Supplemental Material:

Exploring the impacts of unprecedented climate extremes on forest ecosystems: hypotheses to guide modeling and experimental studies

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Supplement Figures:

Table S1. Description of simulation treatments of hypothetical droughts from a 'baseline' case (i.e., no drought treatment) to unprecedented climate extremes (UCEs). Varying drought intensity (precipitation removal) from 5% to 100% removal, in increments of 5%, over drought durations of either 1, 2, or 4 years in length. To explore climate change response, we repeated the drought treatments and increased temperature only (+2K over ambient), eCO_2 concentration to 600 ppm and 800 ppm, and increased temperature and eCO_2 (+2K 600 ppm; +2K 800 ppm) and compared to the reference simulation.

	Drought Intensity	Drought Duration	Temperature (K)	CO_2 (ppm)
Baseline	0%	0 years	Ambient	Ambient
Drought Only (Reference)	5% - 100%	1 year	----	----
Drought Only (Reference)	5% - 100%	2 years	----	----
Drought Only (Reference)	5% - 100%	4 years	----	----
Drought + Temp.	5% - 100%	1 year	+ 2K	----
Drought + Temp.	5% - 100%	2 years	+ 2K	----
Drought + Temp.	5% - 100%	4 years	+ 2K	----
Drought + CO_2	5% - 100%	1 year	----	+ 200 ppm
Drought + CO_2	5% - 100%	2 years	----	+ 200 ppm
Drought + CO_2	5% - 100%	4 years	----	+ 200 ppm
Drought + CO_2	5% - 100%	1 year	----	+ 400 ppm
Drought + CO_2	5% - 100%	2 years	----	+ 400 ppm
Drought + CO_2	5% - 100%	4 years	----	+ 400 ppm
Drought + Temp. + CO_2	5% - 100%	1 year	+ 2K	+ 400 ppm
Drought + Temp. + CO_2	5% - 100%	2 years	+ 2K	+ 400 ppm
Drought + Temp. + CO_2	5% - 100%	4 years	+ 2K	+ 400 ppm

Table S2. Comparison of *in situ* observations and baseline model simulations from ED2 and LPJ-GUESS for the two example study sites, Palo Verde in Costa Rica (Kalacska et al., 2005; Xu et al., 2016) and EucFACE in Australia (Medyln et al., 2016; Duursma et al., 2016). Mean and ± standard deviation.

	Palo Verde Costa Rica	EucFACE Australia
Obs. Biomass (kgC m^{-2})	11.0 (5.2)	12.7 (4.5)
ED2 Biomass (kgC m^{-2})	11.7 (0.3)	5.6 (0.3)
LPJ-GUESS Biomass (kgC m^{-2})	10.4 (0.2)	12.1 (0.2)
Obs. LAI (m^2 m^{-2})	3.8 (1.06)	1.7 (0.6)
ED2 LAI (m^2 m^{-2})	3.3 (0.1)	1.6 (0.2)
LPJ-GUESS LAI (m^2 m^{-2})	4.5 (0.1)	3.2 (1.3)

