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

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33

34   **Abstract**

35

36   Climatic extreme events are expected to occur more frequently in the future, increasing the

37   likelihood of unprecedented climate extremes (UCEs), or record-breaking events. UCEs, such as

38   extreme heatwaves and droughts, substantially affect ecosystem stability and carbon cycling by

39   increasing plant mortality and delaying ecosystem recovery. Quantitative knowledge of such

40   effects is limited due to the paucity of experiments focusing on extreme climatic events beyond

41   the range of historical experience. Here, we use two dynamic vegetation demographic models

42   (VDMs), ED2 and LPJ-GUESS, to investigate the hypothesis that ecosystem responses to UCEs

43   (e.g., unprecedented droughts) differ qualitatively from ecosystem responses to milder extremes,

44   as a result of non-linear ecosystem responses. Additionally, we explore how unprecedented

45   droughts in combination with increasing atmospheric CO_2 and/or temperature may affect

46   ecosystem stability and carbon cycling. We explored these questions using simulations of pre-

47   drought and post-drought conditions at well-studied forest sites in Australia and Costa Rica. Both

48   models produced nonlinear responses to UCEs. Due to the two models having different but

49   plausible representations of processes and interactions, they diverge in sensitivity of biomass loss

50   due to drought duration or intensity, and differ between each site. Biomass losses are most

51   sensitive to drought duration in ED2, but to drought intensity in LPJ-GUESS. Elevated

52   atmospheric CO_2 concentrations (eCO_2) alone did not completely buffer the ecosystems from

53   carbon losses during UCEs in the majority of our simulations. Our findings highlight contrasting

54   differences in process formulations and uncertainties in models, notably related to availability in

55   plant carbohydrate storage and the diversity of plant hydraulic schemes, in projecting potential

56   ecosystem responses to UCEs. The different hypotheses of plant responses to UCEs existing in

57   models reflect knowledge gaps, which should be tested with targeted field experiments. This

58   iterative modeling-experimental framework would help improve predictions of terrestrial

59   ecosystem responses and climate feedbacks.

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1 Introduction

60

61   The increase in extreme climate and weather events, such as prolonged heatwaves and

62 droughts as seen over the last three decades, are expected to continue to increase in frequency

63 and magnitude, leading to progressively longer and warmer droughts on land (IPCC 2012, 2021).

64 Droughts are affecting all areas of the globe, more than any other natural disturbance, and recent

65 droughts have broken long-standing records (Ciais et al., 2005; Phillips et al., 2009; Williams et

66 al., 2012; Matusick et al., 2013; Griffin and Anchukaitis, 2014; Asner et al., 2016; Feldpausch et

67 al., 2016; Seneviratne et al., 2021). Such 'unprecedented climate extremes' (UCEs; "record-

68 breaking events", IPCC (2012)) that are larger in extent and longer-lasting than historical norms

69 can have dramatic consequences for terrestrial ecosystem processes, including carbon uptake and

70 storage and other ecosystem services (Reichstein et al., 2013; Settele, 2014; Allen et al., 2015;

71 Brando et al., 2019; Kannenberg et al., 2020). Thus, to better anticipate the implications of

72 climatic changes for the terrestrial carbon sink and other ecosystem services, we need to better

73 understand how ecosystems respond to extreme droughts and other UCEs.

74   To learn how ecosystems respond to rarely experienced or unprecedented conditions,

75 ecologists can experimentally manipulate environmental conditions (Rustad, 2008; Beier et al.,

76 2012; Meir et al., 2015; Aguirre et al., 2021). However, the majority of such experiments apply

77 moderate treatments, which are mostly weaker in intensity and/or shorter in duration than

78 potential future UCEs (Beier et al., 2012; Kayler et al., 2015; but see Luo et al., 2017), and single

79 experiments have low power to detect effects of stressors on ecosystem responses (Yang et al.,

80 2022). Additionally, most experiments examine low-stature ecosystems, such as grassland,

81 shrubland or tundra, due to lower requirements for infrastructure and financial investment

82 compared to mature forests. However, forests may respond qualitatively differently to UCEs than

83 other ecosystems, in part due to mortality of large trees and strong nonlinear ecosystem

84 responses, with long-lasting consequences for ecosystem-climate feedbacks (Williams et al.,

85 2014; Meir et al., 2015). Ecosystem responses to naturally occurring extreme droughts and

86 heatwaves have been documented (Ciais et al., 2005; Breshears et al., 2009; Feldpausch et al.,

87 2016; Matusick et al., 2016; Ruthrof et al., 2018; Powers et al,. 2020); however, these rapidly-

88 mobilized post-hoc studies often are unable to measure all critical variables and may lack

89 consistently collected data for comparison with pre-drought conditions, thus limiting their

90 inferential power and ability to improve quantitative models. The difficulties of performing

91 controlled real-world experiments of UCEs at broad spatial and temporal scales make process-

92 based modeling a valuable tool for studying potential ecosystem responses to extreme events.

93   Process-based models can be used to explore potential ecosystem impacts using projected

94 climate change over broad spatial and temporal scales (Gerten et al., 2008; Luo et al., 2008;

95 Zscheischler et al., 2014; Sippel et al., 2016), as seen in a few modeling studies that have

96 synthesized and improved our process-level understanding of UCE effects (McDowell et al.,

97 2013; Dietze and Matthes, 2014). However, due to the overly simplified representation of

98 ecological processes in most land surface models (LSMs) – the terrestrial components of Earth

99 System Models (ESMs) used for climate projections – it is doubtful whether most of these

100 models adequately capture ecosystem feedbacks and other responses to UCEs (Fisher and

101 Koven, 2020). For example, only a few ESMs in recent coupled model intercomparison projects

102 (CMIP6) and IPCC climate assessments (Ciais et al., 2013; Arora et al., 2020) include vegetation

103 demographics (Döscher et al., 2022), and most rely on prescribed, static maps of plant functional

104 types (PFTs) (Ahlström et al., 2012). Other LSMs simulate PFT shifts (i.e., dynamic global

105 vegetation models, DGVMs; Sitch et al., (2008)) based on bioclimatic limits, instead of

106 emerging from the physiology- and competition-based demographic rates that determine

107 resource competition and plant distributions in real ecosystems (Fisher et al., 2018). Although a

108 new generation of LSMs with more explicit ecological dynamics and structured demography is

109 emerging (Holm et al., 2020; Koven et al., 2020; Döscher et al., 2022), most current ESMs are

110 limited in ecological detail and realism (e.g., ecosystem structure, demography, and

111 disturbances). Failing to mechanistically represent mortality, recruitment, and disturbance – each

112 of which influences biomass turnover and carbon (C) allocation (Friend et al., 2014) – limits the

113 ability of these models to realistically forecast ecosystem responses to anomalous environmental

114 conditions like UCEs (Fisher et al., 2018).

115   Evaluating and improving the representation of physiological and ecological processes in

116 ecosystem models is critical for reducing model uncertainties when projecting the effects of

117 UCEs on long-term ecosystem dynamics and functioning (Table 1). Vegetation demography,

118 plant hydraulics, enhanced representations of plant trait variation, explicit treatments of resource

119 competition (e.g., height-structured competition for light), and representing major disturbances

120 (e.g., extreme drought) have all been identified as critical areas for advancing current models

121 (Scheiter et al., 2013; Fisher et al., 2015; Weng et al., 2015; Choat et al., 2018; Fisher et al.,

122 2018) and are necessary advances for realistically representing the ecosystem impacts of UCEs.

123 Uncertainty in these processes leads to uncertainty in predicting an ecosystem's pre-drought

124 resistance, which influences the degree of impact and recovery from UCEs (Table 1; Frank et al.,

125 (2015)).

126   In this paper, we explore the potential responses of forest ecosystems to UCEs using two

127 state-of-the-art process-based demographic models (vegetation demographic models, VDMs;

128 Fisher et al., (2018)). We first present conceptual frameworks and hypotheses on potential

129 ecosystem responses to UCEs based on current knowledge. We then present VDM simulations

130 for a range of hypothetical UCE scenarios to illustrate current state-of-the-art model

131 representations of eco-physiological mechanisms expected to drive responses to UCEs. While a

132 variety of UCE-linked biophysical tree disturbance processes (e.g., fire, wind, insect outbreaks)

133 can drive non-linear ecosystem responses, we focus specifically on extreme droughts, which

134 have important impacts on many ecosystems around the world (e.g. Frank et al., 2015, IPCC

135 2021). By studying modeled responses to UCEs, we explore the limits to our current

136 understanding of ecosystem responses to extreme droughts and their corresponding thresholds

137 and tipping points. As anthropogenic forcing has increased the frequency, duration, and intensity

138 of droughts throughout the world (Chiang et al., 2021), we explore how eCO_2 and rising

139 temperatures may affect drought-induced C loss and recovery trajectories, and how the scientific

140 community can iteratively address these questions through experiments and modeling studies.

