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Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes?

1 **Title:** Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall
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28 **Key words:** climate change, precipitation variability, functional traits, drought, tree phenology,
29 belowground processes

30   **Abstract:**

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32   Seasonally dry tropical forests (SDTF) are located in regions with alternating wet and dry

33   seasons, with dry seasons that last several months or more. By the end of the 21st century, climate

34   models predict substantial changes in rainfall regimes across these regions, but little is known

35   about how individuals, species, and communities in SDTF will cope with the hotter, drier

36   conditions predicted by climate models. In this review, we explore different rainfall scenarios

37   that may result in ecological drought in SDTF through the lens of two alternative hypotheses: 1)

38   these forests will be sensitive to drought because they are already limited by water and close to

39   climatic thresholds, or 2) they will be resistant/resilient to intra- and inter-annual changes in

40   rainfall because they are adapted to predictable, seasonal drought. In our review of literature that

41   spans microbial to ecosystem processes, a majority of the available studies suggests that

42   increasing frequency and intensity of droughts on SDTF will likely alter species distributions and

43   ecosystem processes. Though we conclude that SDTF will be sensitive to altered rainfall

44   regimes, many gaps in the literature remain. Future research should focus on geographically

45   comparative studies and well-replicated drought experiments that can provide empirical evidence

46   to improve simulation models used to forecast SDTF responses to future climate change at

47   coarser spatial and temporal scales.

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56 **1. Introduction**

57 Seasonally dry tropical forests (SDTF) once occupied vast amounts of tropical lands—up to 40%

58 of all tropical forest— before large-scale deforestation (Murphy and Lugo 1986). Many of the

59 unique properties of SDTFs hinge on their rainfall regimes. SDTF rainfall regimes are

60 characterized by distinct alternating wet and dry seasons, with some forests having dry seasons

61 (defined as the number of months rainfall $\leq$ 100 mm) of six months or more. However, there is

62 now abundant evidence from models and observations that suggests rainfall regimes in the

63 seasonal tropics are changing, in part due to anthropogenic climate change (Greve *et al* 2014,

64 Chadwick *et al* 2016). These alterations include increasing dry season length over Amazonia and

65 increased variability in the magnitude, timing, and duration of rainfall (Feng *et al* 2013). It is

66 currently not known how ongoing and future changes in rainfall may affect SDTF ecosystems,

67 and whether SDTFs will be robust or sensitive to these changes (Santos *et al* 2014).

68 SDTFs provide a suite of ecosystem services such as water provisioning, flood control, tourism

69 revenue, and pollination, (Maass *et al* 2005), but to date no reviews have considered the extent to

70 which these benefits to society may be compromised by climate change.

71   The goal of this review is to synthesize existing research to address the question: *Are*

72 *SDTFs sensitive or resistant to decreases in rainfall and/or increases in rainfall variability?*

73 Climate change could affect SDTF through either lowered total rainfall amounts, or increased

74 variability in the timing or duration of rainfall, either of which effectively results in rainfall

75 shortages that occur during parts of the year that historically were wetter. Thus, our definition of

76 drought includes both rainfall deficits that these forests may have experienced in the past, as well

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77　as novel droughts which fall outside any previously observed rainfall conditions. Throughout the

78　review we consider two alternative hypotheses: 1) SDTF are sensitive to drought or relative

79　water shortages because they already experience harsh environmental conditions and are near

80　climatic thresholds, or 2) they are resistant because they tolerate or cope with seasonal water

81　deficits. We define drought sensitivity as the changes in biological variables, states, processes, or

82　species distributions that occur when rainfall is at or below the lower limits of what has been

83　previously observed. By contrast, ecological resilience implies the ability to recover from

84　changes in a relatively short amount of time, whereas resistance implies a lack of change in

85　response to anomalously low, prolonged, or recurrent precipitation (Angeler and Allen 2016).

86　Under the hypothesis of SDTF sensitivity, we would expect that if existing SDTFs and their

87　physiological and ecosystem processes are severely limited by rainfall and water availability,

88　they may be extremely vulnerable to changes in rainfall amount, duration, or variability. By

89　contrast, under the alternative hypothesis of resistance/resilience, as most SDTF species have

90　evolved strategies such as leaf deciduousness to tolerate or avoid severe seasonal drought, it is

91　possible that these strategies will result in few alterations in SDTF structure and function in

92　response to future changes in rainfall regimes. Last, it is possible that SDTF responses to drought

93　depend upon the process under consideration, with responses of different dynamics (e.g.

94　decomposition, seedling recruitment) or species displaying a continuum of responses from highly

95　vulnerable to highly resistant or resilient.

96　　　　To evaluate whether SDTF are sensitive or resistant to changes in rainfall, we first define

97　rainfall regimes and the conditions that constitute drought in highly seasonal tropical forests.

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98   Next we evaluate the existing literature to assess evidence that demographic processes,

99   community dynamics, and ecosystem processes in SDTFs are vulnerable or resistant/resilient to

100   changes in rainfall, focusing on above- and belowground separately. We then discuss factors that

101   might modulate responses to changing rainfall regimes, including deforestation and

102   fragmentation, and also summarize work to incorporate SDTFs into simulation models. We

103   conclude by suggesting future work to improve our understanding of SDTFs and climate change.

104   Our review complements recent work that focuses on rainforests (Bonal *et al* 2016) and Amazon

105   basin forests (Olivares *et al* 2015) in that we consider responses to altered rainfall regimes from

106   microbial to ecosystem scales in highly seasonal tropical forests. Because our review is

107   qualitative and synthetic, we relied first on our own knowledge and experience with this

108   literature to select relevant studies. We supplemented this initial set of relevant papers with

109   articles identified via searches of the Web-of-Science database using the search terms "tropical

110   forest" and "drought".

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112   **2. Rainfall and rainless regimes in SDTF**

113   Rainfall within a given SDTF has a distinct seasonal distribution, and seasonal patterns of

114   rainfall can also vary dramatically among SDTFs. Thus, defining the term "drought" in SDTFs

115   can be challenging, as it is possible that a variety of changes to rainfall timing, duration, and/or

116   intensity may result in drought scenarios (Section 2.2).