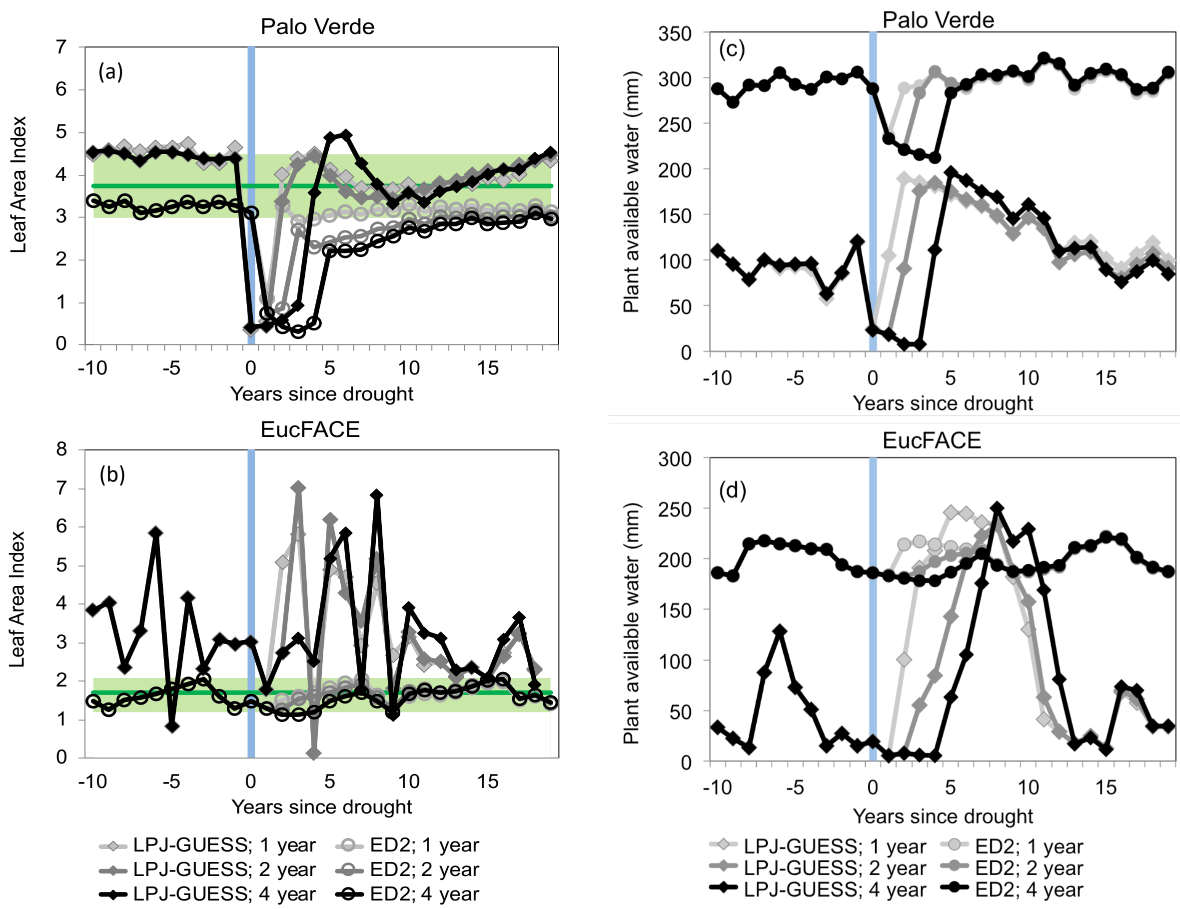

Figure S1. Change in leaf area index (LAI; m^2 m^2) (a-b) and annual plant available water (mm) (c-d) as a result of three drought durations events (1 year, 2 year, and 4 year durations) compared to the pre-drought period (i.e. negative years) and over a 20-year recovery period, for both the LPJ-GUESS and ED2 demography models at the Palo Verde site and EucFACE site. Shaded green area is the observed range in LAI from Kalacska et al., (2005) at Palo Verde and Duursma et al., (2016) at EucFACE. The modeled drought intensity at Palo Verde was 90% precipitation removed, and 50% precipitation removed at EucFACE. Plant available water was calculated over a soil depth of 3 meters in ED2 and 2 meters in LPJ-GUESS.