141

142 **1.1 Conceptual and Analysis Framework for Hypothesis Testing:**

143   This section presents conceptual frameworks that allow us to test two hypotheses on

144 potential responses of plant carbon stocks to UCEs. The first hypothesis is:

145 ***Hypothesis (H1). Terrestrial ecosystem responses to UCEs will differ qualitatively from***

146 ***ecosystem responses to milder extremes because responses are nonlinear. Nonlinearities can***

147 ***arise from multiple mechanisms – including shifts in plant hydraulics, C allocation,***

148 ***phenology, and stand demography – and can vary depending on the pre-drought state of the***

149 ***ecosystem.***

150 We present four conceptual relationships that describe terrestrial ecosystem responses to varying

151 degrees of extreme events (Fig. 1). Change in vegetation C stock is *linearly* related to drought

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152   intensity and/or drought duration (Fig. 1a, H0, null hypothesis), which has some observational

153   support from annual and perennial grassland ecosystems, shrublands and savannas across the

154   globe (Bai et al., 2008; Muldavin et al., 2008; Ruppert et al., 2015). Alternatives to the null

155   (linear) hypothesis are that biomass loss increases non-linearly with increased drought intensity

156   (i.e., reduction in precipitation) represented by a threshold-based relationship (Fig. 1a, H1a),

157   increased drought duration (i.e., prolonged drought with the same intensity) by shifting the linear

158   relationship downwards via increasing slopes (Fig. 1a, H1b), or the combination of both intensity

159   and duration (Fig. 1a, H1c). These hypotheses are supported by observations from the Amazon

160   Basin and Borneo (Phillips et al., 2010) where tree mortality rates increased non-linearly with

161   drought intensity. Similarly, plant hydraulic theories predict nonlinear damage to the plant-water

162   transport systems, and thus mortality risk, as a function of drought stress (Sperry and Love,

163   2015). In particular, longer droughts are more likely to lead to lower soil water potentials,

164   leading to a nonlinear xylem damage function even if stomata effectively limit water loss (Sperry

165   et al., 2016).

166   ***Hypothesis (H2): The effects of increasing atmospheric CO_2 concentration (eCO_2) will***

167   ***alleviate impacts of extreme drought stress through an increase in vegetation productivity and***

168   ***water-use efficiency, but only up to a threshold of drought severity, while increased***

169   ***temperature (and related water stress) will exacerbate tree mortality.***

170   This second hypothesis is based on growing evidence that effects of eCO_2 and climate

171   warming may interact with effects of drought intensity on ecosystems. The CO_2 fertilization

172   effect enhances vegetation productivity (e.g., net primary production, NPP) (Ainsworth and

173   Long, 2005; Norby et al., 2005; Wang et al., 2012), but this fertilization effect is generally

174   reduced by drought (Hovenden et al., 2014; Reich et al., 2014; Gray et al., 2016). Drought events

175   often coincide with increased temperature, which intensifies the impact of drought on

176   ecosystems (Allen et al., 2015; Liu et al., 2017), resulting in nonlinear responses in mortality

177   rates (Adams et al., 2009; Adams et al., 2017a). The evaluation of C cycling in VDMs with

178   doubling of CO_2 (only "beta effect") showed a large carbon sink in a tropical forest (Holm et al.,

179   2020), but the inclusion of climate interactions in VDMs needs to be further explored.

180   Here, we relate ecosystem responses to UCEs by calculating the "integrated carbon (C)

181   loss" (Fig. 1b and see Methods), which integrates C loss from the beginning of the drought until

182   the time when C stocks have recovered to 50% of the pre-drought level. In response to drought,

183   warming, and eCO_2, divergent potential C responses (gains and losses; Fig. 1c) can be expected

184   (Keenan et al., 2013; Zhu et al., 2016; Adams et al., 2017a). For example, a grassland

185   macrocosm experiment found that eCO_2 completely compensated for the negative impact of

186   extreme drought on net carbon uptake due to increased root growth and plant nitrogen uptake,

187   and led to enhanced post-drought recovery (Roy et al., 2016). However, a 16-year grassland

188   FACE and the SoyFACE experiments showed that CO_2 fertilization effects were reduced or

189   eliminated under hotter/drier conditions (Gray et al., 2016; Obermeier et al., 2016). Reich et al.,

190   (2014) also found that CO_2 fertilization effects were reduced in a perennial grassland by water

191   and nitrogen limitation.

192   A corollary to our H2 is that conditions that favor productivity (e.g., longer growing

193   seasons and/or CO_2 fertilization) will enhance vegetation growth leading to "structural

194   overshoot" (SO; Fig. 1d; adapted from and supported by Jump et al., 2017), and can amplify the

195   effects of UCEs. Enhanced vegetation growth coupled with environmental variability can lead to

196   exceptionally high plant-water-demand during extreme drought and water stress, resulting in a

197   "mortality overshoot" (MO; Fig 1d). We conceptualize how oscillations between SO and

198   associated MO could be amplified by increasing climatic variability and UCEs (Fig. 1d).

199   Confidence is low as to how historically unprecedented eCO_2 levels and temperatures will affect

200   ecosystems in the future (i.e., the widening of the shaded areas compared to historical, Fig. 1d).

201   We expect, however that a rapidly changing climate, combined with effects of UCEs as a result

202   of more frequent extreme drought/heat events and drought stress, can exacerbate and amplify

203   SOs and MOs (Jump et al., 2017), leading to increasing C loss, even though various buffering

204   mechanisms exist (cf. (Lloret et al., 2012; Allen et al., 2015)). Relative to our conceptual (Fig.

205   1d), we note that most experimental, observational and modeling studies (Ciais et al., 2005; da

206   Costa et al., 2010; Phillips et al., 2010; Meir et al., 2015) take into account only low to moderate

207   drought intensities or single events, or combine drought with moderate effects of temperature

208   change. As represented by the increasing amplitude of oscillations in Fig. 1d, the interactions

209   between increased temperatures, UCE events, and vegetation feedbacks make ecosystem states

210   become inherently unpredictable, particularly over longer time-scales.

211

2 Methods

212
213   We explored our hypotheses at forested ecosystems in Australia and Central America

214 using two VDMs: the Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) (Smith et

215 al., 2001; Smith et al., 2014) and the Ecosystem Demography model 2 (ED2) (Medvigy et al.,

216 2009; Medvigy and Moorcroft, 2012). These models include detailed process representation of

217 ecosystem demography and dynamic plant growth, recruitment, and mortality, resulting in

218 changes in abundance of different PFTs, as well as vertically stratified tree size- and age-class

219 structure. Community dynamics and age-/size-structure are emergent properties from

220 competition for light, space, water, and nutrients, which dynamically and explicitly scale up from

221 the tree, to stand, to ecosystem level.

222   VDMs have been used to interpret the cascade of ecosystem responses to long-term

223 droughts in the Amazon and are informative when conducting model-data comparisons (Powell

224 et al., 2013), but studies of ecosystem responses to UCEs are lacking. New implementation of

225 plant competition for resources and plant hydraulics in VDMs are improving our understanding

226 of plant-water relations and stresses within plants (Christoffersen et al., 2016; Xu et al., 2016;

227 Fisher et al., 2018; and see Kennedy et al., 2019 for representation in a 'big-leaf' model). Since

228 field data needed to evaluate UCE responses are, by definition, unavailable, we do not perform

229 model-data comparisons. Rather, we use the model results to explore our hypotheses and

230 illustrate their implications for ecosystem responses under UCEs.

231

2.1 LPJ-GUESS and ED2 Model Descriptions

232
233   Both LPJ-GUESS and ED2 resolve vegetation into tree cohorts characterized by their

234 PFT, in addition to age-class in LPJ-GUESS; and size, and stem number density in ED2. Both

235 models are driven by external environmental drivers (e.g., temperature, precipitation, solar

236 radiation, atmospheric CO_2 concentration, nitrogen deposition), and soil properties (soil texture,

237 depth, etc.), and also depend on dynamic ecosystem state, which includes light attenuation, soil

238 moisture, and soil nutrient availability. Establishment and growth of PFTs, and their carbon-,

239 nitrogen- and water-cycles, are simulated across multiple patches per grid cell to account for

240 landscape heterogeneity. Both models characterize PFTs by physiological and bioclimatic

241 parameters, which vary between the models (Smith et al., 2001; Smith et al., 2014; Medvigy et

242 al., 2009; Medvigy and Moorcroft, 2012).

243   The LPJ-GUESS includes three woody PFTs: evergreen, intermediate evergreen, and

244   deciduous PFTs. Mortality in LPJ-GUESS is governed by a 'growth-efficiency'-based function

245   (kg C m^{-2} leaf yr^{-1}), which captures effects of water deficit, shading, heat stress, and tree size on

246   plant productivity relative to its resource-uptake capacity (leaf area), with a threshold below

247   which stress-related mortality risk increases markedly, in addition to background senescence and

248   exogenous disturbances. Stress mortality can be reduced by plants using labile carbon storage,

249   modeled implicitly using a 'C debt' approach, which buffers low productivity, enhancing

250   resilience to milder extremes (more details are given in section 4.1.4). Total mortality can thus be

251   impacted by variation in environmental conditions such as water limitation, low light conditions,

252   and nutrient constraints, as well as current stand structure (Smith et al., 2001; Hickler et al.,

253   2004).