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118   **2.1. Variation in rainfall regimes among and within SDTF**

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119   In tropical latitudes, both total annual rainfall and rainy season length have large spatial

120   variations and generally decrease from equatorial to subtropical regions (Fig. 1). In general,

121   SDTFs have a mean annual temperature >17°C, between 200–2500 mm annual rainfall, and an

122   annual ratio of potential evapotranspiration to precipitation >1 (Murphy and Lugo 1986). The

123   most characteristic feature of SDTF is an extended dry season with a majority of the

124   precipitation (~80%) occurring within the wet season (Maas and Burgos 2011).
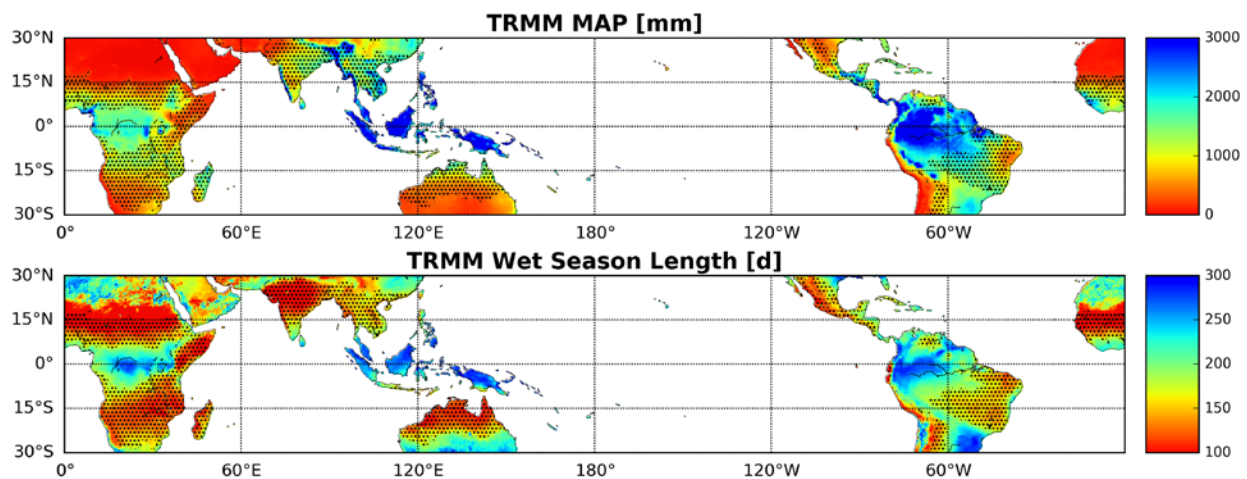

126   **Figure 1.** Map of **a)** annual rainfall in mm, **b)** wet season (defined as 80% of annual rainfall)

127   length in days in equatorial tropics derived from Tropical Rainfall Measuring Mission (TRMM)

128   data. Areas with >200mm rainfall, <180 day wet season and >17 ℃ mean annual temperature are

129   considered SDTFs and are shaded with black hatching.

130   Despite these general patterns, there is considerable inter- and intra-annual variability in

131   rainfall within and among SDTFs. Long-term rainfall records from four well-studied SDTFs

132   illustrate how distinctive seasonality is among sites, and underscore that the terms "wet season"

133   and "dry season" can be overly simplistic (Fig. 2). In Santa Rosa, Costa Rica and Jabiru,

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134   Colombia (Fig. 2a, d) a short drier period (i.e., veranillo) typically occurs during the wet season.

135   Guánica, Puerto Rico (Fig 2b) tends to have a bimodal rainy season with spring and fall (i.e.

136   hurricane season) rains, but neither the spring rains nor the summer dry periods are consistent. In

137   the Yucatán Peninsula in Mexico (Fig. 2c), cold fronts (i.e., Nortes/frentes fríos) that occur

138   during the dry season can bring lower temperatures and rainfall and thus there are three

139   recognized seasons (Nortes, dry season, and wet season).
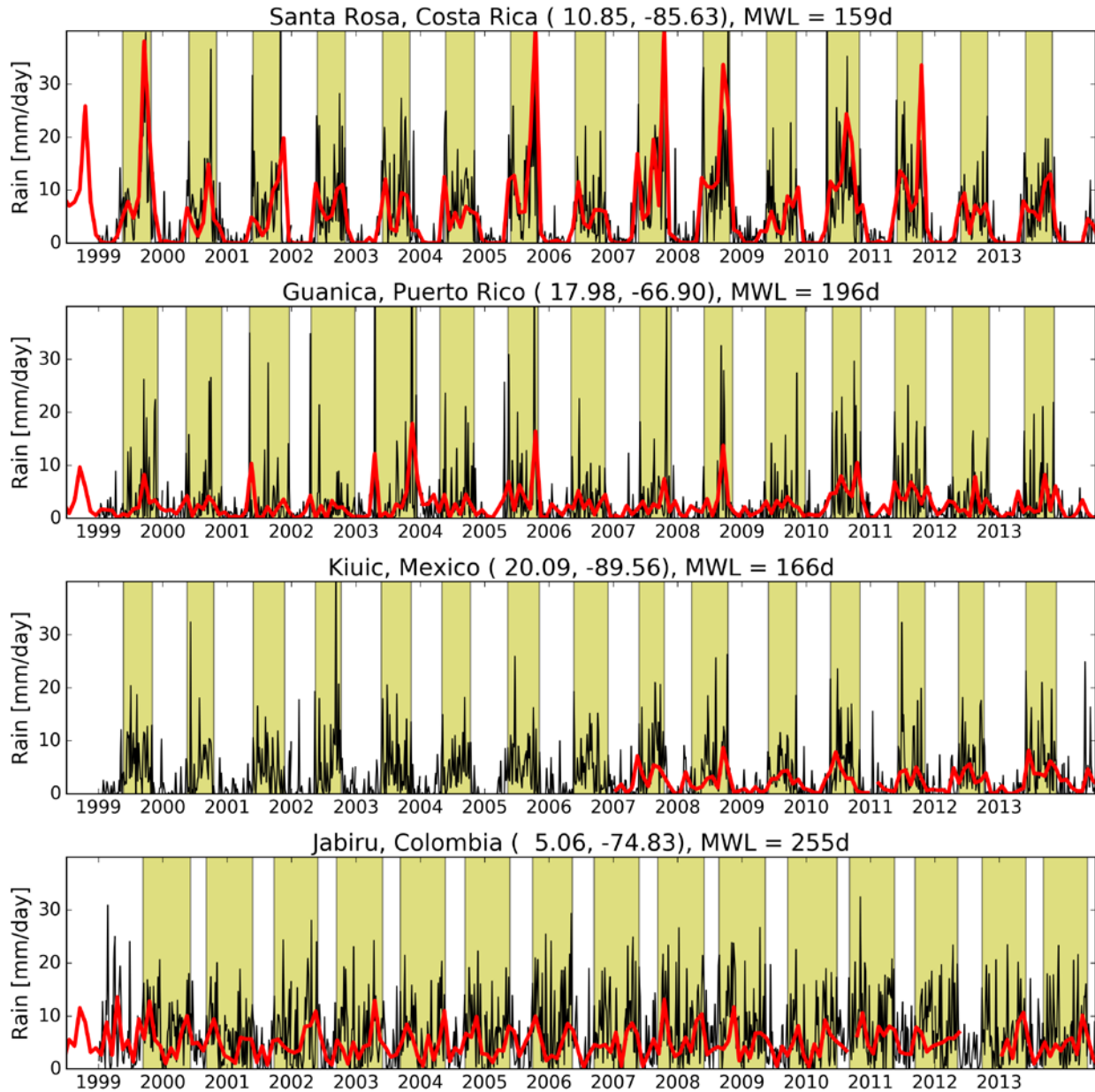
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Figure 2. Annual precipitation at four Neotropical dry forest sites **a)** Santa Rosa, Costa Rica, **b)**

Guánica, Puerto Rico, **c)** Kaxil Kiuic, Mexico and **d)** Jabiru, Colombia. The black line represents

5-day average rainfall from TRMM data. The red line represents in-situ measured monthly

146   average rainfall. Tan shading represents wet season length defined as 80% total annual rainfall

147   and MWL represents mean wet season length in days.