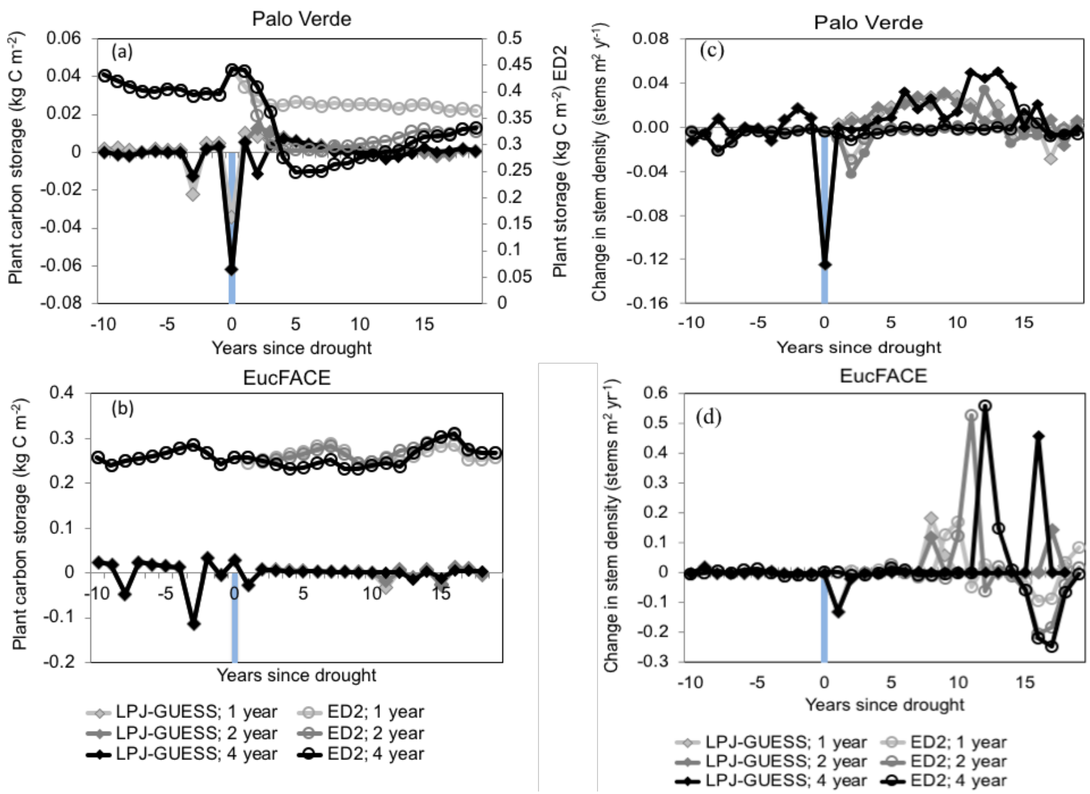

Figure S2. Change in plant carbohydrate storage (kg C m^{-2}) (a-b) and change in stem density (stems m^2 yr^{-1}) (c-d) as a result of three drought durations events (1 year, 2 year, and 4 year durations) compared to the pre-drought period (i.e. negative years) and over a 20-year recovery period, for both the LPJ-GUESS and ED2 demography models at the Palo Verde site and EucFACE site. The modeled drought intensity at Palo Verde was 90% precipitation removed, and 50% precipitation removed at EucFACE.

Supplement Text A:

Meteorological data and initial conditions used to drive ED2 and LPJ-GUESS:

Necessary meteorological drivers for ED2 and LPJ-GUESS include incoming radiation (short-wave and long-wave), air temperature, humidity, and pressure, precipitation and wind speed at sub-daily scale. In-situ meteorological data for Palo Verde is only available since 2008. Using the short-term data as the control climate can lead to biases in ecosystem states and high-frequency cyclic ecosystem dynamics before applying UCEs. Therefore, we use re-analysis data (1970 to 2012) at 0.5 degree resolution from Princeton Global Forcing dataset (Sheffield et al., 2006), and was recycled repeatedly for the Palo Verde simulations.