254   The ED2 version used here (Xu et al., 2016) includes four woody PFTs: evergreen,

255   intermediate evergreen, deciduous, brevi-deciduous, and deciduous stem-succulent. This ED2

256   version includes coupled photosynthesis, plant hydraulics, and soil hydraulic modules (Xu et al.,

257   2016), which together determine plant water stress. The plant hydraulics module tracks water

258   flow along a soil–plant–atmosphere continuum, connecting leaf water potential, stem sap flow,

259   and transpiration, thus influencing controls on photosynthetic capacity, stomatal closure,

260   phenology, and mortality. Leaf water potential depends on time-varying environmental

261   conditions as well as time-invariant PFT traits. Leaf shedding is triggered when leaf water

262   potential falls below the turgor loss point (a PFT trait) for a sufficient amount of time. Leaf

263   flushing occurs when stem water potential remains high (above half of the turgor loss point) for a

264   sufficient time (see Xu et al., 2016 for details). PFTs differ in their hydraulic traits, wood

265   density, specific leaf area, allometries, rooting depth, and other traits. Stress-based mortality in

266   the ED2 version used here includes two main physiological pathways in our current

267   understanding of drought mortality (McDowell et al., 2013): C starvation and hydraulic failure.

268   Mortality due to C starvation in ED2 results from a reduction of C storage, a proxy for non-

269   structural carbohydrate (NSC) storage, which integrates the balance of photosynthetic gain and

270   maintenance cost under different levels of light and moisture availability. Mortality due to

271   hydraulic failure in ED2 is based on the percentage loss of stem conductivity. ED2 also includes

272   a density-independent senescence mortality rate based on wood density.

2.2 Modeling protocol

273

274   We applied LPJ-GUESS and ED2 at two extensively studied field sites. The first is a

275 mature *Eucalyptus* (*E. tereticornis*) warm temperate-subtropical transitional forest that is the site

276 of the Eucalyptus Free Air CO_2 enrichment (EucFACE) experiment in Western Sydney,

277 Australia (Medlyn et al., 2016; Ellsworth et al., 2017; Jiang et al., 2020), with a canopy coverage

278 of 95% (830 trees per ha). The EucFACE site has a mean annual temperature of 17.3°C and

279 receives an annual rainfall of 800 mm (Ellsworth et al., 2017). The evergreen eucalypt trees are

280 on average 22 m tall with a DBH of 21 cm and a stand-level LAI of 1.5. The second site is a

281 seasonally dry tropical forest in the Parque Nacional Palo Verde in Costa Rica (Powers et al.,

282 2009). This site has nutrient rich soils (Powers and Peréz-Aviles, 2013), a mean annual

283 temperature of 25.1°C, and mean annual rainfall of 1440 mm, with a 5-month dry season.

284 Multiple leaf phenological strategies co-occur, including evergreens, brevi-deciduous tree

285 species, as well as deciduous species that drop their leaves during the dry season.

286   We performed a 100-year "baseline" simulation for each model at each site driven by

287 constant, near ambient, atmospheric CO_2 (400 ppm) and recycled historical site-specific climate

288 data (1992-2011 for EucFACE and 1970-2012 for Palo Verde; Sheffield et al., (2006)), absent of

289 drought treatments. A detailed description of the meteorological data and initial conditions used

290 to drive the models is in the Supplementary Text A. No site-level parameter tuning was

291 conducted with the models. To describe the ecosystem impact of UCEs, we simulated 10 years

292 of pre-drought conditions (continuing from the baseline simulation), followed by drought

293 treatments that differed in intensity and duration, followed by a 100-year post-drought recovery

294 period. To explore the effects of drought intensity, we conducted 20 different artificial drought

295 intensity simulations, in which precipitation during the whole year is reduced by 5% to 100% of

296 its original amount, in increments of 5%. To explore the effects of drought duration, the 20

297 different drought intensities are maintained over 1, 2 and 4 years (Table S1). We examined

298 model responses of aboveground biomass, leaf area index (LAI), stem density (number ha^{-1}),

299 plant available soil water (mm), plant C storage (kg C m^{-2}), change in stem mortality rate (yr^{-1}),

300 and PFT composition.

301   To explore how temperature, eCO_2 concentration, and UCE droughts influence forest C

302 dynamics individually and in combination, we implemented the following five experimental

303 scenarios, some realistic and others hypothetical, for each model (Table S1): increased

304   temperature only (+2K over ambient), eCO_2 only (600 ppm and 800 ppm), and both increased

305   temperature and eCO_2 (+2K 600 ppm; +2K 800 ppm). Temperature and eCO_2 manipulations

306   were applied as step increases over the baseline conditions, and are artificial scenarios, as

307   opposed to model-generated climate projections.

308

309   Evaluation of simulation results

310   To relate our simulation results to Fig. 1a, we compared the total biomass loss as a result

311   of each drought treatment by calculating the percentage of biomass reduction at the end of the

312   drought period relative to the baseline (no drought) simulation. To explicitly consider biomass

313   recovery rates over time, we calculated "integrated-C-loss" (Eqs. 1-3), as a result of drought

314   under current climate, which are determined based on the concepts in Fig. 1b. We defined

315   "integrated-C-loss" as the time-integrated carbon in biomass that is lost due to drought relative to

316   what the vegetation would have stored in the absence of drought. That is, it is the difference

317   between biomass in the presence of drought (B_d) at time (t) and biomass in the baseline

318   simulation (no drought; B_{base}), integrated over a defined recovery time period (in kg C m^{-2}

319   yr):

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

320   .   (Eq. 1)

321   To define the bounds of integration, in Eq. 1, t_1 is defined as the time when the maximum

322   amount of plant C is lost as a result of the drought:

$$B_{base}(t_1) - B_d(t_1) = \max_t [B_{base}(t) - B_d(t)]$$

323   (Eq. 2)

324   Then, t_2 is defined implicitly as the time when 50% of the lost biomass has been recovered

325   compared to the baseline:

$$B_{base}(t_2) - B_d(t_2) = \frac{1}{2}(B_{base}(t_1) - B_d(t_1))$$

326   (Eq. 3)

327   Since all integrated-C-loss results are taken as the difference from a non-drought baseline

328   biomass (B_{base}) and all droughts will result in a loss of C.

329   We also use integrated-C-loss to examine the role of drought, temperature and eCO_2

330   change for moderating or exacerbating the impacts of drought on forest C stocks; i.e., to evaluate

331 the hypotheses illustrated in Fig. 1c. To assess these impacts of changing climates, we calculate

332 an "integrated-C-change" (Eq. 4). Defined as the difference between the integrated-C-loss due to

333 drought alone (Eqs. 1-3) under present climate, and the integrated-C-loss due to the combined

334 effects of drought and climate change (i.e., five scenarios of temperature increase and eCO_2):

$$\text{Integrated-C-change} = integrated\ C\ Loss_{Drought} - integrated\ C\ Loss_{Drought+CC}$$

335 (Eq. 4)

336 Because we expect drought to reduce vegetation C stocks, and thus integrated-C-loss to

337 be negative, positive values of integrated-C-change indicate that changes in climatic drivers

338 reduced the C losses from drought (i.e., buffering effects). Negative values of integrated-C-

339 change indicate that the climate change scenario leads to either greater C losses or losses that

340 persist for longer amounts of time (i.e., magnitude and/or duration) compared to a simulation

341 with no climate change (i.e., "reference" run).

342

343 **3 Results**

344 Both models displayed nonlinear responses to drought, in concurrence with Hypothesis

345 H1, but they differ in their behavior and between sites. In general, ED2 shows sensitivity to

346 drought duration (Hypothesis H1b), while LPJ-GUESS shows a stronger sensitivity to drought

347 intensity (Hypothesis H1a). ED2's sensitivity to the duration of drought was mild at Palo Verde

348 (Fig. 2a), and stronger at EucFACE particularly during the 4-year drought with a strong non-

349 monotonic pattern (see explanation below) (Fig. 2b). When reporting only percentage of biomass

350 loss, ED2 predicts close to no UCE response at Palo Verde; with a maximum biomass reduction

351 of only 40% during 95% precipitation removal and a 4-year drought event (i.e., UCE). LPJ-

352 GUESS shows no sensitivity to drought duration but is highly sensitive to drought intensity. C

353 loss predicted by LPJ-GUESS at Palo Verde reached a threshold at ~65% drought intensity, after

354 which forests exhibit strong biomass losses, up to 100% (Fig. 2a). At the EucFACE site, both

355 models predict a critical threshold of biomass loss at 35%-45% drought intensity, with LPJ-

356 GUESS predicting total biomass loss (up to 100%) after this drought intensity threshold (Fig.

357 2b). The EucFACE drought threshold is lower than that of the seasonally dry mixed tropical

358 forest in Palo Verde.

