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

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Abstract

Climatic extreme events are expected to occur more frequently in the future, increasing the likelihood of unprecedented climate extremes (UCEs), or record-breaking events. UCEs, such as extreme heatwaves and droughts, substantially affect ecosystem stability and carbon cycling by increasing plant mortality and delaying ecosystem recovery. Quantitative knowledge of such effects is limited due to the paucity of experiments focusing on extreme climatic events beyond the range of historical experience. Here, we present a road map of how two dynamic vegetation demographic models (VDMs) can be used to investigate hypotheses surrounding ecosystem responses to UCEs (e.g., unprecedented droughts). As a result of nonlinear ecosystem responses to UCEs, that are qualitatively different from responses to milder extremes, we consider both biomass loss and recovery rates over time, by reporting a time-integrated carbon loss as a result of UCE, relative to the absence of drought. Additionally, we explore how unprecedented droughts in combination with increasing atmospheric CO_2 and/or temperature may affect ecosystem stability and carbon cycling. We explored these questions using simulations of pre-drought and post-drought conditions at well-studied forest sites, using the ED2 and LPJ-GUESS models. Due to the two models having different but plausible representations of processes and interactions, they diverge in sensitivity of nonlinear biomass loss due to drought duration or intensity, and differ between each site. Biomass losses are most sensitive to drought duration in ED2, but to drought intensity in LPJ-GUESS. Elevated atmospheric CO_2 concentrations (eCO_2) alone did not completely buffer the ecosystems from carbon losses during UCEs in the majority of our simulations. Our findings highlight contrasting differences in process formulations and uncertainties in models, most notably related to availability in plant carbohydrate storage and the diversity of plant hydraulic schemes, in projecting potential ecosystem responses to UCEs. We provide a summary of the current state and role of many model processes that give way to different underlying hypotheses of plant responses to UCEs, reflecting knowledge gaps, which should be tested with targeted field experiments and an iterative modeling-experimental conceptual framework.

1 Introduction

The increase in extreme climate and weather events, such as prolonged heatwaves and droughts as seen over the last three decades, are expected to continue to increase in frequency and magnitude, leading to progressively longer and warmer droughts on land (IPCC 2012, 2021). Droughts are affecting all areas of the globe, more than any other natural disturbance, and recent droughts have broken long-standing records (Ciais et al., 2005; Phillips et al., 2009; Williams et al., 2012; Matusick et al., 2013; Griffin and Anchukaitis, 2014; Asner et al., 2016; Feldpausch et al., 2016; Seneviratne et al., 2021). Such 'unprecedented climate extremes' (UCEs; "record-breaking events", IPCC (2012)) that are larger in extent and longer-lasting than historical norms can have dramatic consequences for terrestrial ecosystem processes, including carbon uptake and storage and other ecosystem services (Reichstein et al., 2013; Settele, 2014; Allen et al., 2015; Brando et al., 2019; Kannenberg et al., 2020). Thus, to better anticipate the implications of climatic changes for the terrestrial carbon sink and other ecosystem services, we need to better understand how ecosystems respond to extreme droughts and other UCEs.

To learn how ecosystems respond to rarely experienced or unprecedented conditions, ecologists can experimentally manipulate environmental conditions (Rustad, 2008; Beier et al., 2012; Meir et al., 2015; Aguirre et al., 2021). However, the majority of such experiments apply moderate treatments based on a historical sense, which are mostly weaker in intensity and/or shorter in duration than potential future UCEs (Beier et al., 2012; Kayler et al., 2015; but see Luo et al., 2017), and single experiments have low power to detect effects of stressors on ecosystem responses (Yang et al., 2022). Additionally, most experiments examine low-stature ecosystems, such as grassland, shrubland or tundra, due to lower requirements for infrastructure and financial investment compared to mature forests. However, forests may respond qualitatively differently to UCEs than other ecosystems, in part due to mortality of large trees and strong nonlinear ecosystem responses, with long-lasting consequences for ecosystem-climate feedbacks (Williams et al., 2014; Meir et al., 2015). Ecosystem responses to naturally occurring extreme droughts and heatwaves have been documented (Ciais et al., 2005; Breshears et al., 2009; Feldpausch et al., 2016; Matusick et al., 2016; Ruthrof et al., 2018; Powers et al,. 2020); however, these rapidly-mobilized post-hoc studies often are unable to measure all critical variables and may lack consistently collected data for comparison with pre-drought conditions, thus limiting their inferential power and ability to improve quantitative models. The difficulties of performing

controlled real-world experiments of UCEs at broad spatial and temporal scales make process-based modeling a valuable tool for studying potential ecosystem responses to extreme events.

Process-based models can be used to explore potential ecosystem impacts using projected climate change over broad spatial and temporal scales (Gerten et al., 2008; Luo et al., 2008; Zscheischler et al., 2014; Sippel et al., 2016), as seen in a few modeling studies that have synthesized and improved our process-level understanding of UCE effects (McDowell et al., 2013; Dietze and Matthes, 2014). However, due to the overly simplified representation of ecological processes in most land surface models (LSMs) – the terrestrial components of Earth System Models (ESMs) used for climate projections – it is doubtful whether most of these models adequately capture ecosystem feedbacks and other responses to UCEs (Fisher and Koven, 2020). For example, only a few ESMs in recent coupled model intercomparison projects (CMIP6) and IPCC climate assessments (Ciais et al., 2013; Arora et al., 2020) include vegetation demographics (Döscher et al., 2022), and most rely on prescribed, static maps of plant functional types (PFTs) (Ahlström et al., 2012). Other LSMs simulate PFT shifts (i.e., dynamic global vegetation models, DGVMs; Sitch et al., (2008)) based on bioclimatic limits, instead of emerging from the physiology- and competition-based demographic rates that determine resource competition and plant distributions in real ecosystems (Fisher et al., 2018). Although a new generation of LSMs with more explicit ecological dynamics and structured demography is emerging (Holm et al., 2020; Koven et al., 2020; Döscher et al., 2022), most current ESMs are limited in ecological detail and realism (e.g., ecosystem structure, demography, and disturbances). Failing to mechanistically represent mortality, recruitment, and disturbance – each of which influences biomass turnover and carbon (C) allocation (Friend et al., 2014) – limits the ability of these models to realistically forecast ecosystem responses to anomalous environmental conditions like UCEs (Fisher et al., 2018).

Evaluating and improving the representation of physiological and ecological processes in ecosystem models is critical for reducing model uncertainties when projecting the effects of UCEs on long-term ecosystem dynamics and functioning. Vegetation demography, plant hydraulics, enhanced representations of plant trait variation, explicit treatments of resource competition (e.g., height-structured competition for light), and representing major disturbances (e.g., extreme drought) have all been identified as critical areas for advancing current models (Scheiter et al., 2013; Fisher et al., 2015; Weng et al., 2015; Choat et al., 2018; Fisher et al.,

2018; Blyth et al., 2021) and are necessary advances for realistically representing the ecosystem impacts of UCEs. In this perspectives focused paper we look at the differences in these processes, and how they contribute to uncertainty across multiple temporal phases surrounding an extreme event: predicting an ecosystem's pre-disturbance resistance, which influences the degree of impact and recovery from UCEs. Table 1 describes a summary of model mechanisms that affect pre-drought resistance and post-drought recovery and we suggest are critical areas further research (ca. Frank et al., 2015).

In order to inform our discussion, we explore the potential responses of forest ecosystems to UCEs using two state-of-the-art process-based demographic models (vegetation demographic models, VDMs; Fisher et al., (2018)), a unique model exploration-discussion approach to help highlight new paths forward for model advancement. We first present conceptual frameworks and hypotheses on potential ecosystem responses to UCEs based on current knowledge. We then present VDM simulations for a range of hypothetical UCE scenarios to illustrate current state-of-the-art model representations of eco-physiological mechanisms expected to drive responses to UCEs. While a variety of UCE-linked biophysical tree disturbance processes (e.g., fire, wind, insect outbreaks) can drive nonlinear ecosystem responses, we focus specifically on extreme droughts, which have important impacts on many ecosystems around the world (e.g. Frank et al., 2015, IPCC 2021). By studying modeled responses to UCEs, we explore the limits to our current understanding of ecosystem responses to extreme droughts and their corresponding thresholds and tipping points. As anthropogenic forcing has increased the frequency, duration, and intensity of droughts throughout the world (Chiang et al., 2021), we explore how eCO_2 and rising temperatures may affect drought-induced C loss and recovery trajectories, and how the scientific community can iteratively address these questions through experiments and modeling studies. We believe the combination of using cutting-edge VDMs alongside an inspection of current gaps in knowledge will help guide modeling and experimental advances in order to address novel forest responses to climate extremes.

1.1 Conceptual and Modeling Framework for Hypothesis Testing:

We combine conceptual frameworks (Fig. 1) and ecosystem modeling to test two hypotheses on potential responses of plant carbon stocks to UCEs. The first hypothesis is:

Hypothesis (H1). Terrestrial ecosystem responses to UCEs will differ qualitatively from ecosystem responses to milder extremes because responses are nonlinear. Nonlinearities can arise from multiple mechanisms – including shifts in plant hydraulics, C allocation, phenology, and stand demography – and can vary depending on the pre-drought state of the ecosystem.

We present four conceptual relationships that describe terrestrial ecosystem responses to varying degrees of extreme events (Fig. 1). Change in vegetation C stock is related to drought intensity and/or drought duration in a near-linear relationship (Fig. 1a, H0, null hypothesis), which has some observational support from annual and perennial grassland ecosystems, shrublands and savannas across the globe (Bai et al., 2008; Muldavin et al., 2008; Ruppert et al., 2015). We recognize that most ecological systems are nonlinear, thus alternatives to the null hypothesis are that biomass loss increases nonlinearly with increased drought intensity (i.e., reduction in precipitation) represented by a threshold-based relationship (Fig. 1a, H1a), increased drought duration (i.e., prolonged drought with the same intensity) by shifting the near-linear relationship downwards via increasing slopes (Fig. 1a, H1b), or the combination of both intensity and duration (Fig. 1a, H1c). These hypotheses are supported by observations from the Amazon Basin and Borneo (Phillips et al., 2010) where tree mortality rates increased nonlinearly with drought intensity. Similarly, plant hydraulic theories predict nonlinear damage to the plant-water transport systems, and thus mortality risk, as a function of drought stress (Sperry and Love, 2015). In particular, longer droughts are more likely to lead to lower soil water potentials, leading to a nonlinear xylem damage function even if stomata effectively limit water loss (Sperry et al., 2016).

Hypothesis (H2): The effects of increasing atmospheric CO_2 concentration (eCO_2) will alleviate impacts of extreme drought stress through an increase in vegetation productivity and water-use efficiency, but only up to a threshold of drought severity, while increased temperature (and related water stress) will exacerbate tree mortality.

This second hypothesis is based on growing evidence that effects of eCO_2 and climate warming may interact with effects of drought intensity on ecosystems. The CO_2 fertilization effect enhances vegetation productivity (e.g., net primary production, NPP) (Ainsworth and Long, 2005; Norby et al., 2005; Wang et al., 2012), but this fertilization effect is generally

reduced by drought (Hovenden et al., 2014; Reich et al., 2014; Gray et al., 2016). Drought events often coincide with increased temperature, which intensifies the impact of drought on ecosystems (Allen et al., 2015; Liu et al., 2017), resulting in nonlinear responses in mortality rates (Adams et al., 2009; Adams et al., 2017a). The evaluation of C cycling in VDMs with doubling of CO_2 (only "beta effect") showed a large carbon sink in a tropical forest (Holm et al., 2020), but the inclusion of climate interactions in VDMs needs to be further explored.