In-situ meteorological data for EucFACE were obtained from a dataset previously compiled for a simulation study of the EucFACE experimental site (Medlyn et al., 2016). Daily time series of air temperature, precipitation, downward shortwave radiation and photosynthetically-active radiation for 1992-2011 were extracted from the $1 \times 1°$ grid cell encapsulating the site from the Princeton Global Forcing data set (Sheffield et al., 2006). This 20-year time series was recycled repeatedly to force the simulations. For both sites, the baseline simulations were initialized as a near-bare-ground situation, with small amount of tree seedlings equally from each PFT. The baseline spin-up lasted for 100 years (ED2) or 780 years (LPJ-GUESS) using recycling natural climate variability as described above.

Review of Model Parameter Uncertainty

As stated in the manuscript, a goal of this paper is to demonstrate how to use the two VDMs (ED2 and LPJ-GUESS) in order to help generate and test future hypotheses about UCEs. Therefore, we used the models and sites as conceptual "experimental" tools to investigate the given hypotheses and provide a road map for utilizing VDMs. Investigating parameter uncertainty and sensitivity was out of scope for this manuscript. These models are well documented and investigated VDMs, with many previous studies that have looked into parameter uncertainty. Below are a handful of select references (and quick summaries) that explore parameter sensitivities and model uncertainty (in addition to the main manuscripts that tested the two VDMs at the Palo Verde and EucFACE sites (Xu et al., 2016; Medlyn et al., 2016; Medvigy et al., 2019).

- LPJ-GUESS: "Projected forest carbon fluxes (for European forests) are most sensitive to photosynthesis-, water-, and mortality-related parameters, while predictive uncertainties are dominantly induced by environmental drivers and parameters related to water and mortality." (Oberpriller et al., 2022)
- LPJ-GUESS: "The intrinsic quantum efficiency of CO_2 uptake (*alpha_C3*) and the photosynthesis scaling parameter (from leaf to canopy) (*alpha_a*) as the main

contributors of sensitivity for net primary production (NPP) (about 50 %–60 % of the overall sensitivity, Zaehle et al., 2005; Pappas et al., 2013).”

- LPJ-GUESS: The foliage projective cover parameter is sensitivity for net primary production (NPP) (Jiang et al., 2012).
- ED2: After evaluating long-term successional dynamics for a North American Upper Midwest forest authors found that “two parameters related to plant–soil water conductance and growth respiration contributed most to uncertainty in predicted NPP, with both being unobservable empirical coefficients”. And “conclude that parameter uncertainty is more important than structural uncertainty, at least for ED-2.2” (Shiklomanov et al., 2020).
- ED2: See Viskari et al., (2019) for a review on the influence of specifically canopy radiation parameter uncertainty in ED2.

Supplement Text B:

Additional knowledge gaps

With so many compounding interactions contributing to ecosystem resistance, impact, and recovery from droughts, there are still knowledge gaps in compounding processes like response to concurrent or repeated extremes, lag affects, or cascades. However, it is difficult for planned experiments to include multiple stressors and very extreme environmental conditions, thus making it challenging to assess all impacts and whether biological ecosystem components (e.g. plant-soil, plant-atmosphere, C:N, respiration-photosynthesis) will remain coupled under extreme conditions. Unfortunately, there is a lack of data on key characteristics and responses to UCEs, which greatly impacts our understanding and ability to predict ecosystem responses to such events. In addition to the general understanding of ecosystem responses to UCEs, we describe some issues which can lead to compounded and notable responses to UCEs.

Concurrent or repeated extremes: As the frequency of extreme climatic events increases, so does the likelihood of experiencing concurrent/combined or repeated EEs. Combined drought extremes and heat resulted in amplified impacts in the model applications in this study supported by studies showing stronger impact of combined drought-heat extremes on leaf mortality and plant senescence (Dressen et al., 2014). However, the sensitivity of ecosystems to repeated or combined extremes as well as their ability to acclimate remains generally unclear.