359 With respect to C loss over a recovering time period (integrated-C-loss), the two models

360 predict similar drought responses at Palo Verde (Fig. 2c), but not at EucFACE (Fig. 2d). At Palo

361 Verde, the similarity between models in integrated-C-loss reflected longer biomass recovery time

362 but less biomass loss in the short-term in ED2 relative to LPJ-GUESS, which predicted greater

363 biomass loss immediately after drought but shorter recovery time. With the exception of the 1-

364 year drought in ED2, both models predict similar integrated-C-loss across a range of UCEs at

365 Palo Verde, via different pathways. The integrated-C-loss metric revealed a strong non-linear

366 response to drought duration in ED2 (Fig. 2c), while this nonlinearity is less evident when only

367 examining change in biomass (Fig. 2a). The "V"-shaped patterns observed particularly in Fig.

368 2b, arise from interactions between whole-leaf phenology and stomatal responses to drought in

369 ED2. For drought intensities lower than 40%, stomatal conductance is reduced but leaves are not

370 fully shed. Leaf respiration continues, gradually depleting non-structural C pools, followed by a

371 loss of biomass. However, for higher drought intensities, leaf water potentials quickly become

372 systematically lower than leaf turgor loss points and tree cohorts shed all their leaves. This

373 strategy represents an immediate loss of C via leaf shedding, but spares the cohort from slow,

374 respiration-driven depletion of C stocks.

375

376 **3.1 Predicted model responses to UCE droughts combined with increased temperature**

377 **and/or eCO$_2$**

378 Relating to our second hypothesis of additional effects of warming and eCO$_2$, we tested

379 15 treatments in total, repeating the five climate change scenarios for each of the three drought

380 durations. With the addition of climate change impacts, ED2 remained sensitive to the duration

381 of drought, with warming negatively impacting integrated-C-change and most consistently

382 during 2- and 4-year drought durations. ED2 predicts that during the 2- and 4-year droughts at

383 EucFACE, losses are exacerbated when accompanied with warming and even with eCO$_2$, with

384 800 ppm having a more detrimental impact than 600 ppm (Fig. 3a-c). The average integrated-C-

385 change was -111.0 kg C m^{-2} yr across all 15 treatments (Table 2). Only during the 1-year drought

386 duration did drought plus warming and eCO$_2$ have a buffering effect on C stocks, seen in four

387 out of our five scenarios but only during relatively modest droughts intensities (Fig. 3a; i.e.,

388 positive integrated-C-change, see also Table 2).

389 The ED2 simulations of the seasonally dry Palo Verde site (Fig. 3d-f), produced less

390 frequent negative impacts on drought and climate change driven C losses compared to

391 EucFACE, with an average integrated-C-change of -53.9 kg C m^{-2} yr^{-1} across all 15 treatments

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392 (Table 2). During the 2-year drought, applying +2K with eCO$_2$ to 600 ppm showed a slight

393 buffering effect to droughts and the most consistent positive integrated-C-change (Fig. 3e; Table

394 2). Interestingly, an increase in only eCO$_2$ to 800 ppm (no warming) when applied with the 2-

395 and 4-year droughts resulted in the largest loss in integrated-C-change (Fig. 3e-f), larger than the

396 expected 'most severe' scenario; +2K and 800 ppm.

397   Similar to ED2, the LPJ-GUESS model showed a nearly complete negative response in

398 integrated-C-change as a result of UCE drought and scenarios of warming and eCO$_2$ at the

399 EucFACE site (Fig. 3g-i), but mixed and more muted results at Palo Verde (Fig. 3j-l, Table 2).

400 The average integrated-C-change relative to the reference case was -95.4 at EucFACE and -7.8

401 kg C m^{-2} yr at Palo Verde, both less negative compared to ED2. One notable pattern was up until

402 a drought intensity threshold of ~40%, the climate scenarios had no effect or response in

403 integrated-C-change at EucFACE, and the muted response from warming and eCO$_2$ Palo Verde,

404 compared to ED2. Surprisingly, the +2K scenario switched the integrated-C-change to positive,

405 compared to the reference case (Fig. 3g-i; red lines), potentially a physiological process in the

406 model to increased temperatures only that signals an anomalous resiliency response. Similar to

407 the results with no climate change, LPJ-GUESS remained sensitive to the intensity of drought,

408 with ~40% precipitation reduction being a threshold.

409   The models and sites differed with regard to SO and MO responses to increasing drought

410 severity and its interactions with warming and eCO$_2$ (related to conceptual Fig. 1d). ED2 showed

411 a more consistent MO response during UCEs and with additional warming and eCO$_2$ (Fig. 3;

412 negative integrated-C-change), especially at EucFACE, suggesting these ecosystems will remain

413 in a depressed carbon condition driving vegetation mortality, and/or longer recoveries. LPJ-

414 GUESS produced more opportunities for SO with climate change. For example, at EucFACE

415 CO$_2$ fertilization created small SO periods that then led to MO with increasing drought severities,

416 and at Palo Verde all +2K and 600 ppm led to a SO (Fig. 3j-l; Table 2).

417   Both models predicted that C losses due to drought interactions with increased

418 temperature and eCO$_2$ were less severe at the seasonally dry Palo Verde site compared to the

419 somewhat less seasonal, more humid EucFACE site (Table 2), which could be attributed to

420 higher diversity in PFT physiology at Palo Verde. Palo Verde's community composition that

421 emerged following drought included either three (LPJ-GUESS) or four (ED2) PFTs, while only a

422 single PFT existed at EucFACE. With rising temperatures under climate change, UCEs will be

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423 hotter and drier. Nine out of the twelve simulations with both +2K and 600 ppm CO_2, and all but

424 one +2K and 800 ppm CO_2 produced a negative integrated-C-change, implying stronger C losses

425 and/or longer recovery times when droughts are exacerbated by increasing temperatures (Table

426 2).

427

428 4 Discussion

429   We applied two vegetation demographic models (VDMs) to explore two hypotheses

430 regarding a range of modeled response of terrestrial ecosystems to unprecedented climate

431 extremes (UCEs). Key model results include strong nonlinearities (Hypothesis H1) in C response

432 to extreme drought *intensities* in LPJ-GUESS and alternatively drought *durations* in ED2 (at one

433 of two sites), with differences in thresholds between the two models and ecosystems. These

434 nonlinearities may arise from multiple mechanisms that we begin to investigate here, including

435 shifts in plant hydraulics or other functional traits, C allocation, phenology, and stand

436 demography, all which vary among ecosystem types. The models also show exacerbated biomass

437 loss and recovery times in the majority of our scenarios of warming and eCO_2, supporting

438 Hypothesis H2. Below, we elucidate the underlying mechanisms that drive simulated ecosystem

439 response to UCEs based on our simulation results and observational evidence from the literature.

440 We focus on two temporal stages of the UCE: The pre-drought ecosystem stage characterized as

441 the quasi-stable state of the ecosystem prior to a UCE, which can mediate ecosystem resistance

442 and disturbance impact, and the post-drought recovery stage (Table 1).

443

444 4.1 The role of ecosystem processes and states prior to UCEs

445 4.1.1 The role of phenology and phenological strategies prior to UCEs:

446   Observations show that different levels of deciduousness contribute to alternative

447 strategies for tropical tree response to water stress (Williams et al., 2008). For example, during

448 the severe 1997 El Nino drought, brevi-deciduous trees and deciduous stem-succulents within a

449 tropical dry site in Guanacaste Costa Rica retained leaves during the extreme wet-season

450 drought, behaving differently than during normal dry seasons (Borchert et al., 2002). Both

451 models here predict that neither seasonal deciduousness, nor drought-deciduous phenology at the

452 seasonally dry tropical forest, Palo Verde (which consists of trees with different leaf

453 phenological strategies), act to buffer the forest from a large drop in LAI during UCEs (Fig. S1a-

454 b). Even with this large decrease in LAI, ED2 predicted a very weak biomass loss at the time of

455 UCEs (Fig. 2a), suggesting large-scale leaf loss is not a direct mechanism of plant mortality in

456 ED2. At the EucFACE site prior to the simulated extreme drought, LAI was stable in ED2, while

457 LPJ-GUESS displayed strong inter-annual variability in LAI (Fig. S1a-b). This capability of

458 large swings in LAI, and the larger LAI drop (3.0 to 1.7) by LPJ-GUESS could potentially

459 contribute to the considerable mortality response at EucFACE. Models might better capture the

460 different plant phenological responses to UCEs if the PFT phenology schemes better represented

461 morphological and physiological characteristics relevant to plant-water relations (e.g., leaf age;

462 retention of young leaves even during extreme droughts; Borchert et al., (2002); variation in

463 hydraulic traits as a function of leaf habit Vargas et al., (2021)) (Table 3).