Here, we relate ecosystem responses to UCEs by calculating the "integrated carbon (C) loss" (Fig. 1b and see Methods), which integrates C loss from the beginning of the drought until the time when C stocks have recovered to 50% of the pre-drought level. In response to drought, warming, and eCO_2, divergent potential C responses (gains and losses; Fig. 1c) can be expected (Keenan et al., 2013; Zhu et al., 2016; Adams et al., 2017a). For example, a grassland macrocosm experiment found that eCO_2 completely compensated for the negative impact of extreme drought on net carbon uptake due to increased root growth and plant nitrogen uptake, and led to enhanced post-drought recovery (Roy et al., 2016). However, a 16-year grassland FACE and the SoyFACE experiments showed that CO_2 fertilization effects were reduced or eliminated under hotter/drier conditions (Gray et al., 2016; Obermeier et al., 2016). Reich et al., (2014) also found that CO_2 fertilization effects were reduced in a perennial grassland by water and nitrogen limitation.

A corollary to our H2 is that conditions that favor productivity (e.g., longer growing seasons and/or CO_2 fertilization) will enhance vegetation growth leading to "structural overshoot" (SO; Fig. 1d; adapted from and supported by Jump et al., 2017), and can amplify the effects of UCEs. Enhanced vegetation growth coupled with environmental variability can lead to exceptionally high plant-water-demand during extreme drought and water stress, resulting in a "mortality overshoot" (MO; Fig 1d). We conceptualize how oscillations between SO and associated MO could be amplified by increasing climatic variability and UCEs (Fig. 1d). Confidence is low as to how historically unprecedented eCO_2 levels and temperatures will affect ecosystems in the future (i.e., the widening of the shaded areas compared to historical, Fig. 1d). We expect, however that a rapidly changing climate, combined with effects of UCEs as a result of more frequent extreme drought/heat events and drought stress, can exacerbate and amplify SOs and MOs (Jump et al., 2017), leading to increasing C loss, even though various buffering

mechanisms exist (cf. (Lloret et al., 2012; Allen et al., 2015)). Relative to our conceptual (Fig. 1d), we note that most experimental, observational and modeling studies (Ciais et al., 2005; da Costa et al., 2010; Phillips et al., 2010; Meir et al., 2015) take into account only low to moderate drought intensities (such as 50% rain excluded) or single events, or combine drought with moderate effects of temperature change. Where there has been 100% rain exclusion, it was on very small plots of 1.5 m^2 (Meir et al., 2015). As represented by the increasing amplitude of oscillations in Fig. 1d, the interactions between increased temperatures, UCE events, and vegetation feedbacks make ecosystem states become inherently unpredictable, particularly over longer time-scales.

2 Vegetation Demography Model (VDM) Approaches

We argue that VDMs are well suited to address climate change impacts due to the inclusion of detailed process representation of dynamic plant growth, recruitment, and mortality, resulting in changes in abundance of different PFTs, as well as vertically stratified tree size- and age-class structured ecosystem demography. Community dynamics and age-/size-structure are emergent properties from competition for light, space, water, and nutrients, which dynamically and explicitly scale up from the tree, to stand, to ecosystem level. Within this characterization, VDMs also differ between each other and are set up in different configuration, allowing for various testing capabilities. For full names of each model listed below and references, see Table S1. For example, VDMs can aggregate and track the community level disturbance into either patch-tiling sampling (e.g., ED2, FATES, LM3-PPA, ORCHIDEE, JSBACH4.0) or statistical approximations (e.g., LPJ-GUESS, SEIB-DGVM, and CABLE-POP). VDMs could also vary in representing light competition within either multiple canopy layers (e.g., ED2, FATES, LM3-PPA, LPJ-GUESS, SEIB-DGVM) or in a single canopy (e.g., JSBACH4.0, ORCHIDEE, CABLE-POP).

Powell et al. (2013) compared multiple VDMs and LSMs to interpret ecosystem responses to long-term droughts in the Amazon and are informative when conducting model-data comparisons, but studies of the cascade of ecosystem responses and mortality to UCEs are lacking. In a cutting-edge area of development, new mechanistic implementation of plant competition for water and plant hydraulics in VDMs (i.e., hydrodynamics) are improving our understanding of plant-water relations and stresses within plants, such as with TFSv.1-Hydro

(Christoffersen et al., 2016), ED2-hydro (Xu et al., 2016), and FATES-HYDRO (Ma et al., 2021; Fang et al., 2022). Compared to more simplistic representation of plant acquiring soil moisture not connected to plant physiology (e.g., LPJ-GUESS, LM3-PPA, CABLE-POP, SEIB-DGVM). For hydrodynamic representations in 'big-leaf' LSMs such as CLM5, JULES, and Noah-MP-PHS see Kennedy et al., (2019), Eller et al., (2020), and Li et al., (2021) respectively.

The discussion section provides a deeper investigation of model response to UCEs related to droughts. An exhaustive review of all VDMs, and all plant processes is too large to be done here. Existing review papers of different VDM development, processes, and uncertainties can be found here: Fisher et al., (2018); Bonan (2019); Trugman et al., (2019); Hanbury-Brown et al. (2022); Bugmann and Seidl (2022); and specifically related to plant hydraulics see: Mencuccini et al., (2019); Anderegg and Venturas (2020). We use LPJ-GUESS and ED2 as example VDMs in an initial guide framework to explore hypotheses around vegetation mortality and integrated carbon loss from UCEs and climate change impacts, and highlight limiting model processes. Since field data needed to evaluate UCE responses are, by definition, unavailable, we do not perform model-data comparisons. Rather, we use the model results and conceptual framework as a road map to explore our hypotheses and illustrate their implications for ecosystem responses under UCEs, not historical drought events.

2.1 LPJ-GUESS and ED2 Model Descriptions

We explored our hypotheses at forested ecosystems in Australia and Central America using two VDMs: the Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) (Smith et al., 2001; Smith et al., 2014) and the Ecosystem Demography model 2 (ED2) (Medvigy et al., 2009; Medvigy and Moorcroft, 2012). Both LPJ-GUESS and ED2 resolve vegetation into tree cohorts characterized by their PFT, in addition to age-class in LPJ-GUESS; and size, and stem number density in ED2. Both models are driven by external environmental drivers (e.g., temperature, precipitation, solar radiation, atmospheric CO_2 concentration, nitrogen deposition), and soil properties (soil texture, depth, etc.), and also depend on dynamic ecosystem state, which includes light attenuation, soil moisture, and soil nutrient availability. Establishment and growth of PFTs, and their carbon-, nitrogen- and water-cycles, are simulated across multiple patches per grid cell to account for landscape heterogeneity. Both models characterize PFTs by physiological

and bioclimatic parameters, which vary between the models (Smith et al., 2001; Smith et al., 2014; Medvigy et al., 2009; Medvigy and Moorcroft, 2012).

The LPJ-GUESS includes three woody PFTs: evergreen, intermediate evergreen, and deciduous PFTs. Mortality in LPJ-GUESS is governed by a 'growth-efficiency'-based function (kg C m^{-2} leaf yr^{-1}), which captures effects of water deficit, shading, heat stress, and tree size on plant productivity relative to its resource-uptake capacity (leaf area), with a threshold below which stress-related mortality risk increases markedly, in addition to background senescence and exogenous disturbances. Stress mortality can be reduced by plants using labile carbon storage, modeled implicitly using a 'C debt' approach, which buffers low productivity, enhancing resilience to milder extremes (more details are given in section 4.1.4). Total mortality can thus be impacted by variation in environmental conditions such as water limitation, low light conditions, and nutrient constraints, as well as current stand structure (Smith et al., 2001; Hickler et al., 2004).

The ED2 version used here (Xu et al., 2016) includes four woody PFTs: evergreen, intermediate evergreen, deciduous, brevi-deciduous, and deciduous stem-succulent. This ED2 version includes coupled photosynthesis, plant hydraulics, and soil hydraulic modules (Xu et al., 2016), which together determine plant water stress. The plant hydraulics module tracks water flow along a soil–plant–atmosphere continuum, connecting leaf water potential, stem sap flow, and transpiration, thus influencing controls on photosynthetic capacity, stomatal closure, phenology, and mortality. Leaf water potential depends on time-varying environmental conditions as well as time-invariant PFT traits. Leaf shedding is triggered when leaf water potential falls below the turgor loss point (a PFT trait) for a sufficient amount of time. Leaf flushing occurs when stem water potential remains high (above half of the turgor loss point) for a sufficient time (see Xu et al., 2016 for details). PFTs differ in their hydraulic traits, wood density, specific leaf area, allometries, rooting depth, and other traits. Stress-based mortality in the ED2 version used here includes two main physiological pathways in our current understanding of drought mortality (McDowell et al., 2013): C starvation and hydraulic failure. Mortality due to C starvation in ED2 results from a reduction of C storage, a proxy for non-structural carbohydrate (NSC) storage, which integrates the balance of photosynthetic gain and maintenance cost under different levels of light and moisture availability. Mortality due to

hydraulic failure in ED2 is based on the percentage loss of stem conductivity. ED2 also includes a density-independent senescence mortality rate based on wood density.

2.2 Modeling guide

To exemplify how VDMs can be tools to explore new hypotheses related to UCEs we applied the models at two field sites, that were chosen due to being extensively studied and the models used here have already been run at these sites and previously benchmarked against field data (see Xu et al., 2016; Medlyn et al., 2016; Medvigy et al., 2019 for model-data validation). The purpose of this paper was not to do a large multi-site comparison, but rather just select a few for hypothesis testing. In addition, the two sites span a range of vegetation types and are in warm, seasonally dry climates that are more likely to experience droughts in the future (Allen et al., 2017). The first is a mature *Eucalyptus* (*E. tereticornis*) warm temperate-subtropical transitional forest that is the site of the Eucalyptus Free Air CO_2 enrichment (EucFACE) experiment in Western Sydney, Australia (Medlyn et al., 2016; Ellsworth et al., 2017; Jiang et al., 2020). The second site is a seasonally dry tropical forest in the Parque Nacional Palo Verde in Costa Rica (Powers et al., 2009). Site description details can be found in Supplement Text A.

We performed a 100-year "baseline" simulation for each model at each site driven by constant, near ambient, atmospheric CO_2 (400 ppm) and recycled historical site-specific climate data (1992-2011 for EucFACE and 1970-2012 for Palo Verde; Sheffield et al., (2006)), absent of drought treatments. A detailed description of the meteorological data and initial conditions used to drive the models is in the Supplementary Text A. The two models were previously tuned for each site (Xu et al., 2016; Medlyn et al., 2016), and no additional site-level parameter tuning was conducted here due to evaluating responses from hypothetical UCEs. To describe the ecosystem impact of UCEs, we simulated 10 years of pre-drought conditions (continuing from the baseline simulation), followed by drought treatments that differed in intensity and duration, followed by a 100-year post-drought recovery period. To explore the effects of drought intensity, we conducted 20 different artificial drought intensity simulations, in which precipitation during the whole year is reduced by 5% to 100% of its original amount, in increments of 5%. To explore the effects of drought duration, the 20 different drought intensities are maintained over 1, 2 and 4 years (Table S2). We examined model responses of aboveground biomass, leaf area index (LAI), stem density (number ha^{-1}), plant available soil water (mm), plant C storage (kg C m^{-2}), change in stem mortality rate (yr^{-1}), and PFT composition.