148   **2.2. Drought concepts in seasonally dry forests**

149   What does a drought mean in a SDTF? Climatologists have defined a number of indices (e.g.

150   Palmer Drought Severity Index, Standardized Precipitation Index, etc.) to both diagnose and

151   forecast drought based on a combination of data including precipitation, temperature, water

152   supply and demand, and/or soil moisture (Zargar *et al* 2011, Vincente-Serrano *et al* 2015). Here

153   we use an ecological concept of drought, which we define as a reduction in rainfall or a change

154   in the timing or distribution of rainfall or rainless periods that has the potential to directly impact

155   community- or ecosystem-level plant or microbial processes. We use conceptual models of a

156   "generic SDTF" with high contrast wet and dry seasons to differentiate and contrast periodic

157   seasonal drought (i.e. alternating wet and dry seasons, Fig. 3a) from aspects of precipitation

158   regimes that may be altered with climate change. Drought scenarios include a reduction in the

159   total amount of rainfall during the wet season (Fig. 3b), which is the most common type of

160   drought simulated in large-scale, throughfall reduction experiments. This type of drought has

161   clearly occurred in the past in SDTF as low rainfall years, and is expected to increase in the

162   future as one potential consequence of climate change (Dai 2013). In addition to drought defined

163   as exceptionally low annual rainfall totals, there are a number of ways that increased variability

164   of rainfall due to climate change may be perceived as ecological drought or water deficits to

165   organisms. For example, shorter but more intense wet seasons (Fig. 3c) or a shift in when the

166   rainy season occurs (Fig. 3d), may both result in altered dry season lengths with no change in

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167   total yearly rainfall. Moreover, changes in the quantity and timing of rainfall may co-occur (Fig.

168   3e). Last, it is possible that consecutive, multi-year events affect dry forests in additive or

169   multiplicative ways that are different than individual drought years interspersed with non-

170   drought years (Fig. 3f). Thus, there are at least five possible scenarios for how future drought

171   might differ from seasonal rainfall in SDTF including: reduced rainfall during a given year (Fig.

172   3b), altered dry season length (Fig. 3c), altered timing of rainfall (Fig. 3d), reduced rainfall

173   coupled with altered dry season length (Fig. 3e), or multi-year drought of sequential low rainfall

174   years (Fig. 3f).

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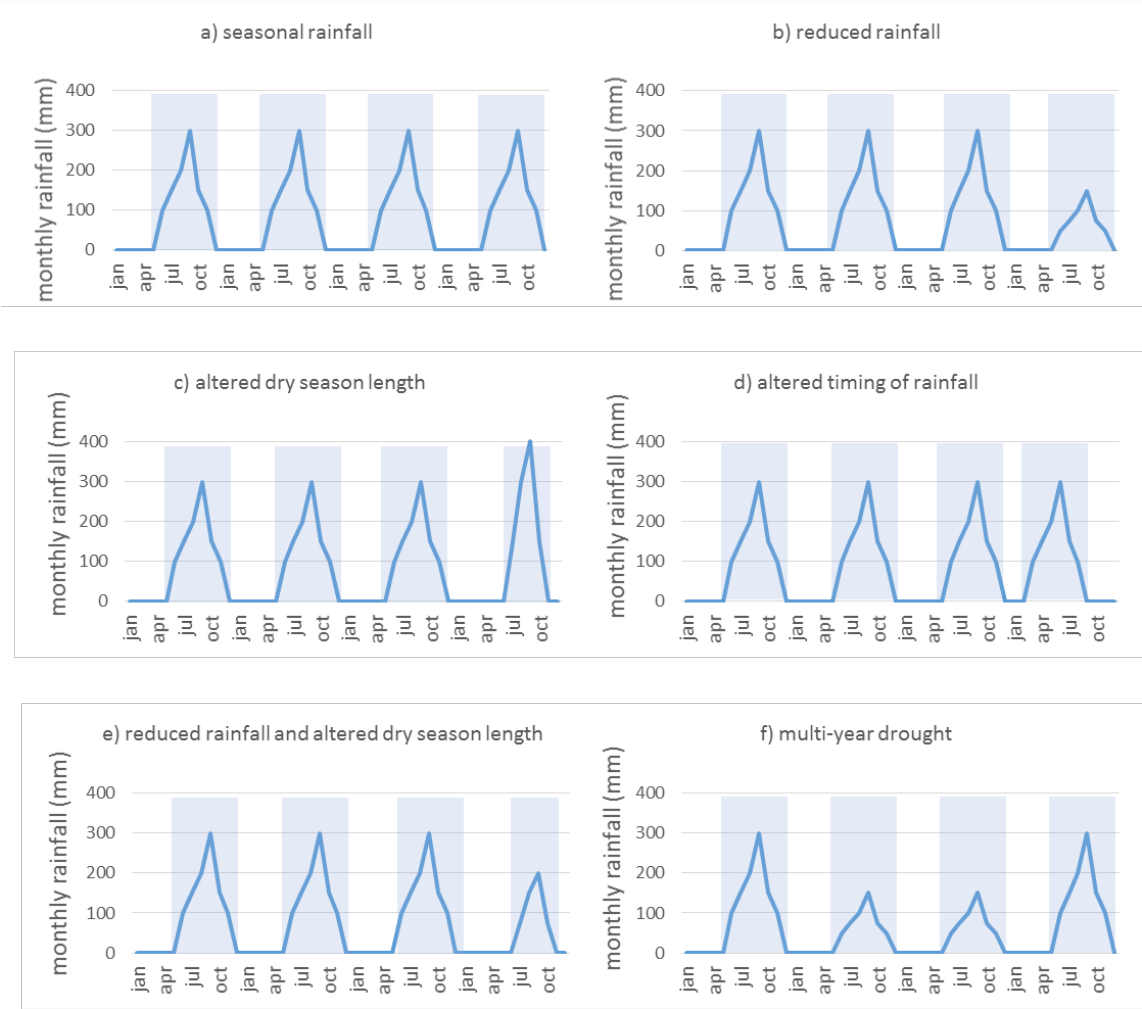
Figure 3. Hypothetical drought scenarios manifested as changes to monthly precipitation for four years. Blue shading defines the wet season **a)** "normal" rainfall regime with alternating wet and dry seasons, **b)** annual rainfall is reduced by 50% during year 4, **c)** the rainy season starts late in year 4, but annual total rainfall remains unchanged, **d)** annual rainfall is equal among years, but the timing of the rainy season is shifted during year 4, **e)** rainfall is reduced by 50% and the timing is shifted for year 4, **f)** multi-annual drought during years 2 and 3.