464

465 **4.1.2 The role of plant hydraulics prior to UCEs:**

466 Susceptibility of plants to hydraulic stress is one of the strongest determinants of

467 vulnerability to drought, with loss of hydraulic conductivity being a major predictor of drought

468 mortality in temperate (McDowell et al., 2013; Anderegg et al., 2015; Sperry and Love, 2015;

469 Venturas et al., 2021) and tropical forests (Rowland et al., 2015; Adams et al., 2017b), as well as

470 a tractable mortality mechanism to represent in process-based models (Choat et al., 2018,

471 Kennedy et al., 2019). Both LPJ-GUESS and ED2 exhibited a wide range in amount and pattern

472 of plant-available-water prior to drought (Fig. S1c-d), leading to large differences in UCE

473 response. LPJ-GUESS predicted lower total plant-available-water at both sites compared to ED2,

474 and subsequently simulated a greater increase in plant-available-water right after the UCEs as a

475 result of greater mortality and decrease in water demand. Due to ED2 using a static mortality

476 threshold from conductivity loss (88%), it likely does not accurately reproduce the wide range of

477 observations of drought-induced mortality. In ED2, large trees, with longer distances to transport

478 water, were at higher risk and suffered higher mortality (Fig. S3), demonstrating how stand

479 demography and size structure can play an important role in ecosystem models (Fisher et al.,

480 2018). There are strong interdependencies and related mechanisms connecting both hydraulic

481 failure (e.g., low soil moisture availability) and C limitation (e.g., stomatal closure) during

482 drought (McDowell et al., 2008; Adams et al., 2017b), and these interactions should be

483 incorporated in ecosystem modeling and further explored (Table 3).

484   **4.1.3. The role of carbon allocation prior to UCEs:**

485   Plants have a variety of strategies to buffer vulnerability to water and nutrient stress

486   caused by extreme droughts, such as allocating more C to deep roots (Joslin et al., 2000; Schenk

487   and Jackson, 2005), investing in mycorrhizal fungi (Rapparini and Peñuelas, 2014), or reducing

488   leaf area without shifting leaf nutrient content (Pilon et al., 1996). Alternatively, presence of

489   deep roots doesn't necessarily lead to deep soil moisture utilization, as seen in a 6-year

490   Amazonian throughfall exclusion experiment where deep root water uptake was still limited,

491   even with high volumetric water content (Markewitz et al., 2010). Elevated CO_2 alone will

492   enhance growth and water-use efficiency (Keenan et al., 2013), reducing susceptibility to

493   drought. However, such increased productivity within a forest stand, and associated structural

494   overshoot during favorable climate windows, can also be reversed by increased competition for

495   light, nutrients, and water during unfavorable UCEs – potentially leading to mortality overshoot

496   (Fig. 1d) and higher C loss. Mortality overshoot could be an explanation for the negative

497   integrated-C-change (i.e., C loss) in the majority of eCO_2-only simulations (18 out of 24

498   scenarios; Table 2).

499   Effects of CO_2 fertilization on plant C allocation strategies are uncertain. As a result,

500   ecosystem models differ in their assumptions on controls of C allocation in response to eCO_2,

501   leading to divergent plant C use efficiencies (Fleischer et al., 2019). Global scale terrestrial

502   models are beginning to include dynamic C allocation schemes, over fixed ratios, that account

503   for concurrent environmental constraints on plants, such as water, and adjust allocation based on

504   resource availability (Weng et al., 2015; Zhu et al., 2019), but the representation of C allocation

505   is still debated and progressing (De Kauwe et al., 2014; Montané et al., 2017; Reyes et al., 2017).

506   It is worth investigating the differences between C allocation based on the allometric partitioning

507   theory (i.e., allocation follows a power allometry function between plant size and organs which

508   is insensitive to environmental conditions; Niklas, 1993), as an alternative to ratio-based optimal

509   partitioning theory (i.e., allocation to plant organs based on the most limiting resources)

510   (McCarthy and Enquist, 2007) or fixed ratios (Table 3), particularly due to VDMs substantial use

511   of allometric relationships. A meta-analysis of 164 studies found that allometric partitioning

512   theory outperformed optimal partitioning theory in explaining drought-induced changes in C

513   allocation (Eziz et al., 2017).

514

4.1.4 The role of plant carbon storage prior to UCEs:

515

516 Studies of neotropical and temperate seedlings show that pre-drought storage of non-

517 structural carbohydrates (NSCs) provides the resources needed for growth, respiration

518 osmoregulation, and phloem transport when stomata close during subsequent periods of water

519 stress (Myers and Kitajima, 2007; Dietze and Matthes, 2014; O'Brien et al., 2014). Furthermore,

520 direct correlations have been shown between NSC depletion and embolism accumulation, and

521 the degree of pre-stress reserves and utilization of soluble sugars (Tomasella et al., 2020). The

522 amount of NSC storage required to mitigate plant mortality during C starvation and interactions

523 with hydraulic failure from severe drought is difficult to quantify, due to the many roles of NSCs

524 in plant function and metabolism (Dietze and Matthes, 2014). For example, NSCs were not

525 depleted after 13 years of experimental drought in the Brazilian Amazon (Rowland et al., 2015).

526 As atmospheric CO_2 increases with climate change, NSC concentrations may increase, as seen in

527 manipulation experiments (Coley, 2002), but interactions with heat, water stress, enhanced leaf

528 shedding, and nutrient limitation complicates this relationship, and needs to be further explored.

529 Despite the recognition of the critical role that plant hydraulic functioning and NSCs play in tree

530 resilience to extremes, knowledge gaps and uncertainties preclude fully incorporating these

531 processes into ecosystem models.

532 Compared to ED2, LPJ-GUESS predicted low plant carbon storage (a model proxy for

533 NSCs) prior to and during drought, and at times became negative, thereby creating C costs (Fig.

534 S2a-b), leading to C starvation and potentially explaining the larger biomass loss in LPJ-GUESS

535 at both sites. Alternatively, ED2 maintained higher levels of NSCs providing a buffer to stress,

536 and mitigating the negative effects of drought. Maintenance of NSCs in ED2, even during

537 prolonged drought (at EucFACE) is due to: (1) trees resorbing a fraction of leaf C during leaf

538 shedding, (2) no maintenance costs for NSC storage in the current version, and (3) no allocation

539 of NSCs to structural growth until NSC storage surpasses a threshold (the amount of C needed to

540 build a full canopy of leaves and associated fine roots), allowing for a buffer to accumulate. In

541 LPJ-GUESS, accumulation and depletion of NSC is recorded as a 'C debt' being paid back in

542 later years. The contrasting responses of the two models to drought, and the likely role of NSCs

543 in explaining differences in model behavior, highlights the need to better understand NSC

544 dynamics and to accurately represent the relevant processes in models (Richardson et al., 2013;

545 Dietze and Matthes, 2014). More observations of C accumulation patterns and how/where NSCs

546   drive growth, respiration, transport and cellular water relations would enable a more realistic

547   implementation of NSC dynamics in models (Table 3).

548

549   **4.1.5 Role of functional trait diversity prior to UCEs:**

550   Currently LPJ-GUESS simulates the Palo Verde community using three PFTs, while ED2 uses

551   four PFTs that differ in photosynthetic and hydraulic traits. The community composition simulated by

552   ED2 is shown to be more resistant to UCEs compared to LPJ-GUESS (Fig. 4), perhaps due to

553   relatively higher functional diversity. This additional diversity helps to buffer ecosystem response to

554   drought by allowing more tolerant PFTs to benefit from reductions in less-tolerant PFTs, thus

555   buffering reductions in ecosystem function (Anderegg et al., 2018). Higher diversity ecosystems were

556   found to protect individual species from negative effects of drought (Aguirre et al., 2021) and enhance

557   productivity resilience following wildfire (Spasojevic et al., 2016); thus, functionally diverse

558   communities may be key to enhancing tolerance to rising environmental stress.

559   Recent efforts to consolidate information on plant traits (Reich et al., 2007; Kattge et al., 2011)

560   have contributed to identifying relationships that can impact community-level drought responses

561   (Skelton et al., 2015; Anderegg et al., 2016a; Uriarte et al., 2016; Greenwood et al., 2017), such as

562   life-history characteristics, and strategies of resource acquisition and conservation as predictors of

563   ecosystem resistance (MacGillivray et al., 1995; Ruppert et al., 2015). While adding plant trait

564   complexity in ESMs may be required to accurately simulate key vegetation dynamics, it necessitates

565   more detailed parameterizations of processes that are not explicitly resolved (Luo et al., 2012). Further

566   investigation of how VDMs represent interactions leading to functional diversity shifts is crucial to

567   this issue. Enquist and Enquist, (2011), as an example, show that long-term patterns of drought (20-

568   years) have led to increases in drought-tolerant dry forest species, which could modulate resistance to

569   future droughts. Higher diversity of plant physiological traits and drought-resistance strategies is

570   expected to enhance community resistance to drought, and models should account for shifts in diverse

571   functionality (Table 3).