To explore how temperature, eCO_2 concentration, and UCE droughts influence forest C dynamics individually and in combination, we implemented the following five experimental scenarios, some realistic and others hypothetical, for each model (Table S2): increased temperature only (+2K over ambient), eCO_2 only (600 ppm and 800 ppm), and both increased temperature and eCO_2 (+2K 600 ppm; +2K 800 ppm). Temperature and eCO_2 manipulations were applied as step increases over the baseline conditions, and are artificial scenarios, as opposed to model-generated climate projections.

2.3 Linking concepts, hypotheses, and model outcomes

To relate our simulation results to Fig. 1a, we compared the total biomass loss as a result of each drought treatment by calculating the percentage of biomass reduction at the end of the drought period relative to the baseline (no drought) simulation. To explicitly consider biomass recovery rates over time, we calculated "integrated-C-loss" (Eqs. 1-3), as a result of drought under current climate, which are determined based on the concepts in Fig. 1b. We defined "integrated-C-loss" as the time-integrated carbon in biomass that is lost due to drought relative to what the vegetation would have stored in the absence of drought. That is, it is the difference between biomass in the presence of drought (B_d) at time (t) and biomass in the baseline simulation (no drought; B_{base}), integrated over a defined recovery time period (in kg C m^{-2} yr):

$$\text{Integrated-C-loss} = \int_{t=t_1}^{t=t_2} (B_{base}(t) - B_d(t))\, dt \quad \text{(Eq. 1)}$$

To define the bounds of integration, in Eq. 1, t_1 is defined as the time when the maximum amount of plant C is lost as a result of the drought:

$$B_{base}(t_1) - B_d(t_1) = \max_t [B_{base}(t) - B_d(t)] \quad \text{(Eq. 2)}$$

Then, t_2 is defined implicitly as the time when 50% of the lost biomass has been recovered compared to the baseline:

$$B_{base}(t_2) - B_d(t_2) = \frac{1}{2}(B_{base}(t_1) - B_d(t_1)) \quad \text{(Eq. 3)}$$

362 Since all integrated-C-loss results are taken as the difference from a non-drought baseline
363 biomass (B_{base}) and all droughts will result in a loss of C.
364 We also use integrated-C-loss to examine the role of drought, temperature and eCO_2
365 change for moderating or exacerbating the impacts of drought on forest C stocks; i.e., to evaluate
366 the hypotheses illustrated in Fig. 1c. To assess these impacts of changing climates, we calculate
367 an "integrated-C-change" (Eq. 4). Defined as the difference between the integrated-C-loss due to
368 drought alone (Eqs. 1-3) under present climate, and the integrated-C-loss due to the combined
369 effects of drought and climate change (i.e., five scenarios of temperature increase and eCO_2):

$$\text{Integrated-C-change} = integrated\ C\ Loss_{Drought} - integrated\ C\ Loss_{Drought+CC} \quad \text{(Eq. 4)}$$

370
371 Because we expect drought to reduce vegetation C stocks, and thus integrated-C-loss to
372 be negative, positive values of integrated-C-change indicate that changes in climatic drivers
373 reduced the C losses from drought (i.e., buffering effects). Negative values of integrated-C-
374 change indicate that the climate change scenario leads to either greater C losses or losses that
375 persist for longer amounts of time (i.e., magnitude and/or duration) compared to a simulation
376 with no climate change (i.e., "reference" run).
377

378 **3 Results**

379 As a basis for the treatment results presented here, we compared the baseline simulations
380 (prior to drought or climate change treatments) of the two VDMs to observations at both sites for
381 biomass and LAI (Table S3, Fig. S1). Both models had similar biomass compared to
382 observations at Palo Verde (10.4 - 11.7 vs. 11.0 kgC m^{-2}), and at EucFACE biomass matched
383 well in LPJ-GUESS (12.1 vs. 12.7 kgC m^{-2}) but was low in ED2 (5.6 kgC m^{-2}). Both models also
384 had similar LAI to observations at Palo Verde (3.3 – 4.5 vs. 3.8 (± 1.06) m^2 m^{-2}), and at
385 EucFACE LAI matched well in ED2 (1.6 vs. 1.7 m^2 m^{-2}), but was high for LPJ-GUESS (3.2 m^2
386 m^{-2}). At EucFACE LAI ranged from 1.2 to 2.1 over a 28-month measurement period (Duursma
387 et al., (2016), but LPJ-GUESS had very large fluctuations in annual LAI outside of these ranges
388 (Fig. S1). These models are well documented and investigated VDMs, with many studies that
389 have looked into parameter uncertainty (see Supplemental Text A for select references that
390 explore model/parameter sensitivity).

Both models displayed nonlinear responses to drought, in concurrence with Hypothesis H1, but they differ in their behavior and between sites. In general, ED2 shows sensitivity to drought duration (Hypothesis H1b), while LPJ-GUESS shows a stronger sensitivity to drought intensity (Hypothesis H1a). ED2's sensitivity to the duration of drought was mild at Palo Verde (Fig. 2a), and stronger at EucFACE particularly during the 4-year drought with a strong non-monotonic pattern (see explanation below) (Fig. 2b). When reporting only percentage of biomass loss, ED2 predicts close to no UCE response at Palo Verde; with a maximum biomass reduction of only 40% during 95% precipitation removal and a 4-year drought event (i.e., UCE). LPJ-GUESS shows very little sensitivity to drought duration but is highly sensitive to drought intensity. C loss predicted by LPJ-GUESS at Palo Verde reached a threshold at ~65% drought intensity, after which forests exhibit strong biomass losses, up to 100% (Fig. 2a). At the EucFACE site, both models predict a critical threshold of biomass loss at 35%-45% drought intensity, with LPJ-GUESS predicting total biomass loss (up to 100%) after this drought intensity threshold (Fig. 2b). The EucFACE drought threshold is lower than that of the seasonally dry mixed tropical forest in Palo Verde.

With respect to C loss over a recovering time period (integrated-C-loss), the two models predict similar drought responses at Palo Verde (Fig. 2c), but not at EucFACE (Fig. 2d). At Palo Verde, the similarity between models in integrated-C-loss reflected longer biomass recovery time but less biomass loss in the short-term in ED2 relative to LPJ-GUESS, which predicted greater biomass loss immediately after drought but shorter recovery time. With the exception of the 1-year drought in ED2, both models predict similar integrated-C-loss across a range of UCEs at Palo Verde, via different pathways. The integrated-C-loss metric revealed a strong nonlinear response to drought duration in ED2 (Fig. 2c), while this nonlinearity is less evident when only examining change in biomass (Fig. 2a). The "V"-shaped patterns observed particularly in Fig. 2b, arise from interactions between whole-leaf phenology and stomatal responses to drought in ED2. For drought intensities lower than 40%, stomatal conductance is reduced but leaves are not fully shed. Leaf respiration continues, gradually depleting non-structural C pools, followed by a loss of biomass. However, for higher drought intensities, leaf water potentials quickly become systematically lower than leaf turgor loss points and tree cohorts shed all their leaves. This strategy represents an immediate loss of C via leaf shedding, but spares the cohort from slow, respiration-driven depletion of C stocks.

3.1 Predicted model responses to UCE droughts combined with increased temperature and/or eCO_2

Relating to our second hypothesis of additional effects of warming and eCO_2, we tested 15 treatments in total, repeating the five climate change scenarios for each of the three drought durations. With the addition of climate change impacts, ED2 remained sensitive to the duration of drought, with warming negatively impacting integrated-C-change and most consistently during 2- and 4-year drought durations. ED2 predicts that during the 2- and 4-year droughts at EucFACE, losses are exacerbated when accompanied with warming, even with eCO_2, with 600 ppm having a more detrimental impact than the more elevated 800 ppm (Fig. 3b-c). The average integrated-C-change was -111.0 kg C m^{-2} yr across all 15 treatments (Table 2). Only during the 1-year drought duration did drought plus warming and eCO_2 have a buffering effect on C stocks, seen in four out of our five scenarios but only during relatively modest droughts intensities (Fig. 3a; i.e., positive integrated-C-change, see also Table 2).

The ED2 simulations of the seasonally dry Palo Verde site (Fig. 3d-f), produced less frequent negative impacts on drought and climate change driven C losses compared to EucFACE, with an average integrated-C-change of -53.9 kg C m^{-2} yr^{-1} across all 15 treatments (Table 2). During the 2-year drought, applying +2K with eCO_2 to 600 ppm showed a slight buffering effect to droughts and the most consistent positive integrated-C-change (Fig. 3e; Table 2). Interestingly, an increase in only eCO_2 to 800 ppm (no warming) when applied with the 2- and 4-year droughts resulted in the largest loss in integrated-C-change (Fig. 3e-f), larger than the expected 'most severe' scenario; +2K and 800 ppm.

Similar to ED2, the LPJ-GUESS model showed a nearly complete negative response in integrated-C-change as a result of UCE drought and scenarios of warming and eCO_2 at the EucFACE site (Fig. 3g-i), but mixed and more muted results at Palo Verde (Fig. 3j-l, Table 2). The average integrated-C-change relative to the reference case was -95.4 at EucFACE and -7.8 kg C m^{-2} yr at Palo Verde, both less negative compared to ED2. One notable pattern was up until a drought intensity threshold of ~40%, the climate scenarios had no effect or response in integrated-C-change at EucFACE, and the muted response from warming and eCO_2 Palo Verde, compared to ED2. Surprisingly, the +2K scenario switched the integrated-C-change to positive, compared to the reference case (Fig. 3g-i; red lines), potentially a physiological process in the

model to increased temperatures only that signals an anomalous resiliency response. Similar to the results with no climate change, LPJ-GUESS remained sensitive to the intensity of drought, with ~40% precipitation reduction being a threshold.

The models and sites differed with regard to SO and MO responses to increasing drought severity and its interactions with warming and eCO_2 (related to conceptual Fig. 1d). ED2 showed a more consistent MO response during UCEs and with additional warming and eCO_2 (Fig. 3; negative integrated-C-change), especially at EucFACE, suggesting these ecosystems will remain in a depressed carbon condition driving vegetation mortality, and/or longer recoveries. LPJ-GUESS produced more opportunities for SO with climate change. For example, at EucFACE CO_2 fertilization created small SO periods that then led to MO with increasing drought severities, and at Palo Verde all +2K and 600 ppm led to a SO (Fig. 3j-l; Table 2).

Both models predicted that C losses due to drought interactions with increased temperature and eCO_2 were less severe at the seasonally dry Palo Verde site compared to the somewhat less seasonal, more humid EucFACE site (Table 2), which could be attributed to higher diversity in PFT physiology at Palo Verde. Palo Verde's community composition that emerged following drought included either three (LPJ-GUESS) or four (ED2) PFTs, while only a single PFT existed at EucFACE. With rising temperatures under climate change, UCEs will be hotter and drier. Nine out of the twelve simulations with both +2K and 600 ppm CO_2, and all but one +2K and 800 ppm CO_2 produced a negative integrated-C-change, implying stronger C losses and/or longer recovery times when droughts are exacerbated by increasing temperatures (Table 2).