3. How might drought scenarios affect above- and belowground processes?

184   Future precipitation regimes are projected to become even more extreme in tropical regions

185   under climate change (Malhi *et al* 2008, Feng *et al* 2013). Climate models predict decreased

186   rainfall and increased dry periods (e.g., Maloney *et al* 2013, Chadwick *et al* 2016, Duffy *et al*

187   2015). Given the marked inter- and intra-annual variability in SDTF rainfall regimes, it is not

188   known how alterations in the magnitude and timing of rainfall will affect the ecological

189   dynamics of species, communities, and ecosystem processes (Vico *et al* 2014).

190   Both above- and belowground biological and ecological processes in SDTF are

191   influenced by water availability, and the effects of increased rainfall variability, timing, or

192   duration could alter these processes in ways that are distinct from responses to the predictable,

193   seasonal water shortages characteristic of SDTFs (Fig. 3a). Here we synthesize predictions of

194   how this variability in rainfall regimes, including the intensity and duration of drought as well as

195   the timing of seasonality, can all affect biological and ecological processes in SDTF at different

196   scales. We focus on above- and belowground processes separately, because they may respond

197   differently to drought and few studies integrate both.

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199   **3.1. Aboveground responses**

200   Changes and variability in rainfall regimes can alter patterns of vegetative growth, physiology,

201   and phenology. Over longer timescales, droughts may shift community dynamics and species

202   distributions.

203   *3.1.1. Tree phenology, physiology, and growth*

204   In SDTF, species are distributed along a continuum of functional strategies from dense-wooded,

205   evergreen species at one extreme to light-wooded, deciduous species at the other (Eamus 1999,

206   Singh and Kushwaha 2005, Mendez-Alonso et al 2012). Species with high wood density have

207   more cell wall material, low storage capacity in stems and narrow vessels, limiting hydraulic

208   efficiency but increased resistance to drought-induced cavitation (Hacke *et al* 2001). These

209   species may further resist drought by tapping subsoil water reserves with deep roots (Borchert

210   1994). By contrast, light-wooded species are less able to withstand xylem cavitation and are

211   more susceptible to hydraulic failure. As a result, these species feature additional strategies to

212   cope with drought such as high sapwood water storage, wide and conductively efficient vessels,

213   and short-lived leaves (Ackerly 2003, Brodribb *et al* 2003, Meinzer *et al* 2008, Méndez-Alonzo

214   *et al* 2012). Despite these broad generalizations, traits such as wood density do not necessarily

215   predict leaf phenology or function at the community scale (Powers and Tiffin 2010), and there is

216   still much to be learned about the variety of mechanisms through which species avoid, tolerate,

217   or escape drought (Delzon 2015). Recently developed high through-put methods including

218   osmometers to quantify turgor loss point and scanners to quantify leaf embolism are useful for

219   identifying the potential drought response of large numbers of species in highly diverse tropical

220   forests (Bartlett *et al* 2012, Delzon 2015, Maréchaux *et al* 2015, Brodribb *et al* 2016).

221   Many hydraulic traits are associated with drought tolerance or avoidance strategies. Leaf

222   water potential at turgor loss point (π_{tlp}) which is related to maintenance of cell turgor in leaves

223   (Tyree and Jarvis 1982), and 50% loss of conductivity (Ψ_{50}) which relates to cavitation

224   resistance (Choat *et al* 2012), are useful traits for predicting species drought responses (Baltzer *et*

225 *al* 2008, Kursar *et al* 2009). Species growing in dry environments have low π_{tlp} (Bartlett *et al*

226 2012) and Ψ_{50} (Maherali *et al* 2004, Choat *et al* 2012), enabling them to maintain stomatal and

227 hydraulic conductance and photosynthetic gas exchange at low soil water potentials (Sack *et al*

228 2003, Baltzer *et al* 2008, Kursar *et al* 2009). However, the narrow safety margins of SDTF

229 species (Ψmin-Ψ50, < 1 MPa, Choat *et al* 2012) indicate high vulnerability to drought (Choat *et*

230 *al* 2012) and therefore future climatic scenarios with reduced rainfall may significantly impact

231 productivity and carbon balance. Moreover, trait-dependent strategies for dealing with water

232 limitation in SDTFs may also interact with other environmental or abiotic variables. For

233 example, shade tolerance is an important resource axis determining cavitation resistance and

234 drought tolerance, with shade-intolerant species more vulnerable to cavitation (Markesteijn *et al*

235 2011).

236   Increased inter-annual rainfall variability, greater intervals between extremely wet and

237 dry years, and particularly a decline in rainfall predicted for SDTFs could influence the relative

238 performance of species with different leaf habits and trait strategies. Decadal declines and/or

239 increased precipitation variability may favor deciduous species (Givnish 2002, Enquist and

240 Enquist 2010) because these species will have shorter periods of time to function without

241 compromising their hydraulic pathway and will probably modify phenological patterns.

242 However, predicting phenological responses requires an understanding of the relationship

243 between phenology and traits such as stem storage capacity (Borchert 1994, Mendez-Alonzo *et*

244 *al* 2013) and leaf age (Borchert *et al* 2002). In scenarios where drought is not intense enough to

245 cause hydraulic failure but is prolonged, species with stomatal closure (isohydric) could reduce

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246   carbon uptake, resulting in carbon starvation and reduced investment in defense, and hence

247   increased mortality by biotic agents (McDowell *et al* 2008, but see Sala *et al* 2010). Moreover,

248   drought may affect biotic interactions between plants and other taxa (e.g. pollination, seed

249   dispersal, frugivory, seed predation, herbivory, and soil microbes), such that climate change

250   effects on plants ramify to other trophic levels (Parmesan and Hanley 2015). There is great

251   potential to use remote sensing to quantify deciduousness and leaf phenology of SDTF canopies

252   across large geographic scales and over time in relation to various climatic drivers (Cuba *et al*

253   2013). For example, Cuba *et al* (2013) showed that deciduousness of forest canopies in the

254   Yucatán peninsula correlate more strongly with temperature than rainfall.

255   Results from throughfall exclusion (TFE) experiments, observations of natural variability

256   among years, rainfall gradients and dendrochronology have shown that drought can impact tree

257   growth and biomass production. To date, TFE experiments have only been performed in tropical

258   forests with annual rainfall >2000 mm, and these studies show that rainforests are more sensitive

259   to drought than is accounted for in models (Meir *et al* 2015). For example, in an Indonesian