572

573   **4.2 The role of ecosystem processes and states in post-UCE recovery**

574   **4.2.1 The role of soil water resources post-UCEs:**

575   Our simulation results generally demonstrated a fast recovery of plant-available-water

576   and LAI at both sites (Fig. S1). Annual plant-available-water substantially increased right after

577   drought by an average of 163 mm at Palo Verde and 213 mm at EucFACE in the LPJ-GUESS

578   simulations, compared to much lower increases in ED2 (50 mm and 12 mm at Palo Verde and

579   EucFACE). This increase in available water post-drought can be attributed to reduced stand

580   density and water competition (Fig. S2c-d; diamonds vs. circles), alleviating the demand for soil

581   resources (water) and subsequent stress, which has also been shown in observations (McDowell

582   et al., 2006; D'Amato et al., 2013). After large canopy tree mortality events there can be

583   relatively rapid recovery of forest biogeochemical and hydrological fluxes (Biederman et al.,

584   2015; Anderegg et al., 2016b; Biederman et al., 2016). These crucial fluxes strongly influence

585   plant regeneration and regrowth, which can buffer ecosystem vulnerability to future extreme

586   droughts. However, this enhanced productivity has a limit. In a scenario where UCEs continue to

587   intensify, causing greater reductions in soil water and reduced ecosystem recovery potential, the

588   SO growth that typically occurs after UCEs may be dampened (Fig. 1d). In water-limited

589   locations, similar to the dry forest sites used here, initial forest recovery from droughts were

590   faster due to thinning induced competitive-release of the surviving trees, and shallow roots not

591   having to compete with neighboring trees for water, allowing for more effective water user

592   (Tague and Moritz, 2019), stressing the importance of root competition and distribution in

593   models (Goulden and Bales, 2019). Tague and Moritz, (2019) also reported that this increased

594   water use efficiency and SO ultimately lead to water stress and related declines in productivity,

595   similar to the MO concept (Jump et al., 2017; McDowell et al., 2006). Since a core strength of

596   VDMs is predicting stand demography during recovery, improved quantification of density-

597   dependent competition following stand dieback would be beneficial for model benchmarking

598   (Table 3).

599

600   **4.2.2 The role of lagged turnover and secondary stressors post-UCEs:**

601   Time lags in forest compositional response and survival to drought could indicate

602   community resistance or shifts to more competitive species and competitive exclusion. During a

603   15-year recovery period from extreme drought at Palo Verde, LPJ-GUESS predicted an increase

604   in stem density (stems m^2 yr^{-1}) (Fig. S2c) compared to ED2, which predicted almost no impact in

605 stem recovery. The mortality "spike" in ED2 due to drought was muted and slightly delayed,

606 contributing to ED2's lower biomass loss and more stable behavior of plant processes over time

607 at Palo Verde. At EucFACE, both models exhibited a pronounced lag effect in stem turnover

608 response, i.e. ~8-12 years after drought (Fig. S2d). After about a decade, strong recoveries and

609 increased stem density occurred, which in ED2 was followed by delayed mortality/thinning of

610 stems. Delayed tree mortality after droughts are common due to optimizing carbon allocation and

611 growth (Trugman et al., 2018), but typically only up to several years post-drought, not a decade

612 or more as seen in the model.

613 The versions of the VDMs used here do not directly consider post-drought secondary

614 stressors such as infestation by insects or pathogens, and the subsequent repair costs due to stress

615 damage, which could substantially slow the recovery of surviving trees. Forest ecologists have

616 long recognized the susceptibility of trees under stress, particularly drought, to insect attacks and

617 pathogens (Anderegg et al., 2015). Tight connections between drought conditions and increased

618 mountain pine beetle activity have been observed (Chapman et al., 2012; Creeden et al., 2014),

619 and can ultimately lead to increased tree mortality (Hubbard et al., 2013). Leaf defoliation is a

620 major concern from insect outbreaks following droughts, and can have large impacts on C

621 cycling, plant productivity, and C sequestration (Amiro et al., 2010; Clark et al., 2010; Medvigy

622 et al., 2012). Implementing these secondary stressors in models could slow the rate of post-UCE

623 recovery and lead to increased post-UCEs tree mortality.

624

625 **4.2.3 The role of stand demography post-UCEs:**

626 Change in stand structure is an important model process to capture, because large trees

627 have important effects on C storage, community resource competition, and hydrology

628 (Wullschleger et al., 2001) (Table 3), and maintaining a positive carbohydrate balance is

629 beneficial in sustaining (or repairing) hydraulic viability (McDowell et al., 2011). There is

630 increasing evidence, both theoretical (McDowell and Allen, 2015) and empirical (Bennett et al.,

631 2015; Rowland et al., 2015; Stovall et al., 2019), that large trees (particularly tall trees with high

632 leaf area) contribute to the dominant fraction of dead biomass after drought events. Under rising

633 temperatures (and decreasing precipitation), VPD will increase, leading to a higher likelihood of

634 large tree death (Eamus et al., 2013; Stovall et al., 2019), driving MO events as hypothesized in

635   Fig. 1d. Consistent with this expectation, ED2 predicted that the largest trees (>100 cm)

636   experienced the largest decreases in basal area to compared to all other size classes (Fig. S3).

637   This drought-induced partial dieback and whole-tree mortality of dominant trees has substantial

638   impacts on stand-level C dynamics, as long-term sequestered C is liberated during the decay of

639   new dead wood (Palace et al., 2008; Potter et al., 2011). In ED2, the intermediate size class (60 -

640   80 cm) increased in basal area following large-tree death, taking advantage of the newly open

641   canopy space. However, small size classes do not necessarily benefit from canopy dieback. For

642   example, in a dry tropical forest, prolonged drought led to a decrease in understory species and

643   small-sized stems (Enquist and Enquist, 2011).

644

645   **4.2.4 The role of functional trait diversity & plant hydraulics post-UCEs:**

646   During the recovery phase from disturbance, competition will likely shift the plant

647   community towards one that is composed of opportunistic, fast-growing pioneer tree species,

648   grasses (Shiels et al., 2010; Carreño-Rocabado et al., 2012), and/or deciduous species, as also

649   seen in previous model results (Hickler et al., 2004). In the treatments presented here, deciduous

650   PFT types were also the strongest to recover after 15 years in both models, surpassing pre-

651   drought values (Fig. 4). It should be noted that ED2 exhibited a strong recovery in the evergreen

652   PFT as well (over two other deciduous PFT types), inconsistent with the above literature (Fig.

653   4b). PFTs in ED2 respond to drought conditions via stomatal closure and leaf shedding,

654   buffering stem water potentials from falling below a set mortality threshold (i.e., 88% of loss in

655   conductivity). This conductivity threshold may need to be reconsidered if further examination

656   reveals an unrealistic advantage under drought conditions for evergreen trees, which exhibited a

657   lower impact from droughts (compared to deciduous and brevi-deciduous PFTs) in ED2.

658   Recovery of surviving trees could be hindered by the high cost of replacing damaged

659   xylem associated with cavitation (McDowell et al., 2008; Brodribb et al., 2010). Many studies

660   have identified "drought legacy" effects of delayed growth or gross primary productivity

661   following drought (Anderegg et al., 2015; Schwalm et al., 2017) and the magnitude of these

662   legacies across species correlates with the hydraulic risks taken during drought itself (Anderegg

663   et al., 2015). The conditions under which xylem can be refilled remain controversial, but it seems

664   likely that many species, particularly gymnosperms, may need to entirely replace damaged

665   xylem (Sperry et al., 2002), and trees worldwide operate within narrow hydraulic safety margins,

666   suggesting that trees in all biomes are vulnerable to drought (Choat et al., 2012). The amount of

667   damaged xylem from a given drought event and recovery rates also vary across trees of different

668   sizes (Anderegg et al., 2018).

