change *Science* **349** 814–8
- Turner M G *et al* 2020 Climate change, ecosystems and abrupt change: science priorities *Phil. Trans. R. Soc. B* **375** 20190105
- Uriarte M, Schwartz N, Powers J S, Marín-Spiotta E, Liao W and Werden L K 2016 Impacts of climate variability on tree demography in second growth tropical forests: the importance of regional context for predicting successional trajectories *Biotropica* **48** 780–97
- Venables W N and Ripley B D 2002 *Modern Applied Statistics with S* 4th edn (New York: Springer)
- Vico G, Way D A, Hurry V and Manzoni S 2019 Can leaf net photosynthesis acclimate to rising and more variable temperatures? *Plant Cell Environ.* **42** 1913–28
- Warner R R and Chesson P 1985 Coexistence mediated by recruitment fluctuations: a field guide to the storage effect *Am. Nat.* **125** 769–87
- Wickham H *et al* 2019 Welcome to the {tidyverse} *J. Open Source Softw.* **4** 1686
- Williams A P, Cook B I and Smerdon J E 2022 Rapid intensification of the emerging southwestern North American megadrought in 2020–2021 *Nat. Clim. Change* **12** 232–4
- Williams A P, Cook E R, Smerdon J E, Cook B I, Abatzoglou J T, Bolles K, Baek S H, Badger A M and Livneh B 2020 Large contribution from anthropogenic warming to an emerging North American megadrought *Science* **368** 314–8
- Wolken J M *et al* 2011 Evidence and implications of recent and projected climate change in Alaska's forest ecosystems *Ecosphere* **2** art124
- Zemp D C, Schleussner C F, Barbosa H M J, Hirota M, Montade V, Sampaio G, Staal A, Wang-Erlandsson L and Rammig A 2017 Self-amplified Amazon forest loss due to vegetation-atmosphere feedbacks *Nat. Commun.* **8** 14681