260   perhumid forest exposed to TFE, wood production decreased by 40% (Moser *et al* 2014) and in

261   an Amazonian forest with a pronounced dry season, the decline reached 30% after seven years of

262   TFE (da Costa *et al* 2010). Similarly, a water addition experiment in a seasonally moist forest in

263   the eastern Amazon showed that stem diameter growth increased with dry season irrigation, but

264   this effect was lagged by one year with tree growth responding to rainfall in the prior year

265   (Vasconcelos *et al* 2012). Studies arrayed along natural rainfall gradients can also be a useful

266   tool for understanding water limitation of ecosystem processes. Litterfall quantities, seasonality,

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267   and nutrient concentrations varied slightly but predictably over a rainfall and successional

268   gradients in the Yucatan peninsula (Lawrence 2005, Read and Lawrence 2003). Another study

269   along this rainfall gradient documented systematic shifts in nutrient cycling, suggesting that N

270   limitation was strongest at lower rainfall sites while P limitation increased with annual rainfall

271   (Campo 2016). Last, dendrochronology and tree ring analysis can provide evidence of the

272   coupling between tree growth and climate for many tropical dry forest species, as the strong

273   seasonality causes many species to have annual growth rings (Rozendaal and Zuidema 2011).

274   For example, a 60+ year record of seven diverse species from a dry forest in Bolivia found

275   positive correlations between ring width and precipitation that also varied with time-scale,

276   suggesting that most SDTF species are generally tolerant of short-term droughts, but vary in their

277   sensitivity to multi-annual droughts (Mendivelso *et al* 2014).

278

279   *3.1.2. Demographic processes and tree community dynamics*

280   Evidence that drought scenarios (Fig. 3) may change community composition of SDTF through

281   differential effects on demographic processes is not as well established for SDTF as it is for

282   moist and wet tropical forest (e.g. Feeley *et al* 2011, Fauset *et al* 2012). Moreover, several

283   factors suggest that demographic responses to drought may vary across the dry forest biome. The

284   prevalence of recruitment modes vary substantially across SDTFs, from primarily relying on

285   establishment from seed (Vieira and Scariot 2006) to regenerating via sprouting (Swaine *et al*

286   1990, Imbert *et al* 1996, Dunphy *et al* 2000, Van Bloem *et al* 2003). Even within specific dry

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287   forests, both sprouting and seedling establishment vary by species, year, and type of disturbance

288   (e.g. fire, hurricanes, clear-cutting, etc.).

289   A number of studies have examined seed bank and seed rain dynamics in dry forests as a

290   function of intra- and inter-annual variation in rainfall (Castilleja 1991, Ray and Brown 1995,

291   Martinez-Garza *et al* 2011, Meave *et al* 2012, dos Santos *et al* 2013). In some locations, seed

292   bank composition differs between the wet and dry seasons (Meave *et al* 2012), which is not

293   surprising if most seeds in SDTF mature or fall during the dry season (Frankie *et al* 1974,

294   Martinez-Garza *et al* 2011). In other locations seed fall is timed more closely to the beginning or

295   peak of the rainy season, when presumably seeds with low viability would have the best chance

296   of establishing (Murphy *et al* 1995, Ray and Brown 1995, Vieira and Scariot 2006) or seed fall

297   would be comprised of species with seeds that mature at various times (Singh and Kushwaha

298   2006). Long dry seasons represent a bottleneck for young seedlings (Swaine *et al* 1990, Gerhardt

299   1993, Ray and Brown 1995, McLaren and McDonald 2003), suggesting that changes to dry

300   season length will affect community composition of recruits. In addition to intra-annual

301   variation, seedbank species richness and density in a remnant caatinga forest in Brazil varied

302   among years and microhabitats, with significant interactions (dos Santos *et al* 2013). Thus, the

303   responses of reproductive phenology to inter-annual variation in rainfall may be individualistic

304   or under phylogenetic control, as was found in a decade-long record of reproductive phenology

305   in a subtropical forest in China, where both flowering and fruiting were positively correlated to

306   indices of ENSO at 2–5 month lags (Chang-Yang *et al* 2015). In one of the most comprehensive

307   studies of recruitment dynamics in tropical dry forest, Maza-Villalobos *et al* (2013) monitored

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308   thousands of individuals 10–100 cm in height over four years in stands representing multiple

309   successional stages in the Chamela-Cuixmala Biosphere Reserve in Mexico. Recruitment into

310   this size class occurred primarily during the wet season, and was severely reduced following an

311   ENSO event. By contrast, mortality rates peaked during the same period although there were

312   complicated lag effects, which may have been caused by depleted storage reserves or ENSO-

313   related effects on pollinator or herbivore community dynamics (Maza-Villalobos *et al* 2013).

314   Marod *et al* (2002) suggested that the diversity of dry forest species' traits including the potential

315   to resprout or maintain viable seedbanks, helps maintain diversity in the face of intra- and inter-

316   annual variability in rainfall in a SDTF in Thailand. Furthermore, the reproductive phenology

317   and productivity of dry forests appear to be highly responsive to episodic rains when rainfall

318   regimes are unpredictable (Diaz and Granadillo 2005). However, this diversity of strategies may

319   reduce species richness under future directional changes in rainfall regimes if only certain

320   combinations of traits are favored, underscoring potential vulnerabilities of SDTFs to changes in

321   rainfall.

322   Long-term studies of community dynamics of adult trees in SDTF systems are rare, but

323   some exist. In a study comparing two forest surveys 20 years apart in Guanacaste, Costa Rica

324   (Enquist and Enquist 2010), extended drought conditions were accompanied by a decrease in the

325   number of trees, mainly in the smallest sizes and in the moister habitats, as well as in the

326   proportion of understory evergreen trees with simple leaves. A 19-year study linking tree

327   mortality to rainfall in a 50-ha plot in Mudumulai, India (Suresh *et al* 2010) found mortality rates

328   and causes varied by size class. In small size classes mortality was mostly due to fire or

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329   elephants, and mortality rates were negatively correlated to rainfall at lags of one, two, or three

330   years. By contrast, mortality rates of trees >30 cm diameter at breast height were far lower than

331   similarly sized trees in wet tropical forests, leading to the suggestion that large SDTF trees are

332   resistant to inter-annual variation in climate (Suresh *et al* 2010). In a 10-year study in

333   Guadeloupe, growth rates were about 50% lower and mortality increased from 1.4% to about 5%

334   during a severe drought in 1994–95 (Imbert and Portecop 2008). By contrast, Hurricane Hugo in

335   1989 increased mortality to 9% and decreased growth rates by 66% (Imbert and Portecop 2008).

336   Such long-term demographic studies are urgently needed to resolve whether and how SDTF

337   composition will change in response to ongoing changes in climate.