4 Discussion

Vegetation demographic models (VDMs) allowed us to uniquely explore two hypotheses regarding a range of modeled response of terrestrial ecosystems to unprecedented climate extremes (UCEs), and setting the stage for the following perspectives to help guide future research. Key model results include strong nonlinearities (Hypothesis H1) in C response to extreme drought *intensities* in LPJ-GUESS and alternatively drought *durations* in ED2 (at one of two sites), with differences in thresholds between the two models and ecosystems. These nonlinearities may arise from multiple mechanisms that we begin to investigate here, including shifts in plant hydraulics or other functional traits, C allocation, phenology, stand size-structure

and/or age demography, and compositional changes, all which vary among ecosystem types. A critical look of driving model mechanisms, which emerged from the hypothetical drought simulations used here, are summarized in Table 3. The models also show exacerbated biomass loss and recovery times in the majority of our scenarios of warming and eCO_2, supporting Hypothesis H2. Below, we discuss the underlying mechanisms that drive simulated ecosystem response to UCEs using the models and sites as conceptual "experimental tools" and observational evidence from the literature. We focus on two temporal stages of the UCE: The pre-drought ecosystem stage characterized as the quasi-stable state of the ecosystem prior to a UCE, which can mediate ecosystem resistance and disturbance impact, and the post-drought recovery stage (Table 1).

4.1 The role of ecosystem processes and states prior to UCEs

4.1.1 The role of phenology and phenological strategies prior to UCEs:

Observations show that diversity of deciduousness contributes to successful alternative strategies for tropical forest response to water stress (Williams et al., 2008). For example, during the severe 1997 El Nino drought, brevi-deciduous trees and deciduous stem-succulents within a tropical dry site in Guanacaste Costa Rica retained leaves during the extreme wet-season drought, behaving differently than during normal dry seasons (Borchert et al., 2002). Both models here predict that neither seasonal deciduousness, nor drought-deciduous phenology at the seasonally dry tropical forest, Palo Verde (which consists of trees with different leaf phenological strategies), act to buffer the forest from a large drop in LAI during UCEs (Fig. S1a-b). Even with this large decrease in LAI, ED2 predicted a very weak biomass loss at the time of UCEs (Fig. 2a), suggesting large-scale leaf loss is not a direct mechanism of plant mortality in ED2. Leaf loss is one component of total carbon turnover flux equations in terrestrial models, in addition to woody loss, fine-roots, and reproductive tissues. Having a better understanding of when extreme levels of phenological turnover contribute to stand-level mortality could be improved. Among other turnover hypothesis explored, Pugh et al. (2020) found that phenological turnover fluxes where just as important as mortality fluxes in driving forest turnover time in the VDMs: LPJ-GUESS, CABLE-POP, ORCHIDEE, but not the LSM JULES. At the EucFACE site prior to the simulated extreme drought, LPJ-GUESS displayed strong inter-annual variability

514 in LAI (Fig. S1a-b). This capability of large swings in LAI (5.8 to 0.8) by LPJ-GUESS could
515 contribute to model uncertainty and the considerable mortality response at EucFACE. Modeled
516 LAI was the largest source of variability in another ecosystem model, CABLE, when evaluating
517 the simulated response to CO_2 fertilization (Li et al., 2018). VDMs could be improved by better
518 capturing different plant phenological responses to UCEs by better representing a range of leaf-
519 level morphological and physiological characteristics relevant to plant-water relations such as
520 leaf age, retention of young leaves even during extreme droughts, (Borchert et al., (2002)), and
521 variation in hydraulic traits as a function of leaf habit (Vargas et al., (2021)) (Table 3). Two such
522 examples are seen in the FATES model where the possibility for "trimming" the lowest leaf
523 layer can occur when leaves are in negative carbon balance due to light limitation thus
524 optimizing maintenance costs and carbon gain, as well as leaf age classifications providing
525 variations in leaf productivity and turnover.
526
527 **4.1.2 The role of plant hydraulics prior to UCEs:**
528 Susceptibility of plants to hydraulic stress is one of the strongest determinants of
529 vulnerability to drought, with loss of hydraulic conductivity being a major predictor of drought
530 mortality in temperate (McDowell et al., 2013; Anderegg et al., 2015; Sperry and Love, 2015;
531 Venturas et al., 2021) and tropical forests (Rowland et al., 2015; Adams et al., 2017b), as well as
532 a tractable mortality mechanism to represent in process-based models (Choat et al., 2018,
533 Kennedy et al., 2019). Both LPJ-GUESS and ED2 exhibited a wide range in amount and pattern
534 of plant-available-water prior to drought (Fig. S1c-d), contributing to large differences in UCE
535 response. LPJ-GUESS, which does not simulate hydrodynamics, predicted lower total plant-
536 available-water at both sites compared to ED2, and subsequently simulated greater mortality and
537 a greater increase in plant-available-water right after the UCEs as a result of less water demand.
538 Due to ED2 using a static mortality threshold from conductivity loss (88%), it likely does not
539 accurately reproduce the wide range of observations of drought-induced mortality. In ED2, large
540 trees, with longer distances to transport water, were at higher risk and suffered higher mortality
541 (Fig. 4), demonstrating how stand demography, size structure, and tapering of xylem conduits
542 can play an important role in ecosystem models (Petit et al., 2008; Fisher et al., 2018). Of the
543 VDMs that are beginning to incorporate a continuum of hydrodynamics (e.g., ED2 (described in
544 Methods 2.1 section) and FATES-HYDRO (Fang et al., 2022, based on Christoffersen et al.,

2016), they are able to solve for transient water from soils to roots, through the plant and connect with transpiration demands. Therefore instead of the plant water stress function being based on soil water potentials, it is replaced with more realistic connections with leaf water potentials. Mortality is then caused by hydraulic failure via embolism controlled by the critical water potential (P_{50}) that leads to 50% loss of hydraulic conductivity. For advancements in tree level hydrodynamic modeling see the FETCH3 model (Silva et al., 2022), for justification for plant hydrodynamics in conjunction with multi-layer vertical canopy profiles see Bonan et al., (2021). There are strong interdependencies and related mechanisms connecting both hydraulic failure (e.g., low soil moisture availability) and C limitation (e.g., stomatal closure) during drought (McDowell et al., 2008; Adams et al., 2017b), and these interactions should be incorporated in ecosystem modeling and further explored (Table 3).

4.1.3. The role of carbon allocation prior to UCEs:

Plants have a variety of strategies to buffer vulnerability to water and nutrient stress caused by extreme droughts, such as allocating more C to deep roots (Joslin et al., 2000; Schenk and Jackson, 2005), investing in mycorrhizal fungi (Rapparini and Peñuelas, 2014), or reducing leaf area without shifting leaf nutrient content (Pilon et al., 1996). Alternatively, presence of deep roots doesn't necessarily lead to deep soil moisture utilization, as seen in a 6-year Amazonian throughfall exclusion experiment where deep root water uptake was still limited, even with high volumetric water content (Markewitz et al., 2010). Elevated CO_2 alone will enhance growth and water-use efficiency (Keenan et al., 2013), reducing susceptibility to drought. However, such increased productivity within a forest stand, and associated structural overshoot during favorable climate windows, can also be reversed by increased competition for light, nutrients, and water during unfavorable UCEs – potentially leading to mortality overshoot (Fig. 1d) and higher C loss. Mortality overshoot, as a result of structural overshoot, could be an explanation for the negative integrated-C-change (i.e., C loss) in the majority of eCO_2-only simulations (18 out of 24 scenarios; Table 2).

Effects of CO_2 fertilization on plant C allocation strategies are uncertain. As a result, ecosystem models differ in their assumptions on controls of C allocation in response to eCO_2, leading to divergent plant C use efficiencies (Fleischer et al., 2019). Global scale terrestrial models are beginning to include optimal dynamic C allocation schemes, over fixed ratios, that account for concurrent environmental constraints on plants, such as water, and adjust allocation

based on resource availability such as in LM3-PPA (Weng et al., 2015), but the representation of C allocation is still debated and progressing (De Kauwe et al., 2014; Montané et al., 2017; Reyes et al., 2017). Options for carbon allocation strategies can based on the allometric partitioning theory (i.e., allocation follows a power allometry function between plant size and organs which is insensitive to environmental conditions; Niklas, 1993), as an alternative to ratio-based optimal partitioning theory (i.e., allocation to plant organs based on the most limiting resources) (McCarthy and Enquist, 2007) or fixed ratios (Table 3), and the strategies should be further investigated particularly due to VDMs substantial use of allometric relationships. A meta-analysis of 164 studies found that allometric partitioning theory outperformed optimal partitioning theory in explaining drought-induced changes in C allocation (Eziz et al., 2017). Further eco-evolutionarily-based approaches such as optimal response or game-theoretic optimization, as well as entropy-based approaches are useful when wanting to simulate higher levels of complexity (reviewed in Franklin et al. 2012). With more frequent UCEs and the need for plants to reduce water consumption, a shift in the optimal strategy of allocation between leaves and fine roots should change. The goal functions (e.g., fitness proxy) used in optimal response modeling can account for these shifts in costs and benefits of allocation between all organs (Franklin et al. 2009, 2012).

4.1.4 The role of plant carbon storage prior to UCEs:

Studies of neotropical and temperate seedlings show that pre-drought storage of non-structural carbohydrates (NSCs) provides the resources needed for growth, respiration osmoregulation, and phloem transport when stomata close during subsequent periods of water stress (Myers and Kitajima, 2007; Dietze and Matthes, 2014; O'Brien et al*.,* 2014). Furthermore, direct correlations have been shown between NSC depletion and embolism accumulation, and the degree of pre-stress reserves and utilization of soluble sugars (Tomasella et al., 2020). The amount of NSC storage required to mitigate plant mortality during C starvation and interactions with hydraulic failure from severe drought is difficult to quantify, due to the many roles of NSCs in plant function and metabolism (Dietze and Matthes, 2014). For example, NSCs were not depleted after 13 years of experimental drought in the Brazilian Amazon (Rowland et al., 2015). As atmospheric CO_2 increases with climate change, NSC concentrations may increase, as seen in manipulation experiments (Coley, 2002), but interactions with heat, water stress, enhanced leaf

shedding, and nutrient limitation complicates this relationship, and needs to be further explored. Despite the recognition of the critical role that plant hydraulic functioning and NSCs play in tree resilience to extremes, knowledge gaps and uncertainties preclude fully incorporating these processes into ecosystem models.

Compared to ED2, LPJ-GUESS predicted low plant carbon storage (a model proxy for NSCs) prior to and during drought, and at times became negative, thereby creating C costs (Fig. S2a-b), leading to C starvation and potentially explaining the larger biomass loss in LPJ-GUESS at both sites. Alternatively, ED2 maintained higher levels of NSCs providing a buffer to stress, and mitigating the negative effects of drought. Maintenance of NSCs in ED2, even during prolonged drought (at EucFACE) is due to: (1) trees resorbing a fraction of leaf C during leaf shedding, (2) no maintenance costs for NSC storage in the current version, and (3) no allocation of NSCs to structural growth until NSC storage surpasses a threshold (the amount of C needed to build a full canopy of leaves and associated fine roots), allowing for a buffer to accumulate. In LPJ-GUESS, accumulation and depletion of NSC is recorded as a 'C debt' being paid back in later years. The contrasting responses of the two models to drought, and the likely role of NSCs in explaining differences in model behavior, highlights the need to better understand NSC dynamics and to accurately represent the relevant processes in models (Richardson et al., 2013; Dietze and Matthes, 2014). More observations of C accumulation patterns and how/where NSCs drive growth, respiration, transport and cellular water relations would enable a more realistic implementation of NSC dynamics in models (Table 3).

