1 **Structural overshoot of tree growth with climate variability and the global spectrum of**

2 **drought-induced forest dieback**

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27   **Abstract**

28   Ongoing climate change poses significant threats to plant function and distribution. Increased

29   temperatures and altered precipitation regimes amplify drought frequency and intensity,

30   elevating plant stress and mortality. Large-scale forest mortality events will have far-reaching

31   impacts on carbon and hydrological cycling, biodiversity, and ecosystem services. However,

32   biogeographical theory and global vegetation models poorly represent recent forest die-off

33   patterns. Furthermore, since trees are sessile and long-lived, their responses to climate

34   extremes are substantially dependent on historical factors. We show that periods of

35   favourable climatic and management conditions that facilitate abundant tree growth can lead

36   to structural overshoot of above-ground tree biomass due to a subsequent temporal mismatch

37   between water demand and availability. When environmental favourability declines,

38   increases in water and temperature stress that are protracted, rapid, or both, drive a gradient

39   of tree structural responses that can modify forest self-thinning relationships. Responses

40   ranging from premature leaf senescence and partial canopy dieback to whole-tree mortality

41   reduce canopy leaf area during the stress period, and for a lagged recovery window

42   thereafter. Such temporal mismatches of water requirements from availability can occur at

43   local to regional scales throughout a species geographical range. Since climate change

44   projections predict large future fluctuations in both wet and dry conditions, we expect forests

45   to become increasingly structurally mismatched to water availability and thus over-built

46   during more stressful episodes. By accounting for the historical context of biomass

47   development, our approach can explain previously problematic aspects of large-scale forest

48   mortality, such as why it can occur throughout the range of a species and yet still be locally

49   highly variable, and why some events seem readily attributable to an ongoing drought while

50   others do not. This refined understanding can facilitate better projections of structural

51 overshoot responses, enabling improved prediction of changes to forest distribution and

52 function from regional to global scales.

53

54 **Introduction**

55 Changing climate patterns pose significant threats to plant and ecosystem function and

56 species distributions (Kelly & Goulden, 2008). In many areas, increased temperatures and

57 altered precipitation regimes combine to exacerbate drought stress from hotter droughts,

58 significantly elevating plant mortality, from water-limited Mediterranean forests to tropical

59 moist forests (IPCC, 2014; Allen *et al.*, 2015, Greenwood *et al.*, in press). Of particular

60 concern are broad-scale forest die-off events where rapid mortality occurs over 10s to 1000s

61 of km^2 of forest, which could offset any positive tree-growth effects of CO_2 fertilisation and

62 longer growing seasons from warming temperatures during the second half of the 20th

63 Century (Norby & Zak, 2011; Nabuurs *et al.*, 2013; Ruiz-Benito *et al.*, 2014; van der Sleen *et*

64 *al.*, 2015). Furthermore, widespread forest growth reductions and increases in the extent and

65 magnitude of die-off events are anticipated as climate warms and becomes more extreme and

66 as current climatic extremes become more frequent (Adams *et al.*, 2009; van Oijen *et al.*,

67 2013; Allen *et al.*, 2015; Frank *et al.*, 2015; Charney *et al.*, 2016; Greenwood *et al.*, in press).

68 Extensive forest die-offs would have far-reaching consequences through impacts on carbon

69 and hydrological cycling, biodiversity, and goods and environmental services to local human

70 populations (Anderegg *et al.*, 2015; Frank *et al.*, 2015; Trumbore *et al.*, 2015).

71

72 Ongoing environmental changes are already altering the distribution of species across the

73 globe (Walther *et al.*, 2002; Parmesan, 2006). Contemporary plant range changes have been

74 readily identified in woody species, with range expansions and increases in population

75 density resulting from enhanced growth and reproduction at the upper and poleward edge of

76   species distributions as the climate warms (Sturm *et al.*, 2001; Harsch *et al.*, 2009). Negative

77   changes in plant water balance due to elevated temperature and/or decreased precipitation are

78   expected to locally constrain productivity and elevate mortality (e.g. Juday *et al.*, 2015), with

79   effects being particularly evident at the equatorial and low altitude (or hotter and drier)

80   margins of species distributions (Bigler *et al.*, 2007; Sarris *et al.*, 2007; Allen *et al.*, 2010;

81   Carnicer *et al.*, 2011; Linares & Camarero, 2011; Sánchez-Salguero *et al.*, 2012). Indeed,

82   recent evidence from populations at the equatorial and low altitude range-edge of forest-

83   forming tree species has shown elevated mortality and growth decline linked to rising

84   temperatures and drought stress over the last half-century (Jump *et al.*, 2006; van Mantgem &

85   Stephenson, 2007; Beckage *et al.*, 2008; Piovesan *et al.*, 2008). Drought-linked tree mortality

86   might, therefore, be expected to concentrate along already hotter and drier margins of a

87   species' distribution. However, this is not always the case, with recent drought-linked die-off

88   also occurring throughout species ranges while some range edge populations can be relatively

89   unaffected by regional drought (Jump *et al.*, 2009; Allen et al. 2010; Hampe & Jump, 2011;

90   Allen *et al.*, 2015; Cavin & Jump, 2016). Consequently, simple biogeographical explanations

91   cannot adequately explain the full range of drought-linked tree mortality patterns observed.