338

3.2. Belowground responses

340   The effects of drought on belowground processes has received much less attention relative to

341   aboveground dynamics. However, variability in rainfall regimes and resulting changes in soil

342   moisture can also impact root dynamics and relationships between trees and symbionts, and

343   ultimately these processes feedback to affect nutrient cycling and carbon storage.

344   *3.2.1. Root dynamics*

345   Fine roots are plants' primary organ for water and nutrient uptake, and plants can shift allocation

346   to roots vs. shoots in order to maximize resource uptake. This suggests that fine root dynamics

347   could be particularly sensitive to drought, either through direct effects of water deficits or

348   indirect effects mediated by nutrient availability or other factors. In SDTF, fine root dynamics

349   are synchronized to seasonal changes in rainfall but also respond to inter-annual precipitation

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350   anomalies (Kummerow *et al* 1990, Gei and Powers 2015). In addition to responding to variation

351   in soil moisture and hence rainfall, other factors such as spatial variability in nutrients can affect

352   fine root production and turnover (Roy and Singh 1995, Castellanos *et al* 2001, Powers and

353   Peréz-Aviles 2013). Seedlings of SDTF species form deeper roots compared to species from

354   tropical wet forests (Poorter and Markesteijn 2008), which could be a strategy to tolerate periods

355   of soil drought. Within SDTF, root architecture may vary systematically over environmental

356   gradients such as secondary succession or rainfall gradients. For example, a comparison of

357   rooting depth among seedlings of 23 dry forest species showed a trade-off from vertical foraging

358   to water storage during secondary succession, indicating that species differ in their belowground

359   vulnerability to drought at early life stages (Paz *et al* 2015). Campo and Merino (2016) compared

360   SDTFs along a precipitation and forest composition gradient in the Yucatán and found increased

361   soil carbon storage in drier sites, due to lower decomposition and higher chemical recalcitrance

362   of fine roots.

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364   *3.2.2. Belowground symbionts and microbial community composition*

365   Plant-soil interactions may regulate carbon cycle responses to climate change at different spatial

366   and temporal scales (Bardgett *et al* 2013, Van der Putten *et al* 2016). Plant relationships with

367   mycorrizhal fungi are particularly relevant for the carbon cycle given that plants transfer

368   photosynthate carbon to fine roots where these fungi proliferate (Bardgett *et al* 2008, Orwin *et al*

369   2011). Plants differ in the type of mycorrhizal associations (Read *et al* 2004), and therefore have

370   varied mechanisms for nutrient acquisition including the uptake of inorganic and organic forms

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371   of nitrogen (N) and phosphorus (P) (Harrison *et al* 2007, Bardgett *et al* 2008, Leigh *et al* 2009,

372   Orwin *et al* 2011). In particular, arbuscular mycorrhizal fungi (AMF) are present in most SDTF

373   plants (Siqueira *et al* 1998, Zangaro *et al* 2003, Mangan *et al* 2010), as well as ectomycorrhizal

374   host trees (Högberg 1992, Hasselquist *et al* 2011), with important implications for nutrient

375   cycling (Waring *et al* 2015). Both AMF (Augé 2004) and ectomycorrhizae (Lehto and Zwiazek

376   2011) may improve water acquisition of host plants, which could impact how SDTF trees

377   respond to drought.

378   Although numerous studies report on the presence, abundance, or diversity of AMF

379   (Allen *et al* 1998, Guadarrama *et al* 2008, Zangaro *et al* 2012) and ectomycorrhizae (Hasselquist

380   *et al* 2011) in SDTFs, very few studies have assessed how these fungi may influence the

381   response of SDTF species to drought, or how plant-soil interactions impact the water and

382   nutrient cycles in these forests. For instance, Gavito *et al* (2008) experimentally explored the

383   effects of drought on the establishment of plant-AMF associations and found no evidence of

384   adaptations to water stress in any of the plants or of the AMF communities. By contrast, drought

385   limited the formation of mycorrhizal associations, although plants inoculated with AMF

386   experienced lower water stress.

387   Another important plant-microbe symbiosis—symbiotic N fixation by legumes—can be

388   affected by abiotic stresses including drought, high temperature, and salinity. Soil water

389   limitation inhibits nodule initiation, growth and development, function, and longevity (Serraj *et*

390   *al* 1999). Water stress also affects rhizobial survival and growth and population structure in soil

391   (Hungria and Vargas 2000). Moreover, the regulation of N_2 fixation could be altered under water

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392   stress through reduced carbon supply from the plant, oxygen permeability changes, or feedback

393   inhibition by ureides accumulated in nodules and shoots (Valentine *et al* 2010). In SDTFs,

394   nodulation fluctuates seasonally (Teixeira *et al* 2006, González-Ruiz *et al* 2008, Gei and Powers

395   2015) and so nodules in dry forest legumes are likely to be short lived. Changes in drought

396   intensity or in dry season length in these forests could alter nodule "phenology" or lifespan by

397   inducing their premature senescence. Drought stress can also delay or stop normal nodule

398   development, as well as decrease the success of bacterial root-infection resulting in formation of

399   ineffective nodules (Räsänen and Lindström 2003), which could be detrimental especially to

400   seedlings. High temperatures could exacerbate these effects by decreasing survival of rhizobia,

401   affecting the exchange of molecular signals between host plants and rhizobia, and inhibiting

402   root-hair formation and the root-infection process (Hungria and Vargas 2000). However,

403   mycorrhizal inoculation could alleviate the effects of drought stress and improve N_2 fixation

404   (Redecker *et al* 1997). It is noteworthy that the majority of studies addressing microbial

405   responses to seasonal or exceptional drought in SDTFs have focused on plant symbionts (e.g.

406   mycorrhizae, rhizobia). However, we still have much to learn about how free-living

407   microorganisms are affected by drought. For example, the impact of drought on soil pathogens

408   can vary from beneficial to adverse. On the one hand, wetter conditions have been shown to be

409   more conducive for pathogen reproduction and dispersal (Swinfield *et al* 2012), therefore under

410   drier conditions there could potentially be lower numbers of soil pathogens. On the other hand,

411   pathogens have been shown to increase the chances of mortality in drought-stressed individuals

412   (Allen *et al* 2010, Spear *et al* 2015) through more easily infecting trees already under stress

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413   brought on by drought conditions, subsequently leading to mortality (decline spiral model;

414   Manion 1991, Manion and Lachance 1992).

415   *3.2.3. Ecosystem processes and nutrient cycling*

416   Belowground ecosystem processes in tropical dry forests are sensitive to intra- and inter-annual

417   variation in precipitation (Rohr *et al* 2013). For example, decomposition of leaf litter is

418   controlled by the timing and magnitude of precipitation events (Anaya *et al* 2012), and annual

419   decay rate constants increase with precipitation across SDTFs (Campo and Merino 2016).