669   Plasticity in nutrient acquisition traits, intraspecific variation in plant hydraulic traits

670   (Anderegg et al., 2015), and changes in allometry (e.g., Huber values) can have large effects on

671   acclimation to extreme droughts. This suggests some capacity for physiological adaptation to

672   extreme drought, as seen by short-term negative effects from drought and heat extremes being

673   compensated for in the longer term (Dreesen et al., 2014). Still, given the shift towards more

674   extreme droughts with climate change, vegetation mortality thresholds are likely to be exceeded,

675   as reported in Amazonian long-term plots where mortality of wet-affiliated genera has increased

676   while simultaneously new recruits of dry-affiliated genera are also increasing (Esquivel-Muelbert

677   et al., 2019). Increasing occurrences of heat events, water stress and high VPD will lead to

678   extended closure of stomata to avoid cavitation, progressively reducing CO_2 enrichment benefits

679   (Allen et al., 2015). Where CO_2 fertilization has been seen to partially offset the risk of

680   increasing temperatures, the risk response was mediated by plant hydraulic traits (Liu et al.,

681   2017), yet interactions with novel extreme droughts were not considered. The VDM simulations

682   suggest that the combination of elevated warming and eCO_2 will exacerbate consequences of

683   UCEs by reductions in both C stocks and post-drought biomass recovery speeds (Fig. 3).

684   Therefore, future UCE recovery may not be easily predicted from observations of historical post-

685   disturbance recovery. An associated area for further investigation is to better understand the

686   hypothesized interplay between amplified mortality from hotter UCEs followed by structural

687   overshoot regrowth during wetter periods (Fig. 1d), which could potentially buffer net ecosystem

688   C impacts through time (Table 3).

689

5 Conclusions

691   Model limitations and unknowns exposed by our simulations highlight current challenges

692   in our ability to understand and forecast UCE effects on ecosystems. These limitations reflect a

693   general lack of empirical experiments focused on UCEs. Insufficient data means that relevant

694   processes may currently be poorly represented in models, and models may then misrepresent C

695   losses during UCEs. The two VDMs used here had different sensitivities to drought duration and

696   intensity. These model uncertainties could potentially be addressed by improved datasets on

697   thresholds of conductivity loss at high drought intensities, the role of trait diversity (e.g. different

698   strategies of drought deciduousness) in buffering ecosystem drought responses, and a better

699   grasp of plant storage stocks before, during, and after multi-year droughts. Our study takes some

700   initial steps to identify and assess model uncertainties in terms of mechanisms and magnitudes of

701   responses to UCEs, which can then be used to inform and develop field experiments targeting

702   key knowledge gaps as well as to prioritize ongoing model development (Table 3). This iterative

703   model-experiment framework offers strong potential to drive progress in improving our

704   understanding of terrestrial ecosystem responses to UCEs and climate feedbacks, while

705   informing the development of the next generation of models.

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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. Mechanisms listed in the two right columns refer to real ecosystems and are not necessarily represented in models, even if the process or state variable is represented in a given model. 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); + Vargas et al., (2021).

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 modulate vulnerability to death; drought-deciduousness reduces vulnerability to drought *, with higher water potential at turgor loss point and leaf vulnerability to embolism [+]	Leaf lifespan tends to increase from pioneer to late-successional species in some ecosystems (e.g., tropical forests)
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 ^^	Allocation among fine roots, xylem, & leaves affects recovery time & GPP/LAI trajectory

4) Non-Structural Carbohydrate (NSC) Storage	ED2: Yes LPJ-G: Yes	Buffers 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
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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764 **Table 2** Impact of eCO$_2$ and/or temperature on the integrated-C-change (kg C m^{-2} yr) relative to

765 drought treatments with no additional warming or eCO$_2$, for both models, and both sites seen in

766 Fig. 3. Quantified as average and minimum integrated-C-change across all 20 drought intensities

767 for step-change scenarios of warming and eCO$_2$. The percentage of each scenario that was

768 negative in integrated-C-change (i.e., decreases in C loss). Green values represent positive

769 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

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771 **Table 3** Summary of suggestions emerging from the hypothetical drought simulations used here

772 of the driving mechanisms (e.g., ecosystem or plant processes and state variables) to explore for

773 future research in manipulation experiments, data collection, and model development and testing,

774 as related to furthering our understanding of UCE resistance and 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 the 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.

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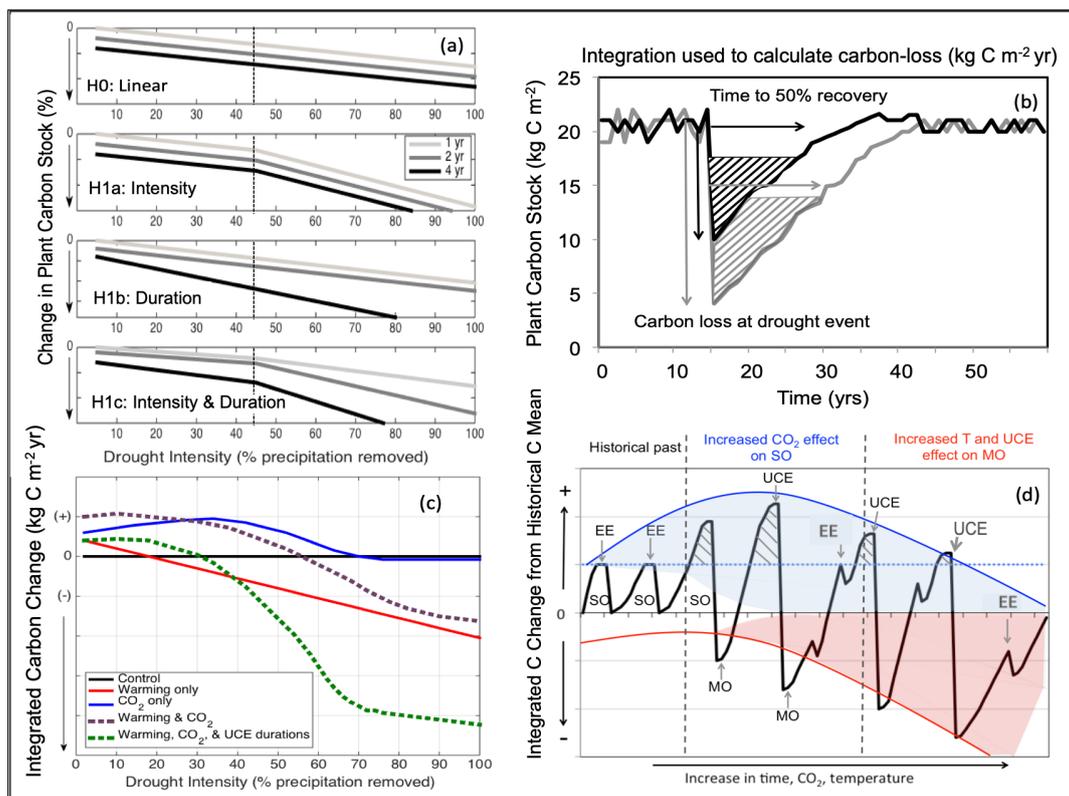
Figure 1 Conceptual diagrams showing impacts of extreme droughts (unprecedented climate extremes, UCEs; i.e., record-breaking droughts) on plant C stocks. (a) **Conceptual response diagram**: potential loss in C stock as a function of increasing drought intensity (0-100% precipitation removal) and drought 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 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

791   "integrated-C-change" (kg C m^{-2} yr) due to eCO$_2$ (blue line), rising temperature (red line),

792   interaction between eCO$_2$ and temperature (dashed purple), and combined interactions among

793   eCO$_2$, temperature, and UCEs of prolonged durations (green line), all relative to a reference

794   drought of normal duration with no warming (black line). Integrated-C-change denotes the

795   difference in integrated-C-loss (see panel b) between a scenario of changing climatic drivers and

796   the reference drought (control). **(d) Conceptual UCE amplification diagram**: hypothetical

797   amplified change in forest C stocks to eCO$_2$ and temperature relative to the pre-warming

798   historical past (based on Jump et al. (2017)). Change in C stock greater than zero indicates a

799   'structural overshoot' (SO) due to favorable environmental conditions and/or recovery from an

800   extreme drought-heat event (EE). Hashed black areas indicate a structural overshoot due to

801   eCO$_2$, which occurs over the historical CO$_2$ levels (dashed blue line). Initially, an eCO$_2$ effect

802   leads to a larger increase in structural overshoot (due to CO$_2$ fertilization), driving more extreme

803   vegetation mortality ('mortality overshoot' - MO) relative to historical dieback events and thus a

804   greater decrease in C stock. Increased warming through time increasingly counteracts any CO$_2$

805   fertilization effect; while the amplitude of post-UCE C stock recoveries remains large, net C

806   stock values eventually decline (downward curvature) due to more pronounced loss in C stocks

807   (and greater ecosystem state change) from hotter UCEs.

808   SO = structural overshoot, MO = mortality overshoot, EE = historically extreme drought-heat

809   event, UCE = unprecedented climate extreme.