4.1.5 Role of functional trait diversity prior to UCEs:

Currently LPJ-GUESS simulates the Palo Verde community using three PFTs, while ED2 uses four PFTs that differ in photosynthetic and hydraulic traits. The community composition simulated by ED2 is shown to be more resistant to UCEs compared to LPJ-GUESS (Fig. 5), perhaps due to relatively higher functional diversity (via more PFTs with additional phenological and hydraulic diversity). This additional diversity helps to buffer ecosystem response to drought by allowing more tolerant PFTs to benefit from reductions in less-tolerant PFTs, thus buffering reductions in ecosystem function (Anderegg et al., 2018). Higher diversity ecosystems were found to protect individual species from negative effects of drought (Aguirre et al., 2021) and enhance productivity resilience following

637 wildfire (Spasojevic et al., 2016); thus, functionally diverse communities may be key to enhancing
638 tolerance to rising environmental stress.
639 Recent efforts to consolidate information on plant traits (Reich et al., 2007; Kattge et al., 2011)
640 have contributed to identifying relationships that can impact community-level drought responses
641 (Skelton et al., 2015; Anderegg et al., 2016a; Uriarte et al., 2016; Greenwood et al., 2017), such as
642 life-history characteristics, and strategies of resource acquisition and conservation as predictors of
643 ecosystem resistance (MacGillivray et al., 1995; Ruppert et al., 2015). While adding plant trait
644 complexity in ESMs may be required to accurately simulate key vegetation dynamics, it necessitates
645 more detailed parameterizations of processes that are not explicitly resolved (Luo et al., 2012). Further
646 investigation of how VDMs represent interactions leading to functional diversity shifts is crucial to
647 this issue. Enquist and Enquist, (2011), as an example, show that long-term patterns of drought (20-
648 years) have led to increases in drought-tolerant dry forest species, which could modulate resistance to
649 future droughts. Higher diversity of plant physiological traits and drought-resistance strategies is
650 expected to enhance community resistance to drought, and models should account for shifts in diverse
651 functionality (Table 3).
652
653 **4.2 The role of ecosystem processes and states in post-UCE recovery**
654 **4.2.1 The role of soil water resources post-UCEs:**
655 Our simulation results generally demonstrated a fast recovery of plant-available-water
656 and LAI at both sites (Fig. S1). Annual plant-available-water substantially increased right after
657 drought by an average of 163 mm at Palo Verde and 213 mm at EucFACE in the LPJ-GUESS
658 simulations, compared to much lower increases in ED2 (50 mm and 12 mm at Palo Verde and
659 EucFACE). This increase in available water post-drought can be attributed to reduced stand
660 density and water competition (Fig. S2c-d; diamonds vs. circles), alleviating the demand for soil
661 resources (water) and subsequent stress, which has also been shown in observations (McDowell
662 et al., 2006; D'Amato et al., 2013). After large canopy tree mortality events there can be
663 relatively rapid recovery of forest biogeochemical and hydrological fluxes (Biederman et al.,
664 2015; Anderegg et al., 2016b; Biederman et al., 2016). These crucial fluxes strongly influence
665 plant regeneration and regrowth, which can buffer ecosystem vulnerability to future extreme
666 droughts. However, this enhanced productivity has a limit. In a scenario where UCEs continue to

intensify, causing greater reductions in soil water and reduced ecosystem recovery potential, the SO growth that typically occurs after UCEs may be dampened (Fig. 1d). In water-limited locations, similar to the dry forest sites used here, initial forest recovery from droughts were faster due to thinning induced competitive-release of the surviving trees, and shallow roots not having to compete with neighboring trees for water, allowing for more effective water user (Tague and Moritz, 2019), stressing the importance of root competition and distribution in models (Goulden and Bales, 2019). Tague and Moritz, (2019) also reported that this increased water use efficiency and SO ultimately lead to water stress and related declines in productivity, similar to the MO concept (Jump et al., 2017; McDowell et al., 2006). Since a core strength of VDMs is predicting stand demography during recovery, improved quantification of density-dependent competition following stand dieback would be beneficial for model benchmarking (Table 3).

4.2.2 The role of lagged turnover and secondary stressors post-UCEs:

Time lags in forest compositional response and survival to drought could indicate community resistance or shifts to more competitive species and competitive exclusion. During a 15-year recovery period from extreme drought at Palo Verde, LPJ-GUESS predicted an increase in stem density (stems m^2 yr^{-1}) (Fig. S2c) compared to ED2, which predicted almost no impact in stem recovery. The mortality "spike" in ED2 due to drought was muted and slightly delayed, contributing to ED2's lower biomass loss and more stable behavior of plant processes over time at Palo Verde. At EucFACE, both models exhibited a pronounced lag effect in stem turnover response, i.e. ~8-12 years after drought (Fig. S2d). After about a decade, strong recoveries and increased stem density occurred, which in ED2 was followed by delayed mortality/thinning of stems. Delayed tree mortality after droughts is common due to optimizing carbon allocation and growth (Trugman et al., 2018), but typically only up to several years post-drought, not a decade or more as seen in the model.

The versions of the VDMs used here do not directly consider post-drought secondary stressors such as infestation by insects or pathogens, and the subsequent repair costs due to stress damage, which could substantially slow the recovery of surviving trees. Forest ecologists have long recognized the susceptibility of trees under stress, particularly drought, to insect attacks and

pathogens (Anderegg et al., 2015). Tight connections between drought conditions and increased mountain pine beetle activity have been observed (Chapman et al., 2012; Creeden et al., 2014), and can ultimately lead to increased tree mortality (Hubbard et al., 2013). Leaf defoliation is a major concern from insect outbreaks following droughts, and can have large impacts on C cycling, plant productivity, and C sequestration (Amiro et al., 2010; Clark et al., 2010; Medvigy et al., 2012). Implementing these secondary stressors in models could slow the rate of post-UCE recovery and lead to increased post-UCEs tree mortality.

4.2.3 The role of stand demography post-UCEs:

Change in stand structure is an important model process to capture, because large trees have important effects on C storage, community resource competition, and hydrology (Wullschleger et al., 2001) (Table 3), and maintaining a positive carbohydrate balance is beneficial in sustaining (or repairing) hydraulic viability (McDowell et al., 2011). There is increasing evidence, both theoretical (McDowell and Allen, 2015) and empirical (Bennett et al., 2015; Rowland et al., 2015; Stovall et al., 2019), that large trees (particularly tall trees with high leaf area) contribute to the dominant fraction of dead biomass after drought events. Under rising temperatures (and decreasing precipitation), VPD will increase, leading to a higher likelihood of large tree death (Eamus et al., 2013; Stovall et al., 2019), driving MO events as hypothesized in Fig. 1d. Consistent with this expectation, ED2 predicted that the largest trees (>100 cm) experienced the largest decreases in basal area to compared to all other size classes (Fig. 4). This drought-induced partial dieback and mortality of large dominant trees has substantial impacts on community-level C dynamics, as long-term sequestered C is liberated during the decay of new dead wood (Palace et al., 2008; Potter et al., 2011). In ED2, the intermediate size class (60 - 80 cm) increased in basal area following large-tree death, taking advantage of the newly open canopy space. However, small size classes do not necessarily benefit from canopy dieback. For example, in a dry tropical forest, prolonged drought led to a decrease in understory species and small-sized stems (Enquist and Enquist, 2011).

Due to VDMs being able to exhibit dynamic biogeography they are more useful at predicting shifts in community composition beyond LSMs capabilities. Further areas of advancement (described in Franklin et al. (2020)) is including models of natural selection, self-organization, and entropy maximization which can substantially improve community dynamic

responses in varying environments such as UCEs. Eco-evolutionary optimality (EEO) theory can also help improve functional trait representation in global process-based models (reviewed in Harrison et al., 2021), through hypotheses in plant trait trade-offs and mechanistic links between processes such as resource demand, acquisition, and plant's competitiveness and survival; traits associated with high degrees of sensitivity in models. The power of prognostic VDMs to predict shifts in demography and community migration with climate change is large, but rarely is being constrained with plant-level EEO theory, and thus will likely need to use stand level competition and coexistence principles of how plants self-organize (Franklin et al. 2020).

4.2.4 The role of functional trait diversity & plant hydraulics post-UCEs:

In field experiments, higher disturbance rates have shifted the recovery trajectory and competition of the plant community towards one that is composed of opportunistic, fast-growing pioneer tree species, grasses (Shiels et al., 2010; Carreño-Rocabado et al., 2012), and/or deciduous species, as also seen in model results (Hickler et al., 2004). In the treatments presented here, deciduous PFT types were also the strongest to recover after 15 years in both models, surpassing pre-drought values (Fig. 5). It should be noted that ED2 exhibited a strong recovery in the evergreen PFT as well, inconsistent with the above literature (Fig. 5b). PFTs in ED2 respond to drought conditions via stomatal closure and leaf shedding, buffering stem water potentials from falling below a set mortality threshold (i.e., 88% of loss in conductivity). This conductivity threshold may need to be reconsidered if further examination reveals an unrealistic advantage under drought conditions for evergreen trees, which exhibited a lower impact from droughts (compared to deciduous and brevi-deciduous PFTs) in ED2. Nitrogen cycling feedbacks were not investigated here, but could also be an explanation for a strong evergreen PFT recovery.

Recovery of surviving trees could be hindered by the high cost of replacing damaged xylem associated with cavitation (McDowell et al., 2008; Brodribb et al., 2010). Many studies have identified "drought legacy" effects of delayed growth or gross primary productivity following drought (Anderegg et al., 2015; Schwalm et al., 2017) and the magnitude of these legacies across species correlates with the hydraulic risks taken during drought itself (Anderegg et al., 2015). The conditions under which xylem can be refilled remain controversial, but it seems likely that many species, particularly gymnosperms, may need to entirely replace damaged

xylem (Sperry et al., 2002), and trees worldwide operate within narrow hydraulic safety margins, suggesting that trees in all biomes are vulnerable to drought (Choat et al., 2012). The amount of damaged xylem from a given drought event and recovery rates also vary across trees of different sizes (Anderegg et al., 2018).

Plasticity in nutrient acquisition traits, intraspecific variation in plant hydraulic traits (Anderegg et al., 2015), and changes in allometry (e.g., Huber values) can have large effects on acclimation to extreme droughts. This suggests some capacity for physiological adaptation to extreme drought, as seen by short-term negative effects from drought and heat extremes being compensated for in the longer term (Dreesen et al., 2014). Still, given the shift towards more extreme droughts with climate change, vegetation mortality thresholds are likely to be exceeded, as reported in Amazonian long-term plots where mortality of wet-affiliated genera has increased while simultaneously new recruits of dry-affiliated genera are also increasing (Esquivel-Muelbert et al., 2019). Increasing occurrences of heat events, water stress and high VPD will lead to extended closure of stomata to avoid cavitation, progressively reducing CO_2 enrichment benefits (Allen et al., 2015). Where CO_2 fertilization has been seen to partially offset the risk of increasing temperatures, the risk response was mediated by plant hydraulic traits (Liu et al., 2017) using a soil–plant–atmosphere continuum (SPAC) model, yet interactions with novel extreme droughts were not considered. The VDM simulations suggest that the combination of elevated warming and potential structural overshoot from eCO_2 (or inaccurate representation in NSCs allocation/usage priority) will exacerbate consequences of UCEs by reductions in both C stocks and post-drought biomass recovery speeds (Fig. 3). Therefore, future UCE recovery may not be easily predicted from observations of historical post-disturbance recovery. An associated area for further investigation is to better understand the hypothesized interplay between amplified mortality from hotter UCEs followed by structural overshoot regrowth during wetter periods (Fig. 1d), which could potentially lead to continual large swings in MO and SO and vulnerable net ecosystem C fluxes through time (Table 3).