420   Similarly, mineralization of N and P are strongly tied to rainfall patterns. Soil microbial biomass,

421   carbon pools and the biomass C:N ratio are higher during the dry season and in drier vs. wetter

422   sites (Singh *et al* 1989, Anaya *et al* 2007, Bejarano *et al* 2014). The onset of the rainy season is

423   accompanied by a rapid increase in nutrient mineralization rates and triggers immobilization of

424   N and P into microbial biomass (Singh *et al* 1989, Campo *et al* 1998, Austin *et al* 2004). In

425   addition, the lack of rain during the dry season and during drought lowers soil respiration rates in

426   dry tropical forests (Adachi *et al* 2009, Wood and Silver 2012), decoupling the positive

427   correlation between soil temperature and respiration (Wood *et al* 2013).

428   The slower turnover of labile carbon and nutrient pools in drier forests may contribute to

429   the negative relationship between soil carbon sequestration and mean annual precipitation across

430   Mexican tropical dry forests (Campo and Merino 2016). At broader spatial scales, however, the

431   relationship between soil organic carbon and aridity is hump-shaped (Delgado-Baquerizo *et al*

432   2013), suggesting that extremely dry conditions may have a negative impact on ecosystem

433   carbon storage via decreases in carbon inputs from plant productivity or via physical processes

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434   such as erosion and fire. Similarly, the relationship between soil moisture and respiration may

435   also be hump-shaped moving from dry to wet forests (Orchard and Cook 1983, Wood and Silver

436   2012), as carbon mineralization is limited by water in dry soils and oxygen in inundated soils.

437   Therefore, the effects of shifting rainfall patterns in tropical dry forests are likely to have

438   complex effects on belowground carbon storage, which ultimately depend on feedbacks among

439   historical precipitation regimes, plant responses to drought, and microbial biomass growth and

440   substrate use efficiency.

441

442   **4. Regional factors that might modulate responses to drought at different timescales**

443   Variability in rainfall regimes and drought influence both above- and belowground ecosystem

444   processes directly. However, drought can also indirectly influence SDTFs at differing timescales,

445   and conversely, context-specific factors, other disturbances such as land-use change and forest

446   fragmentation, and/or spatial heterogeneity—operating at both short (Section 4.1) and longer

447   timescales (Section 4.2)—may modify the responses of SDTFs to rainfall variability.

448

449   **4.1. Short or contemporary timescales**

450   Predictions of SDTF responses to drought scenarios (e.g. Fig. 3) are complicated by a number of

451   factors that also interact with drought or modulate ecosystem responses to drought. First,

452   elevated temperatures typically accompany drought, and both can contribute to reduced growth

453   and/or elevated tree mortality (Allen *et al* 2010). Second, drought may exacerbate the effects of

454   other disturbances, such as delayed mortality brought on by hurricanes (Van Bloem *et al* 2006,

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455   Imbert and Portecop 2008). Third, drought can also increase the occurrence, duration, or severity

456   of other disturbances such as fires or insect/pathogen outbreaks; thus, drought may be the

457   ultimate but not proximate driver of ecosystem dynamics. Similarly, landscape context (e.g.

458   topography, distance from streams, etc.), abiotic factors such as soil fertility and depth, and

459   distribution of forest patches in different successional stages may modify ecosystem responses to

460   drought (Powers *et al* 2015), such that certain areas of a landscape are more susceptible than

461   others to altered rainfall.

462   The most extensive contiguous area of SDTF can be found across South America (Miles

463   *et al* 2006), the region where conservation of SDTF is also highest (accounts for 71.8% of total

464   protected SDTF). Regions such as Africa, Southeast Asia, and Australasia, which are susceptible

465   to anthropogenic conversion of SDTF, are extensively fragmented (Miles *et al* 2006). Forest

466   fragmentation can be detrimental to these highly and uniquely diverse systems. Seed recruitment

467   is limited across small habitat fragments, which can subsequently lead to losses in biological and

468   genetic diversity (Nunez-Avila *et al* 2013).

469   Last, we speculate that the great climatic diversity that characterizes SDTF (Fig. 1),

470   suggests that not all SDTFs will respond to changes in drought in a similar fashion. For example,

471   forests such as those in Santa Rosa, Costa Rica that experience very strong alternating wet and

472   dry seasons with highly predictable start and end dates (Fig. 3a) may be more sensitive to

473   changes in the timing of the wet and dry seasons (Fig. 3c, d) than the total amount of annual

474   rainfall. By contrast, SDTFs where rainfall is low but variable throughout the year such as in

475   Guánica, Puerto Rico, may be more affected by the total amount of annual rainfall rather than its

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476 timing (Fig. 3b). Unfortunately, no studies we are aware of have tested the hypothesis that

477 STDF with different rainfall regimes respond differently (or similarly) to climate change, or

478 which mechanisms might account for this; thus, comparative studies that characterize ecological

479 patterns and processes within and across the STDF biome remains a high priority for future

480 research.

481

482 **4.2. Decadal to evolutionary timescales**

483 Tropical forests are dynamic and have undergone directional shifts in composition and structure

484 over decades to millennia (Phillips and Gentry 1994, Condit 1998, Laurance *et al* 2004, Chave *et*

485 *al* 2008, Feeley *et al* 2011). In SDTFs, species composition is strongly correlated to variables

486 related to precipitation and temperature such as water storage capacity (Santos *et al* 2012), water

487 deficit (Neves *et al* 2015), or evapotranspiration (Saiter *et al* 2015). Short-term changes in

488 species composition and forest structure have important consequences for ecosystem response to

489 global change. Previous studies across the tropics emphasize the importance of differential

490 species responses to drought governed by functional traits (Holbrook *et al* 1995, Meir and

491 Pennington 2011). Decreasing rainfall in SDTFs may favor acquisitive, drought-deciduous

492 species as rainfall becomes insufficient to replenish deep soil water reserves (Borchert 1994,

493 Enquist and Enquist 2010). However, decreased rainfall seasonality may favor slow-growing,

494 evergreen species with conservative water-use strategies (Givnish 2002, Craven *et al* 2013).

495 Over evolutionary time scales, paleo-studies have shown that SDTFs are strongly drought

496 tolerant (Meir and Pennington 2011). The ecological stability of SDTFs, with slow rates of

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497   compositional change and immigration rates, may constrain evolutionary responses to intensified

498   selective pressures. Species adapted to the seasonality of SDTF show patterns of monophyly and

499   old stem ages, suggesting persistence over evolutionary timescales (Pennington and Lavin 2015).

500   SDTF populations in Peru and Bolivia, for example, have been stable for up to 10 million years

501   through the drier climates of the Pleistocene. Indeed, SDTFs were more extensive during cooler,

502   drier glacial periods (Pennington *et al* 2009b).