Lag effects: Ecosystems must re-establish resilience following an extreme event, but the time needed for a system to do so is difficult to predict due to unanticipated lag effects of extreme events on ecosystem functioning. Previous drought exposure has been linked to long-term mortality of forest trees in the eastern US (Berdanier and Clark, 2016) and to decreased short-term leaf survival in response to additional extreme events (Dreesen et al., 2014) suggesting a time period following disturbance where forests are particularly susceptible to additional stressors. Also, transgenerational effects of drought on leaf stoichiometry (C:N) with direct consequences for ecosystem-level C storage has been detected in perennial plant seedlings (Walter et al., 2016). However, such lag effects are generally difficult to study and are therefore generally poorly understood.

Cascades: Despite our understanding that feedbacks among ecosystem components are likely to impact environmental functioning along multiple pathways and ultimately the terrestrial carbon cycle (Reichstein et al., 2013), empirical studies of cascades are rare (but see Jentsch et al., 2011 for plant-soil measurements). In particular, our ability to predict response thresholds is poor, and additional uncertainty in predicting ecosystem responses occurs because thresholds can be passed at any organizational level within an organism (e.g. leaf, individual, plant community levels; Frank et al., 2015; Gutschick and BassiriRad, 2003) and among organisms (e.g. different sensitivities of soil fungi vs. bacteria to different disturbances; Muhr et al., 2009).

Secondary disturbance: The combination of extreme events and secondary disturbances may increase the susceptibility of carbon loss from ecosystems (e.g., Hicke et al., 2016). For example, extreme droughts and heatwaves promote forest fires by increasing both fuel flammability and lightning strike frequency (Wendler et al., 2011). Substantial forest damage can also occur through phenological changes of forest vegetation or biotic pests or pathogens. Warm winters can weaken wintertime pest mortality and increase pest growth rates (Bale et al., 2002; Cornelissen, 2011), shifting insect phenologies and triggering outbreaks. Water-stressed trees are susceptible to foliar and woody damage from forest insect and pathogens (Jactel et al., 2012, Flowers and Gonzalez-Meler, 2015; Kolb et al., 2016), and combined drought-stress and insect outbreaks can cause massive forest die-off (Allen et al., 2010; Anderegg et al., 2015b) leading to unprecedented levels of tree mortality such as those recorded in western North America (Breshears et al., 2005; Raffa, 2008). Warm winters may advance the leaf-out of deciduous species (Parmesan and Yohe, 2003), increasing their susceptibility to secondary disturbances, such as frost-damage (Gu et al., 2011; Polgar and Primack, 2011). Studies have directly linked such coupled disturbances to a decrease in seasonal C accumulation and to shifts in the development of reproductive structures (Augspurger, 2009), but the global consequences of such phenological shifts and coupled-disturbances has not been quantified (?).

Thresholds: Large-scale ecosystem studies are costly and so rarely include gradients or multiple treatment levels (but see Kreyling et al., 2014). Therefore our ability to detect and understand tipping points is still very limited. Models could play a significant role in identifying ‘zones of sensitivity’ that can be targeted in field experiments.

References:

Augspurger, C. K.: Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate deciduous forest, Func, Ecol., 23: 1031–1039. doi:10.1111/j.1365-2435.2009.01587.x, 2009.

Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K., Butterfield, J., Buse, A., Coulson, J. C., Farrar, J., Good, J. E. G., Harrington, R., Hartley, S., Jones, T. H., Lindroth, R. L., Press, M. C., Symrnioudis, I., Watt, A. D. and Whittaker, J. B.: Herbivory in global climate change research: direct effects of rising temperature on insect herbivores, Glob. Change Biol., 8: 1–16. doi:10.1046/j.1365-2486.2002.00451.x, 2002.

Berdanier, A. B. and Clark, J. S.: Multiyear drought-induced morbidity preceding tree death in southeastern U.S. forests, Ecol Appl, 26: 17–23. doi:10.1890/15-0274, 2016.

Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Randy G. Balice, Romme, WH, Kastens, JH, Floyd, M L, Belnap, J, Anderson, JJ, Myers, OB, and Meyer, CW.: Regional Vegetation Die-off in Response to Global-Change-Type Drought, PNAS, 102, 15144–15148, 2005.

Cornelissen, T.: Climate change and its effects on terrestrial insects and herbivory patterns. Neotrop. entomol. 40, 155-163, http://dx.doi.org/10.1590/S1519-566X2011000200001, 2011.

Duursma, R.A., Gimeno, T.E., Boer, M.M., Crous, K.Y., Tjoelker, M.G. and Ellsworth, D.S.: Canopy leaf area of a mature evergreen *Eucalyptus* woodland does not respond to elevated atmospheric [CO_2] but tracks water availability. Glob. Change Biol., 22, 1666-1676. https://doi.org/10.1111/gcb.13151, 2016.

Flowers C.E. and M.A. Gonzalez-Meler: Responses of temperate forest productivity to insect and pathogen disturbances, Ann Rev Plant Sci, 66:547-569, 2015.

Frank, D., Reichstein, M., Bahn, M., Thonicke, K., Frank, D., Mahecha, M. D., Smith, P., van der Velde, M., Vicca, S., Babst, F., Beer, C., Buchmann, N., Canadell, J. G., Ciais, P., Cramer, W., Ibrom, A., Miglietta, F., Poulter, B., Rammig, A., Seneviratne, S. I., Walz, A., Wattenbach, M., Zavala, M. A. and Zscheischler, J.: Effects of climate extremes on the terrestrial carbon cycle: concepts, processes and potential future impacts, Glob. Change Biol., 21, 2861–2880, doi:10.1111/gcb.12916, 2015.

Gutschick, V. P. and BassiriRad, H.: Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences, New Phytol., 160, 21–42, doi:10.1046/j.1469-8137.2003.00866.x, 2003.

Hicke, J.A., A.J.H. Meddens, C.A. Kolden: Recent tree mortality in the western United States from bark beetles and forest fires, Forest Science 62, 141-153, 2016.

Jactel, H., Petit, J., Desprez-Loustau, M.-L., Delzon, S., Piou, D., Battisti, A. and Koricheva, J.: Drought effects on damage by forest insects and pathogens: a meta-analysis, Glob. Change Biol., 18, 267–276. doi:10.1111/j.1365-2486.2011.02512.x, 2012.

Jentsch, A., Kreyling, J., Elmer, M., Gellesch, E., Glaser, B., Grant, K., Hein, R., Lara, M., Mirzae, H., Nadler, S. E., Nagy, L., Otieno, D., Pritsch, K., Rascher, U., Schädler, M., Schloter, M., Singh, B. K., Stadler, J., Walter, J., Wellstein, C., Wöllecke, J. and Beierkuhnlein, C.: Climate extremes initiate ecosystem-regulating functions while maintaining productivity, J. of Ecol., 99, 689–702, doi:10.1111/j.1365-2745.2011.01817.x, 2011.

Jiang, Y., Zhuang, Q., Schaphoff, S., Sitch, S., Sokolov, A., Kicklighter, D., and Melillo, J.: Uncertainty analysis of vegetation distribution in the northern high latitudes during the 21st century with a dynamic vegetation model, Ecol. Evol., 2, 593-614, https://doi.org/10.1002/ece3.85, 2012.

Kalacska, M.E.R., Sánchez-Azofeifa, G.A., Calvo-Alvarado, J.C., Rivard, B. and Quesada, M.: Effects of Season and Successional Stage on Leaf Area Index and Spectral Vegetation Indices in Three Mesoamerican Tropical Dry Forests. Biotropica, 37: 486-496. https://doi.org/10.1111/j.1744-7429.2005.00067.x, 2005.