5 Summary of perspectives for model advancement

Model limitations and unknowns exposed by our simulations and literature review highlight current challenges in our ability to understand and forecast UCE effects on ecosystems. These limitations reflect a general lack of empirical experiments focused on UCEs. Insufficient

data means that relevant processes may currently be poorly represented in models, and models may then misrepresent C losses during UCEs. The two VDMs used here had different sensitivities to drought duration and intensity. These model uncertainties could potentially be addressed by improved datasets on thresholds of conductivity loss at high drought intensities, the role of trait diversity (e.g., different strategies of drought deciduousness and EEO theory) in buffering ecosystem drought responses, and a better grasp of allocation to plant C storage stocks before, during, and after multi-year droughts. Our study takes some initial steps to identify and assess model gaps in terms of mechanisms and magnitudes of responses to UCEs, which can then be used to inform and develop field experiments targeting key knowledge gaps as well as to prioritize ongoing model development (Table 3). Our intention was not to do an exhaustive list of UCE simulation experiments, and additional modeling perturbations and experiments would be useful outcomes of future studies. For example, we begin to investigate duration of droughts but we did not consider frequency of back-to-back UCEs. This iterative model-experiment framework of using VDMs as hypothesis testing tools offers strong potential to drive progress in improving our understanding of terrestrial ecosystem responses to UCEs and climate feedbacks, while informing the development of the next generation of models.

Code Availability. The source code for the ED2 model can be downloaded and available publicly at https://github.com/EDmodel/ED2. The source code for the LPJ-GUESS model can be downloaded and available publicly at http://web.nateko.lu.se/lpj-guess/download.html. All model simulation data will be available in a Dryad repository.

Data Availability. Authors received the required permissions to use the site level meteorological data used in this study. Otherwise, no ecological or biological data were used in this study.

Author Contributions. JH wrote the manuscript with significant contributions from AR, BS, JD, DM, with input and contributions from all authors. XX and MM were the primary leads running the model simulations, with model assistance and strong feedback from DM and BS. All authors made contributions to this article, and agree to submission.

Competing Interests. The contact author has declared that neither they nor their co-authors have any competing interests.

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Table 1. Hypothesized plant processes and ecosystem state variables affecting pre-drought resistance and post-drought recovery in the context of unprecedented climate extremes (UCEs). The "Included in Model?" column indicates which processes or state variables are represented in each of the two models studied in this paper. The mechanisms listed in the two right columns refer to real-world ecosystems and are not necessarily represented in the ED2 and LPJ-GUESS models. Contents of the table are based on a non-exhaustive literature review, expert knowledge, and modeling results presented here. Symbols refer to the following literature sources: * Borchert et al., 2002; Williams et al., (2008); ** Dietze and Matthes, (2014); O'Brien et al., 2014; *** ENQUIST and ENQUIST, (2011); Greenwood et al., (2017); Powell et al., (2018); ^ Rowland et al., (2015); McDowell et al., (2013); Anderegg et al., (2015); ^^ Joslin et al., 2000; Markewitz et al., (2010); ^^^ Powell et al., (2018); ^^^^ Bennett et al., (2015); Rowland et al., (2015); ~ Hubbard et al., (2013); ~ ~ McDowell et al., (2006); D'Amato et al., (2013); + Zhu et al., (2018); Vargas et al., (2021); % Trugman et al., (2019); %% Franklin et al., (2012); %% Franklin et al., (2020).

Process or State Variable	Included in model?	Mechanisms affecting pre-UCE drought resistance influencing impact	Mechanisms affecting post-UCE drought recovery
Processes			
1) Phenology Schemes	ED2: Yes LPJ-G: Yes	- Leaf area and metabolic activity modulates vulnerability to death - Drought-deciduousness reduces vulnerability to drought *, with higher water potential at turgor loss point and less leaf vulnerability to embolism +	- Leaf lifespan tends to increase from pioneer to late-successional species in some ecosystems (e.g., tropical forests) and is a balance between C gain and its cost
2) Plant Hydraulics	ED2: Yes LPJ-G: No	- Cavitation resistance traits ^ - Turgor loss, hydraulic failure (stem embolism) lead to increased plant mortality and enhanced vulnerability to secondary stressors.	- Replacement cost of damaged xylem slows recovery of surviving trees
3) Dynamic Carbon Allocation	ED2: Yes LPJ-G: Yes	- Increased root allocation could offset soil water deficit under gradual onset of drought ^^ - Leaf C allocation strategies should be connected to hydraulic processes %	- Allocation among fine roots, xylem, & leaves affects recovery time & GPP/LAI trajectory - Eco-evolutionary optimality theory %%

4) Non-Structural Carbohydrate (NSC) Storage	ED2: Yes LPJ-G: Yes	- NSCs buffer C starvation mortality due to reduced primary productivity. - Maintenance of hydraulic function & avoiding hydraulic failure **	- Low NSC could increase vulnerability to secondary stressors during recovery
State Variables			
1) Plant-Soil Water Availability	ED2: Yes LPJ-G: Partly	- Low soil water potential increases risk of tree C starvation, turgor loss and hydraulic failure	- After stand dieback reduced demand for soil resources &/or reduced shading - Increased soil water enhances regeneration/ regrowth, buffers vulnerability to long-term drought ~ ~
2) Plant Functional Diversity	ED2: Yes LPJ-G: Yes	- Presence of drought-tolerant species modulates resistance at community level. - Shallow-rooting species more vulnerable ^^^ ***	- Changed resource spectra shift competitive balance in favor of grasses and pioneer trees
3) Stand Demography	ED2: Yes LPJ-G: Yes	- Larger tree size enhances vulnerability to drought and secondary stressors due to higher maintenance costs ^^^^	- Mortality of canopy individuals favors understory species and smaller size-classes - Self-organizing principles %%%
4) Compounding Stressors	ED2: No LPJ-G: No	- Reduced resistance to insects and pathogens due to physiological/mechanical/ hydraulic damage & depletion of NSC	- Infestation by insects and pathogens, repair of damage due to secondary stressors, slows recovery of surviving trees ~

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Table 2 Impact of eCO_2 and/or temperature on the integrated-C-change (kg C m^{-2} yr) relative to drought treatments with no additional warming or eCO_2, for both models, and both sites seen in Fig. 3. Quantified as average and minimum integrated-C-change across all 20 drought intensities for step-change scenarios of warming and eCO_2. The percentage of each scenario that was negative in integrated-C-change (i.e., decreases in C loss). Green values represent positive integrated-C-change.

EucFACE		*ED2*			*LPJ-GUESS*		
		Average integrated C change	Largest integrated C change	% climate scenario was negative	Average integrated C change	Largest integrated C change	% climate scenario was negative
1 year	600 ppm	**2.2**	0.0	33.3	-74.6	-396.6	36.8
	800 ppm	-10.6	-73.0	50.0	-124.1	-416.0	57.9
	2K	**2.3**	-0.5	16.7	**21.3**	-20.8	15.8
	2K, 600 ppm	**0.5**	-8.2	61.1	-67.5	-201.5	78.9
	2K, 800 ppm	**1.8**	-0.4	22.2	-145.9	-400.1	47.4
2 year	600 ppm	-105.6	-456.7	77.8	-85.2	-260.6	63.2
	800 ppm	-199.0	-522.9	83.3	-106.3	-350.1	42.1
	2K	-10.3	-34.7	77.8	**14.2**	-35.2	31.6
	2K, 600 ppm	-204.9	-666.1	77.8	-47.6	-128.8	84.2
	2K, 800 ppm	-12.4	-61.6	50.0	-167.0	-421.9	68.4
4 year	600 ppm	-125.5	-306.2	83.3	-122.6	-277.4	94.7
	800 ppm	-277.1	-423.3	100.0	-212.2	-523.7	89.5
	2K	-61.8	-188.6	72.2	**12.9**	-13.8	31.6
	2K, 600 ppm	-385.9	-674.2	94.4	-79.1	-197.3	94.7
	2K, 800 ppm	-277.9	-737.7	72.2	-247.0	-503.8	100.0
	Average	-111.0	-277.0	64.8	-95.4	-276.5	62.5
Palo Verde		*ED2*			*LPJ-GUESS*		
1 year	600 ppm	-1.6	-6.2	77.8	-11.0	-32.4	78.9
	800 ppm	**6.7**	-0.2	11.1	-39.2	-154.0	100.0
	2K	-1.0	-15.3	38.9	-33.4	-75.1	100.0
	2K, 600 ppm	**2.5**	-1.1	22.2	**6.5**	-4.6	52.6
	2K, 800 ppm	-6.6	-16.6	77.8	-121.1	-237.7	100.0
2 year	600 ppm	**15.1**	-16.7	38.9	**27.3**	-6.0	10.5
	800 ppm	-229.2	-756.6	66.7	**20.6**	-17.2	26.3
	2K	-8.2	-71.8	50.0	**32.0**	-12.7	15.8
	2K, 600 ppm	**24.8**	-5.7	11.1	**36.2**	-1.2	5.3
	2K, 800 ppm	-152.9	-348.1	77.8	**8.0**	-54.5	36.8
4 year	600 ppm	-11.1	-37.3	94.4	**3.4**	-25.1	26.3
	800 ppm	-260.2	-694.8	94.4	-25.2	-132.6	57.9
	2K	-39.0	-133.8	66.7	-7.7	-45.9	68.4
	2K, 600 ppm	**1.0**	-16.4	38.9	**6.1**	-4.1	31.6
	2K, 800 ppm	-148.5	-429.3	83.3	-20.0	-75.5	78.9
	Average	-53.9	-170.0	56.7	-7.8	-58.6	52.6

871 **Table 3** Summary of suggested critical look of driving mechanisms (e.g., ecosystem or plant
872 processes and state variables) which emerged from the hypothetical drought simulations used
873 here to explore for future research in manipulation experiments, data collection, and model
874 development and testing, as related to furthering our understanding of UCE resistance and
875 recovery.

	UCE Drought Resistance & Recovery Summary
Processes	**Suggestions of driving mechanisms to further explore in data and models**
1) Phenology Schemes	Represent morphological and physiological traits relevant to plant-water relations; drought- deciduousness can reduce vulnerability to drought; phenology of evergreens needs more investigation.
2) Plant Hydraulics	Interactions between hydraulic failure (e.g. low soil moisture availability) and C limitation (e.g. stomatal closure) during drought should be included in models. Account for turgor loss, hydraulic failure traits, costs to recover damaged xylem.
3) Dynamic Carbon Allocation	C allocation based on eco-evolutionary optimality (EEO) and allometric partitioning theory in addition, or replacing ratio-based optimal partitioning theory, and fixed ratios. Explore root allocation that could offset soil water deficits.
4) Non-structural Carbohydrate (NSC) Storage	Deciding best practices for NSC representation in models. Better understanding of NSC storage required to mitigate plant mortality during C starvation and interactions with avoiding hydraulic failure during severe droughts.
States Variables	
1) Plant-Soil Water Availability	Better quantification of the amount and accessibility of plant-available water for surviving trees, and tradeoff between increased structural productivity but vulnerability to subsequent droughts. Future relevance, or benefit, of lower water demand due to thinning with UCEs.
2) Plant Functional Diversity	Understand how higher diversity of plant physiological traits and drought-resistance strategies will enhance community resistance to drought; models still need to account for shifts in diverse functionality, including deciduousness shifts and interplay of regrowth structural overshoot followed by amplified mortality from hotter UCEs.
3) Stand Demography	Large trees more vulnerable to drought; need data on changes in C stock with UCEs in high-density smaller tree stands vs. stands with larger trees. Using 'self-organization' principles for modeling stand level competition and coexistence under UCEs.