503   Under future climate scenarios, regions such as rainforests in eastern Amazonia (Malhi *et*

504   *al* 2008) and savanna and grasslands in India (Chaturvedi *et al* 2011) may become climatically

505   suitable for SDTFs, theoretically resulting in an expansion of this major biome. In order to

506   expand into adjacent areas, SDTF species will need to disperse to track the shifting climatic

507   envelope; however, paleo-evidence suggests that SDTFs are highly dispersal limited (Pennington

508   *et al* 2009b, Pennington and Lavin 2015). Moreover, the suitability of new areas for SDTF

509   species may further depend on soil nutrient status, fire frequencies, and/or increasingly

510   fragmented landscapes; in nutrient poor soils a transition into a savanna type ecosystem is more

511   likely (Meir and Pennington 2011). SDTF species also lack necessary adaptations to fire (Dexter

512   *et al* 2015) and moisture stress from higher temperatures or prolonged drought conditions could

513   increase their vulnerability (Pulla *et al* 2015). The large rates of historic deforestation suffered by

514   SDTF (Miles *et al* 2006) and current fragmented status may also affect future composition and

515   dynamics through declines in species pools or other processes. Collectively, these factors call

516   into question the ability of SDTFs to expand to adjacent areas in geologically short periods of

517   time. Nevertheless, many Neotropical SDTF species show wide distributions over precipitation

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518   gradients, indicating that they are climatologically more "generalists" compared to wet forest

519   species, which have low tolerance for dry conditions (Esquivel Muelbert *et al* 2016).

520

521   **5. Lessons from terrestrial ecosystem models**

522   Numerical ecosystem models can be useful tools for understanding SDTF responses to drought.

523   Such models quantitatively synthesize numerous assumptions and hypotheses related to the real

524   system that they represent. Model-simulated ecosystem responses to climate change or

525   variability, including droughts, are logical consequences of underlying assumptions and

526   hypotheses. Evaluation of model simulations therefore permits analysis of the ideas forming the

527   ecological basis of the model. We focus here specifically on vegetation demographic models

528   (VDMs), which are characterized by the representation and tracking of multiple (1) plant size

529   classes, (2) plant functional types, and (3) micro-environments with a grid cell. We do not review

530   results from big-leaf dynamic global vegetation models because such models rarely consider tree

531   types associated with SDTFs (Sitch *et al* 2015) and have generally not been evaluated against

532   SDTF field data.

533   Holm *et al* (2012) carried out the first simulations of a SDTF using an individual-based

534   VDM, ZELIG-TROP. Their simulations of Puerto Rican SDTFs were generally consistent with

535   field measurements of forest structure and basal area over the past three decades. They found that

536   forest recovery from disturbance was highly sensitive to soil moisture, with low values of soil

537   moisture slowing forest recovery by more than a century compared to forests that had "ordinary"

538   levels of soil moisture. Seiler *et al* (2014) used the LPJ-GUESS model to simulate tropical

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539   forests in Bolivia. Their model was able to capture the observed transition between evergreen

540   forests and deciduous dry forests, and they identified thresholds for precipitation and water

541   deficit beyond which leaf abscission becomes a competitive advantage. In their simulations and

542   in satellite observations, annual GPP of SDTFs was more sensitive to rainfall anomalies than that

543   of wet tropical forests. When the LPJ-GUESS model was forced with the precipitation

544   projections that have been projected for Bolivia at the end of the 21st century, Seiler *et al* (2015)

545   found that the pure effect of decreased rainfall was a >70% reduction in SDTF vegetation

546   carbon. Xu *et al* (2016) were the first to incorporate an explicit plant hydraulic scheme into

547   model simulations focusing on SDTFs. In Costa Rica and throughout Mesoamerica, they found

548   that plant hydraulics greatly improved the model's ability to simulate responses to seasonal

549   drought, including litterfall and phenological variation among plant functional types (PFTs).

550   They also realistically simulated PFT-dependent responses of woody growth to inter-annual

551   variability in rainfall. Overall, PFT responses to drought were strongly mediated by other

552   prescribed traits including the leaf turgor loss point, xylem hydraulic conductivity, and rooting

553   depth.

554   These studies suggest that SDTFs would be highly sensitive to increased drought.

555   However, work to improve model simulations of SDTFs is needed. Potentially critical processes

556   such as hydraulic failure are generally missing from models (Anderegg *et al* 2012). Belowground

557   parameterizations are poorly constrained (Warren *et al* 2014), and implications of trade-offs

558   between above- and belowground allocation should be explored (Doughty *et al* 2015).

559   Functional diversity is clearly important for model simulations (Anderegg 2015, Xu *et al* 2016),

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560   but further testing of this aspect would be useful. Finally, we recommend that model

561   development be coordinated with experimental manipulations and ongoing observational

562   analyses.

563   **6. Conclusions and Future Work**

564   Our initial question was whether seasonally dry tropical forests, their species, and their

565   ecological dynamics are resistant/resilient to intra- and inter-annual changes in rainfall—

566   reflecting adaptations to predictable, seasonal drought—or whether they are sensitive, as they

567   may already be limited by water and close to climatic thresholds. The available data, from

568   diverse sources such as observations of seedlings, TFE experiments, dendrochronology, and

569   modeling collectively suggest that the structure and function of SDTF will change as droughts

570   become more frequent or severe or rainfall becomes more variable (Chadwick *et al* 2016; Feng

571   *et al* 2013; Greve *et al* 2014). These changes are likely to result in reduced carbon storage as has

572   been seen in Amazonia (Phillips *et al* 2009), altered biodiversity and species ranges (Enquist

573   2002), lowered potentials for reforestation and secondary forest regrowth (Uriarte *et al* 2016) and

574   diminished capacities to provide ecosystem services. Many of these processes may display lags,

575   such that the effects of droughts are only manifested after several years. Moreover, drier tropical

576   forests may be slower to recover from intense or prolonged droughts (i.e. may have lower

577   engineering resilience *sensu* Angeler and Allen 2016) compared to wetter tropical forests, similar

578   to results from a meta-analysis of drought effects on temperate zone forests that found that dry

579   ecosystems took the longest to reestablish normal growth rates after extreme drought (Anderegg

580   *et al* 2015).

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581   Seasonally dry tropical forest ecosystems contain unique and threatened biodiversity

582   (Pennington *et al* 2009a) and provide many ecosystem services that affect human well-being

583   (Maass *et al* 2005). Despite our conclusion that SDTFs are sensitive to changes in drought

584   intensity, frequency, or timing, there are many remaining gaps in our knowledge. In particular,

585   future work should establish well-replicated drought simulations or experiments, distributed

586   across the range of dry forest climatic variation and biogeography. Comparative studies across

587   the SDTF biome to understand which tropical dry forests and their tree species incur high

588   mortality during droughts, and the mechanisms that underlie these responses is also a high

589   priority, as are studies that integrate below- and aboveground responses to drought. Together,

590   these experiments and observations should be used to improve simulation models, which in turn

591   may be used to forecast SDTF responses to altered climates across coarser spatial scales and over

592   a range of potential climate change scenarios.

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