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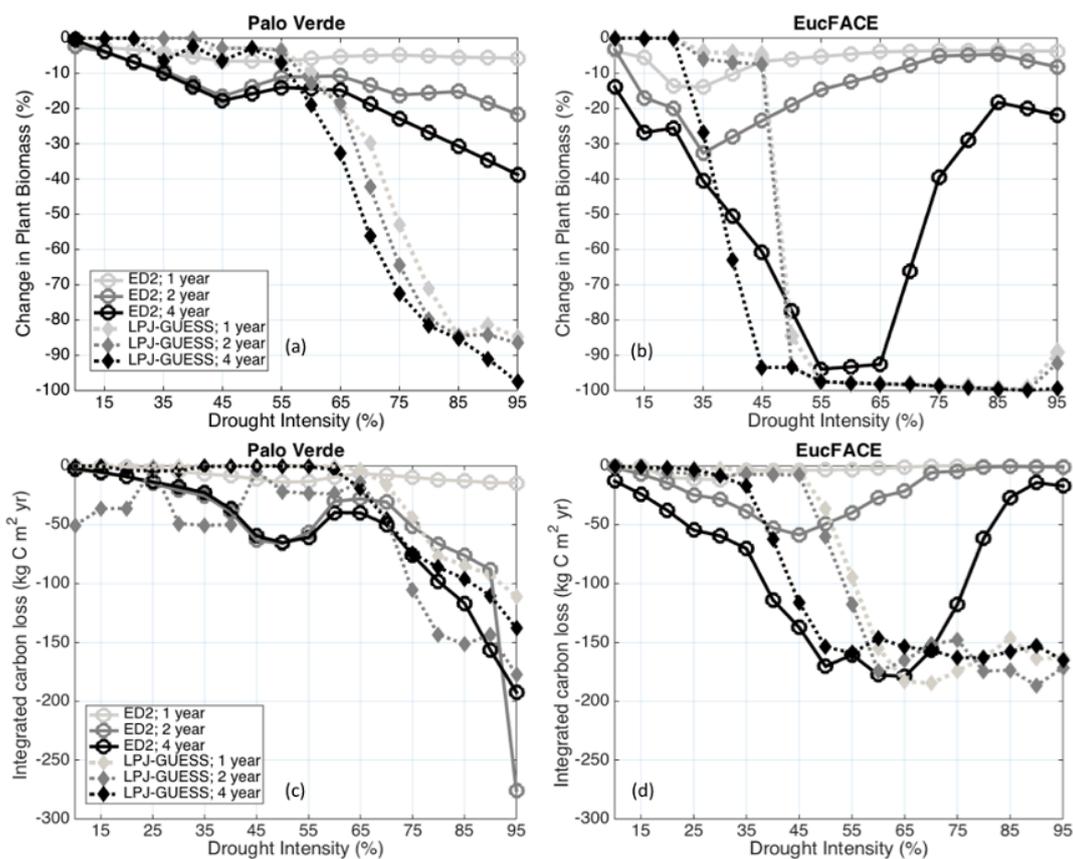
Figure 2 Modeled change in biomass (%) at the end of drought periods of different lengths (1, 2, and 4-year droughts) and intensities (up to 95% precipitation removed) at (a) Palo Verde, and (b) EucFACE, for the ED2 and LPJ-GUESS models. Modeled integrated-C-loss (C reduction due to extreme drought integrated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

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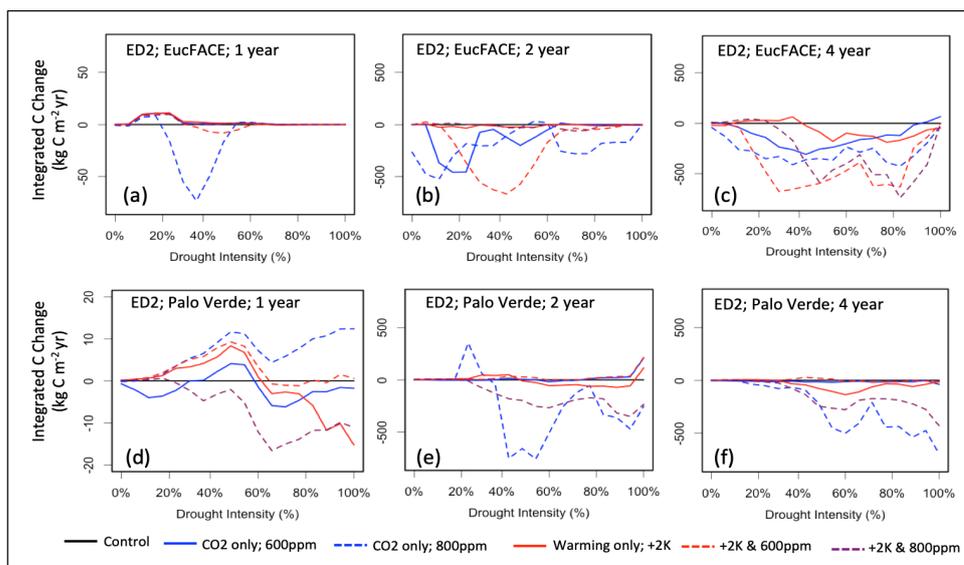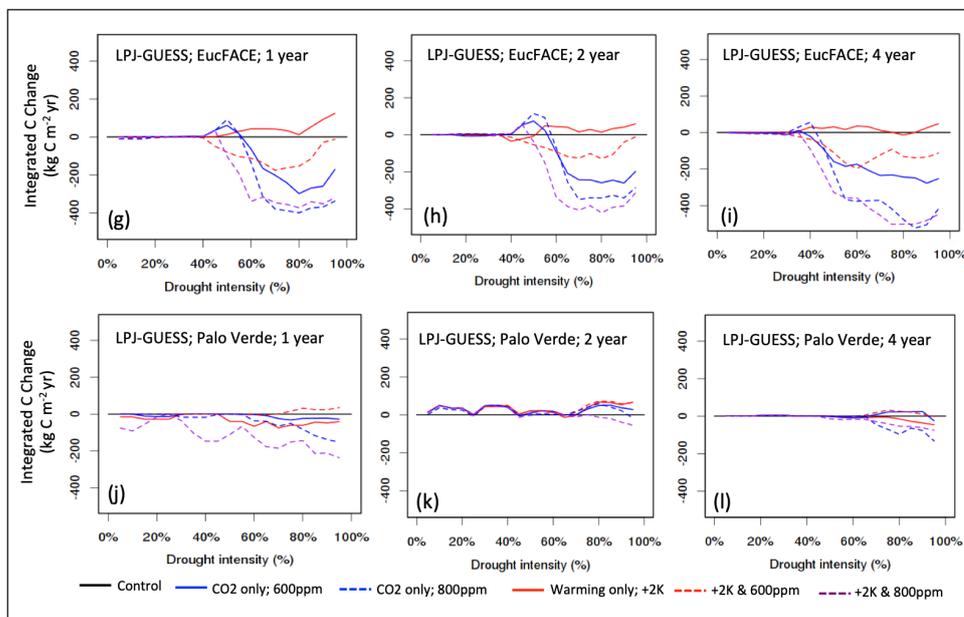
Figure 3 Vegetation C response to interactions between drought intensity (0% to 100%
precipitation reduction), drought durations (1, 2, 4-year droughts), and idealized scenarios of
warming and eCO$_2$ compared to the reference simulation, simulated by two VDMs; ED2 (a-f)
and LPJ-GUESS (g-l) at two sites (EucFACE and Palo Verde). The scenarios include a control
(current temperature; 400 ppm atmospheric CO$_2$), two eCO$_2$ scenarios (600 ppm or 800 ppm),

825   elevated temperature (2 K above current), and a combination of eCO_2 (600 ppm or 800 ppm) and

826   higher temperature. Vegetation response is quantified as "integrated-C-change" (in kg C m^{-2} yr;

827   Eq. 4), which is defined as the difference in integrated-C-losses due to drought between a given

828   scenario of change in climatic drivers and the control. Negative values for integrated-C-change

829   indicate that warming and/or eCO_2 leads to stronger C losses and/or longer recovery, while

830   positive values for integrated-C-change indicates a buffering effect.

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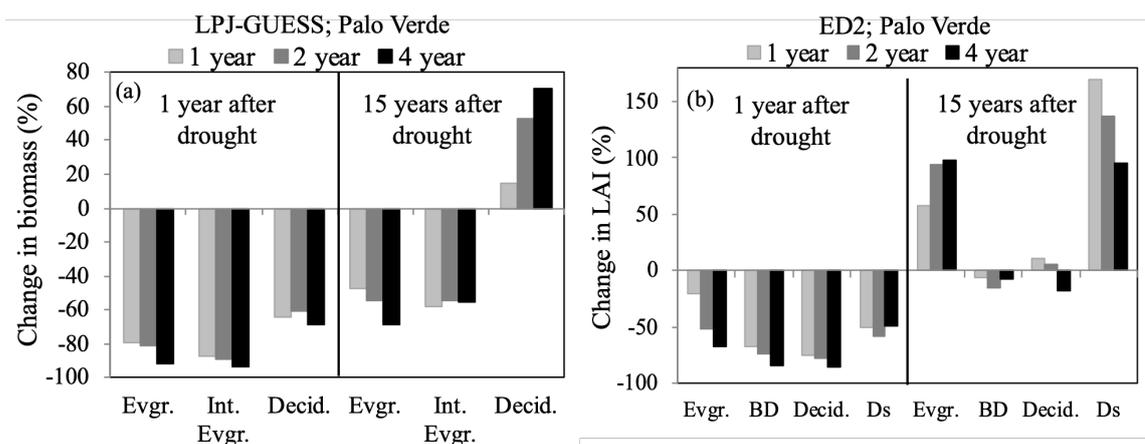
Figure 4 Percent change in community composition, represented by plant functional type (PFT),

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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