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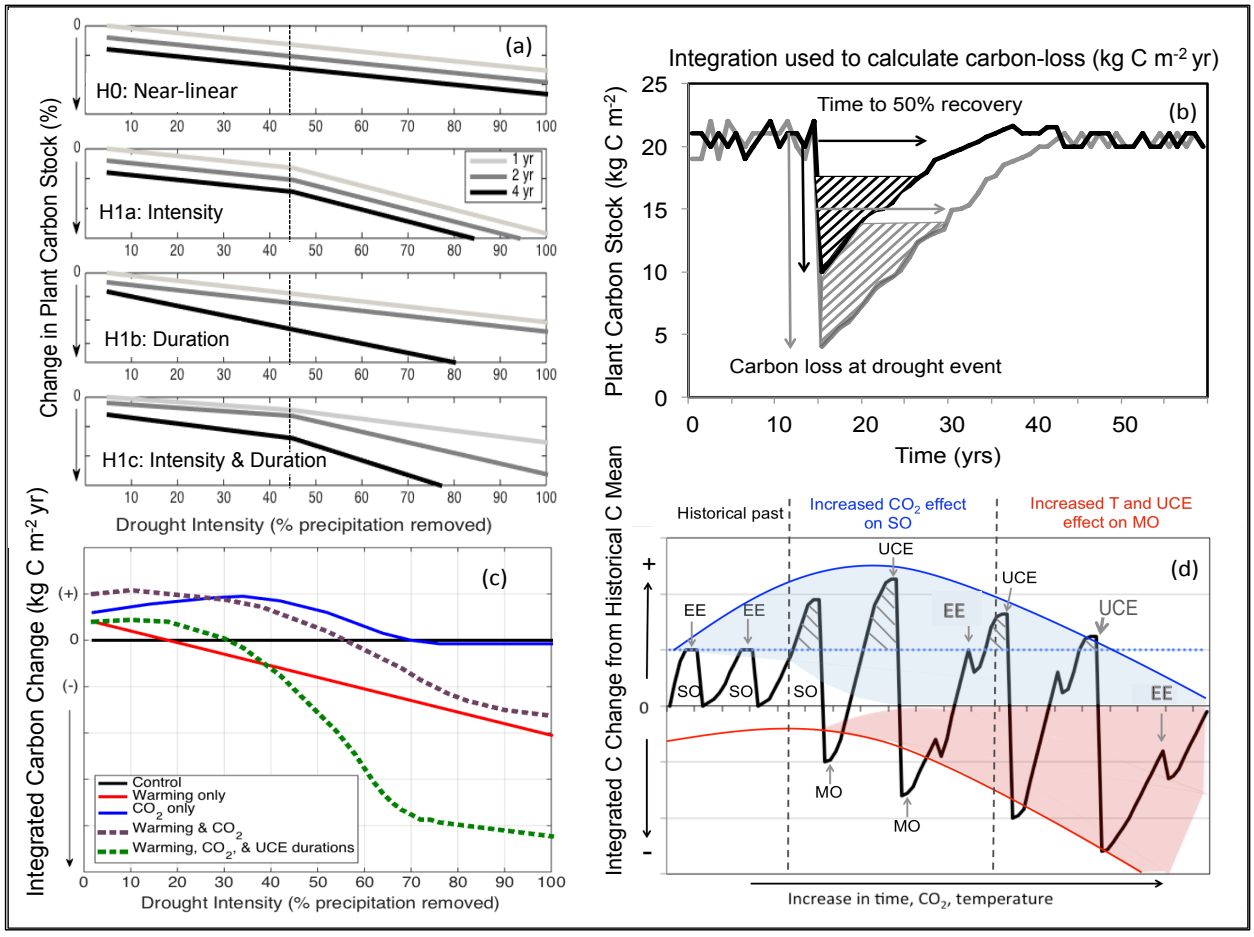

Figure 1 Conceptual diagrams showing impacts of extreme droughts (unprecedented climate extremes, UCEs; i.e., record-breaking droughts) on plant C stocks. (a) **Conceptual response diagram**: potential loss in C stock as a function of increasing drought intensity (0-100% precipitation removal) and drought duration (1, 2 or 4 years of drought). In this example, an arbitrary threshold of 45% precipitation reduction and 4-year drought duration is assumed to correspond to a UCE. The "null hypothesis" (H0, top panel) is a near-linear response of C stocks to droughts. Alternative hypotheses include nonlinear and threshold responses to drought intensity (H1a), drought duration via different slope responses (H1b), and combined effects of both drought intensity and durations (H1c). (b) **Conceptualized UCE C loss diagram**: responses of forest C stocks to a large (grey) and small (black) UCE. "Integrated-C-loss" (kg C m^{-2} yr) denotes the integral of the C loss over time and is calculated from the two arrows: the total loss in C (kg C m^{-2}) due to drought, and the time (yr) to recover 50% of the pre-drought C stock. (c) **Conceptualized UCE-climate C change diagram:** hypothetical response in terrestrial

892 "integrated-C-change" (kg C m^{-2} yr) due to eCO_2 (blue line), rising temperature (red line),
893 interaction between eCO_2 and temperature (dashed purple), and combined interactions among
894 eCO_2, temperature, and UCEs of prolonged durations (green line), all relative to a reference
895 drought of normal duration with no warming (black line). Integrated-C-change denotes the
896 difference in integrated-C-loss (see panel b) between a scenario of changing climatic drivers and
897 the reference drought (control). (d) **Conceptual UCE amplification diagram**: hypothetical
898 amplified change in forest C stocks to eCO_2 and temperature relative to the pre-warming
899 historical past (based on Jump et al. (2017)). Change in C stock greater than zero indicates a
900 'structural overshoot' (SO) due to favorable environmental conditions and/or recovery from an
901 extreme drought-heat event (EE). Hashed black areas indicate a structural overshoot due to
902 eCO_2, which occurs over the historical CO_2 levels (dashed blue line). Initially, an eCO_2 effect
903 leads to a larger increase in structural overshoot (due to CO_2 fertilization), driving more extreme
904 vegetation mortality ('mortality overshoot' - MO) relative to historical dieback events and thus a
905 greater decrease in C stock. Increased warming through time increasingly counteracts any CO_2
906 fertilization effect; while the amplitude of post-UCE C stock recoveries remains large, net C
907 stock values eventually decline (downward curvature) due to more pronounced loss in C stocks
908 (and greater ecosystem state change) from hotter UCEs.
909 SO = structural overshoot, MO = mortality overshoot, EE = historically extreme drought-heat
910 event, UCE = unprecedented climate extreme.
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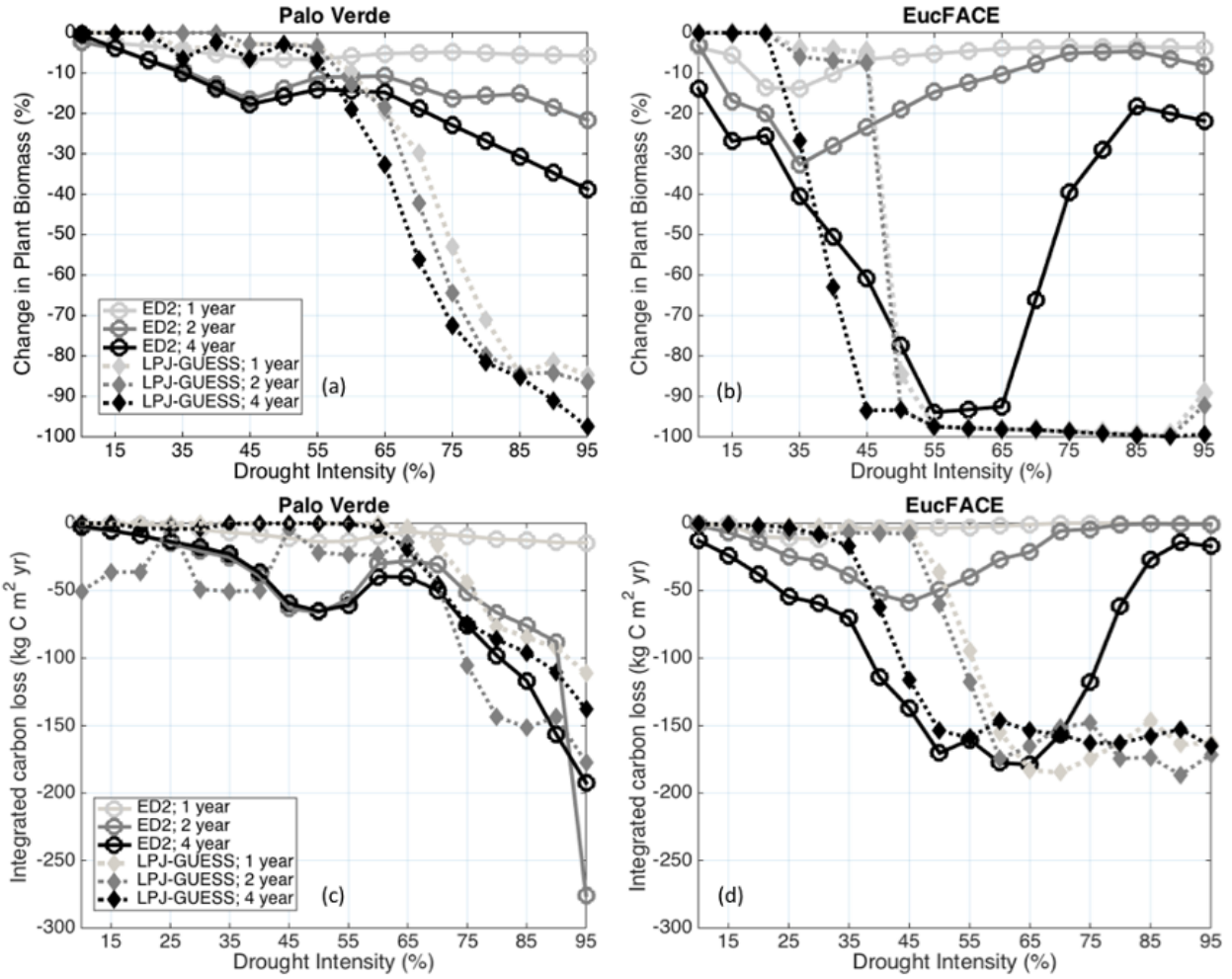

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913 **Figure 2** Modeled change in biomass (%) at the end of drought periods of different lengths (1, 2,
914 and 4-year droughts) and intensities (up to 95% precipitation removed) at (a) Palo Verde, and (b)
915 EucFACE, for the ED2 and LPJ-GUESS models. Modeled integrated-C-loss (C reduction due to
916 extreme drought integrated over time until biomass recovers to 50% of the non-drought baseline
917 biomass) at (c) Palo Verde and (d) EucFACE.