Medlyn, B.E., De Kauwe, M.G., Zaehle, S., Walker, A.P., Duursma, R.A., Luus, K., Mishurov, M., Pak, B., Smith, B., Wang, Y.-P., Yang, X., Crous, K.Y., Drake, J.E., Gimeno, T.E., Macdonald, C.A., Norby, R.J., Power, S.A., Tjoelker, M.G. & Ellsworth, D.S.: Using models to guide field experiments: a priori predictions for the CO2 response of a nutrient- and water-limited native Eucalypt woodland, Glob. Change Biol., 22, 2834-2851, 2016.

Muhr, J., Borken, W. and Matzner, E.: Effects of soil frost on soil respiration and its radiocarbon signature in a Norway spruce forest soil, Glob. Change Biol., 15, 782–793, doi:10.1111/j.1365-2486.2008.01695.x, 2009.

Oberpriller, J., Herschlein, C., Anthoni, P., Arneth, A., Krause, A., Rammig, A., Lindeskog, M., Olin, S., and Hartig, F.: Climate and parameter sensitivity and induced uncertainties in carbon stock projections for European forests (using LPJ-GUESS 4.0), Geosci. Model Dev., 15, 6495–6519, https://doi.org/10.5194/gmd-15-6495-2022, 2022.

Pappas, C., Fatichi, S., Leuzinger, S., Wolf, A., and Burlando, P.: Sensitivity analysis of a process-based ecosystem model: Pinpointing parameterization and structural issues, J. Geophys. Res.-Biogeo., 118, 505–528, https://doi.org/10.1002/jgrg.20035, 2013.

Parmesan, C and G. Yohe: A globally coherent fingerprint of climate change impacts across natural systems, Nature, 421, 37-42, 2003.

Polgar, C. A. and Primack, R. B.: Leaf-out phenology of temperate woody plants: from trees to ecosystems, New Phytol., 191, 926–941, doi:10.1111/j.1469-8137.2011.03803.x, 2011.

Raffa, K. F.: Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions, BioScience, 58, 501-517, 2008.

Reichstein, M, Bahn, M, Ciais, P, Frank, D, Mahecha, MD, Seneviratne, SI, Zscheischler, J, Beer, C, Buchmann, N, Frank, DC, Papale, D, Rammig, A, Smith, P, Thonicke, K, van der Velde, M, Vicca, S, Walz, A and Wattenbach, M.: Climate extremes and the carbon cycle, Nature, 500, 287-295, 2013.

Sheffield, J., Goteti, G. & Wood, E.F.: Development of a 50-year high-resolution global dataset of meteorological forcings for land surface modeling, J. Clim., 19, 3088–3111, 2006.

Shiklomanov, AN, Bond-Lamberty, B, Atkins, JW, Gough, CM.: Structure and parameter uncertainty in centennial projections of forest community structure and carbon cycling, Glob. Change Biol., 26, 6080– 6096, https://doi.org/10.1111/gcb.15164, 2020.

Viskari T., Shiklomanov A., Dietze M.C., Serbin S.P.: The influence of canopy radiation parameter uncertainty on model projections of terrestrial carbon and energy cycling, PLoS ONE 14, e0216512, https://doi.org/10.1371/journal.pone.0216512, 2019.

Walter, J., Harter, D. E. V., Beierkuhnlein, C. and Jentsch, A.: Transgenerational effects of extreme weather: perennial plant offspring show modified germination, growth and stoichiometry, J Ecol, doi:10.1111/1365-2745.12567, 2016.

Wendler G, Conner J, Moor B, Shulski M, Stuefer M.: Climatology of Alaskan wildfires with special emphasis on the extreme year of 2004, Theoretical and Applied Climatology, 104, 459–472, 2011.

Zaehle, S., Sitch, S., Smith, B., and Hatterman, F.: Effects of parameter uncertainties on the modeling of terrestrial biosphere dynamics, Global Biogeochem. Cy., 19, GB3020, https://doi.org/10.1029/2004GB002395, 2005.