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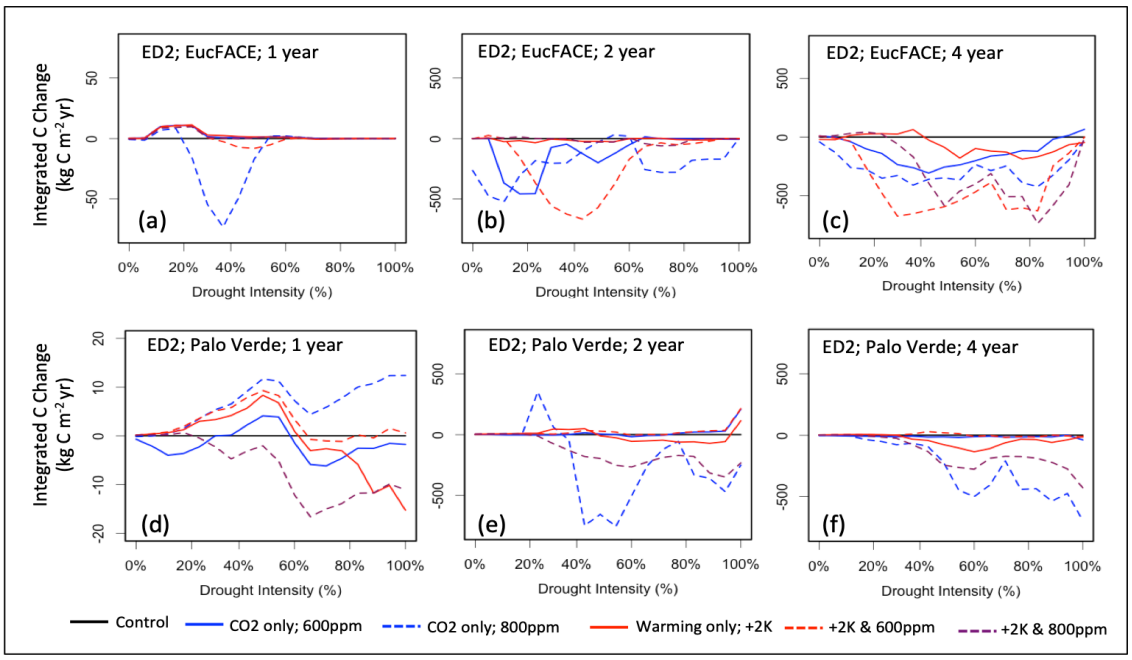

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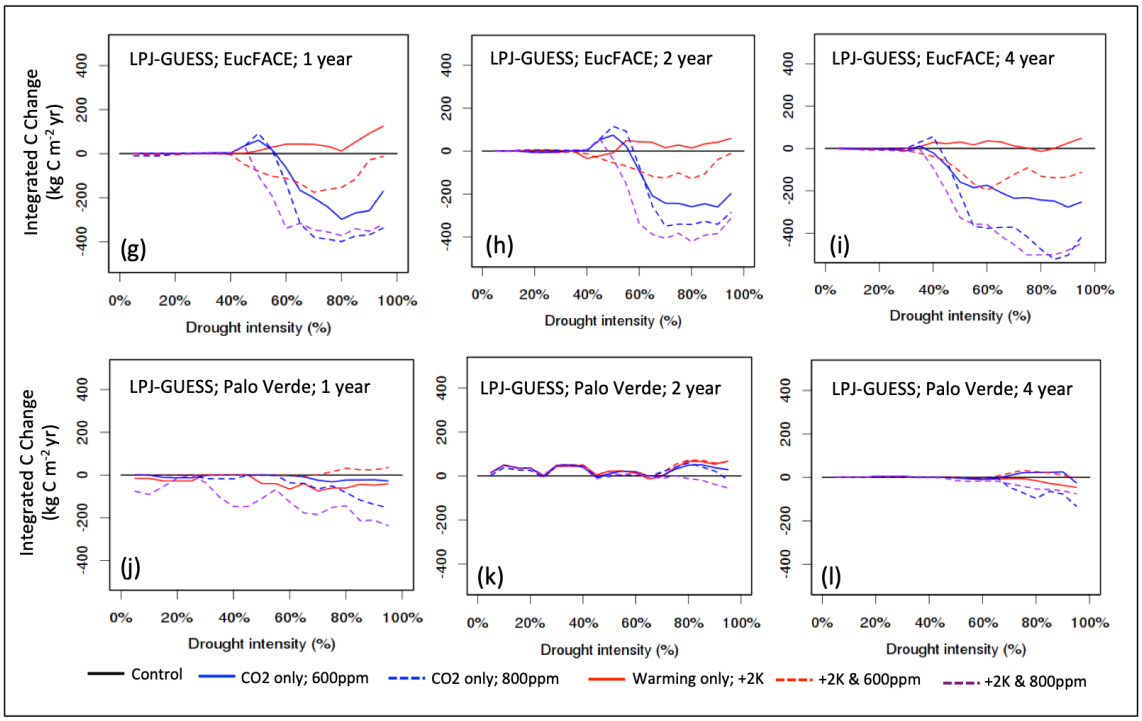

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921 **Figure 3** Vegetation C response to interactions between drought intensity (0% to 100%
922 precipitation reduction), drought durations (1, 2, 4-year droughts), and idealized scenarios of
923 warming and eCO_2 compared to the reference simulation, simulated by two VDMs; ED2 (a-f)
924 and LPJ-GUESS (g-l) at two sites (EucFACE and Palo Verde). The scenarios include a control
925 (current temperature; 400 ppm atmospheric CO_2), two eCO_2 scenarios (600 ppm or 800 ppm),

elevated temperature (2 K above current), and a combination of eCO_2 (600 ppm or 800 ppm) and higher temperature. Vegetation response is quantified as "integrated-C-change" (in kg C m^{-2} yr; Eq. 4), which is defined as the difference in integrated-C-losses due to drought between a given scenario of change in climatic drivers and the control. Negative values for integrated-C-change indicate that warming and/or eCO_2 leads to stronger C losses and/or longer recovery, while positive values for integrated-C-change indicates a buffering effect.

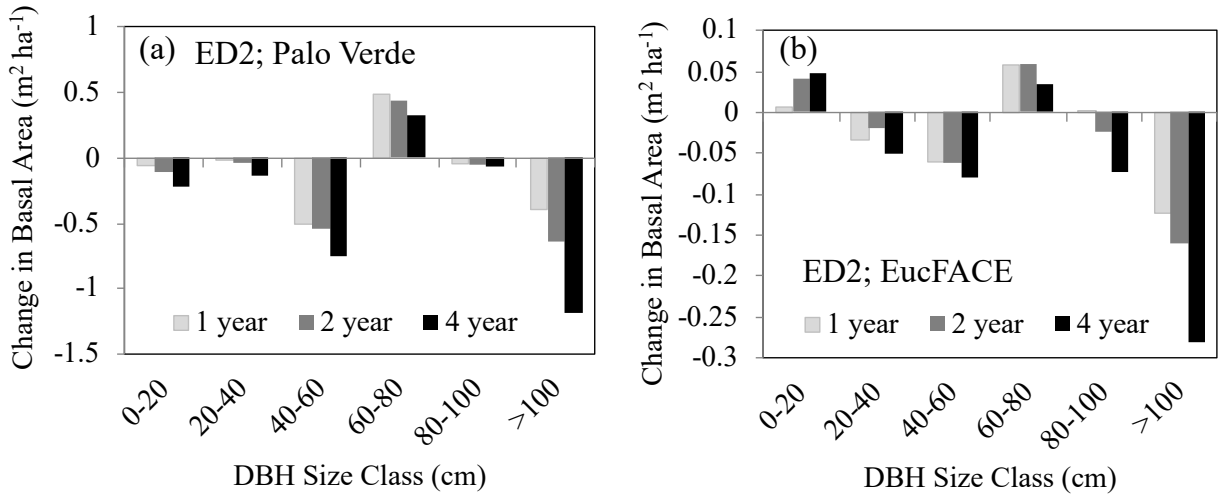

Figure 4 Change in basal area (m^2 ha^{-1}) immediately following either 1, 2, or 4 year droughts for six increasing size class bins (DBH, cm) as predicted by the ED2 model for (a) the Palo Verde site, with 90% precipitation removed, and (b) the EucFACE site with 50% precipitation removed.

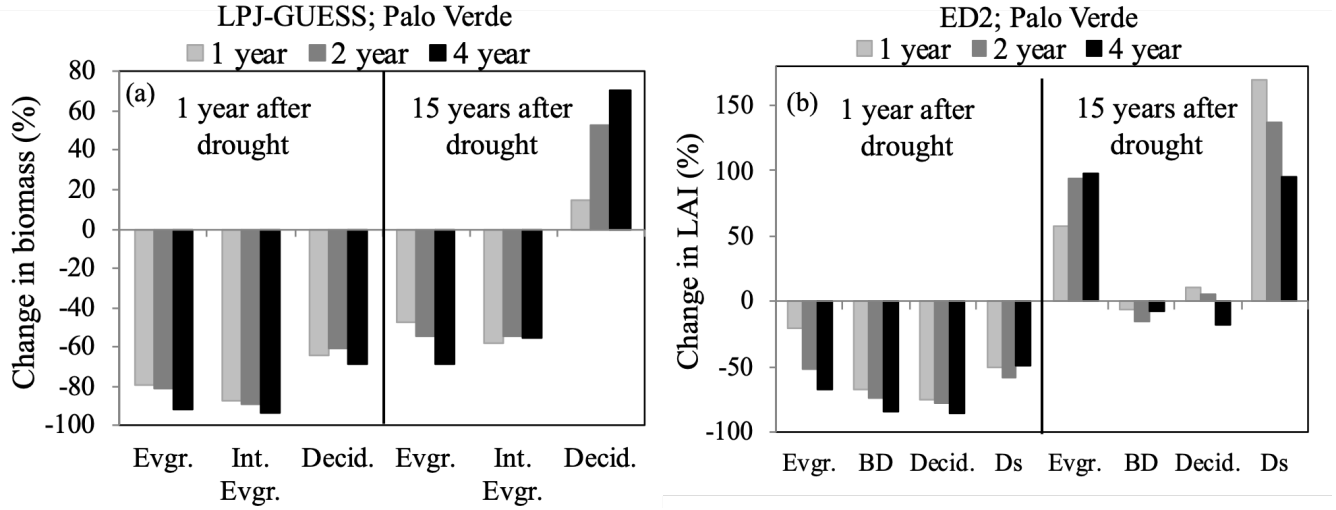

Figure 5 Percent change in community composition, represented by plant functional type (PFT), the year following three drought durations of UCEs (1, 2, and 4-year droughts and 90% precipitation removed) as well as 15 years after droughts, for the tropical Palo Verde site by (a) LPJ-GUESS reported in biomass change, and (b) ED2 reported in LAI change. Even though Ds had the strongest recovery, it should be noted it was the least abundant PFT at this site. Evgr. = evergreen, Int. Ever. = intermediate evergreen, Decid. = deciduous, BD = brevi-deciduous, Ds = deciduous stem-succulent. EucFACE data not shown because only one PFT present (evergreen tree).

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