92

93   Despite the recognised effects of intense droughts and increased temperatures on tree

94   mortality, the die-off patterns observed worldwide are poorly reproduced by global

95   vegetation models (McDowell *et al.*, 2013; Steinkamp & Hickler, 2015). Forests are complex

96   ecosystems, and the responses to climate extremes are dependent on a range of factors

97   including species composition, species-specific plant functional traits (Anderegg *et al.*,

98   2016a), intraspecific variability, biotic interactions, legacy effects, such as "ecological

99   memory" of past climate, management, or natural disturbances (Johnstone *et al.*, 2016), and

100   stand structure (Fensham *et al.*, 2005; Allen *et al.*, 2015). Another major factor commonly

101 confounding interpretations of the relationships between the drivers and effects of forest

102 dieback is the temporal mismatch between relatively rapid climatic fluctuations in water

103 deficit and temperature and the slower lagged morphological responses of trees. The

104 complexity of the interactions among multiple inciting and exacerbating factors associated

105 with diverse forest mortality processes are highlighted by the varied and divergent patterns

106 and causes attributed to mortality events, even within a particularly well-studied species such

107 as piñon pine (Meddens *et al.*, 2015).

108

109 Our knowledge of physiological causes of drought-linked tree mortality has advanced rapidly

110 over recent years as our understanding of the importance of both hydraulic failure and

111 carbon-related aspects, as well as their interaction, has developed (McDowell, 2011; Sevanto

112 *et al.*, 2014; Hartmann *et al.*, 2015; Mencuccini *et al.*, 2015). Likewise, the importance of

113 substrate and biotic interactions, particularly insect pest outbreaks, in exacerbating mortality

114 is well-understood at a general level (Franklin *et al.*, 1987; Anderegg *et al.*, 2015; Fensham *et*

115 *al.*, 2015; Hartmann *et al.*, 2015; Meddens *et al.*, 2015). However, a strong disparity persists

116 between observed die-off events and our predictive capacity (McDowell *et al.*, 2013).

117 Consequently, there is an urgent need to develop a more integrated approach to

118 understanding broad-scale mortality, incorporating historical and landscape context as well as

119 more immediate environmental drivers (Hartmann *et al.*, 2015).

120

121 Here, we consider tree mortality responses to drought, showing that an approach that

122 combines past environmental conditions with current tree structure can improve our

123 understanding of drought-linked mortality events. We begin by considering plant responses

124 to reduced water availability, before looking at the role of stand structure and management in

125 determining response to changes in water availability from a variety of forest ecosystems. We

126   conclude with proposals to improve monitoring and modelling approaches with the aim of

127   improving our predictive capacity of forest dieback across the globe.

128

129   **Plant-level adjustments to increased water scarcity**

130   Alterations to the availability of resources limiting plant function and growth can be both

131   direct (e.g. water, light and nutrients) or indirect (e.g. through disturbance, pests, pathogens).

132   Plants typically respond to changes in resource availability via the gain or loss of biomass,

133   suggesting that plant biomass should track the recent availability of the limiting resource

134   (Chollet *et al.*, 2014). Commonly, significant time lags in response can occur due to the

135   comparative slowness of plant morphological adjustments (e.g. carbon allocation, Arneth et

136   al., 1998) relative to potentially more rapid changes in resource availability, which could be

137   partially compensated by water storage in plants and soil (Sevanto et al., 2006). However,

138   fluctuations in water availability are of critical importance since the water-storage capacity of

139   most plants is low relative to total daily water demand, even in large trees. This relatively low

140   water-storage capacity renders plants at particularly high risk of structural and functional

141   injury through water deficit on much shorter time scales than through reduction of other

142   resources that can be stored within plant tissues and reallocated (Vaadia *et al.*, 1961; Chapin

143   *et al.*, 1990). Trees generally take advantage of wetter conditions by growing more above-

144   ground biomass (e.g. taller stems and more leaf area), necessary to better compete for light

145   and space when water is abundant. However, when the water limitations of drier climatic

146   conditions inevitably return, this newly developed biomass may become unsustainable and

147   vulnerable to structural dieback. We term this process of increased above-ground biomass

148   development due to more favourable water availability in the past and the consequent

149   temporal mismatch between water availability and demand, *structural overshoot* (SO).

150

151 Drought-resistance strategies are varied and range from drought escape (ephemeral species)

152 to drought avoidance (e.g. through efficient stomatal control, drought-deciduousness,

153 increased root:shoot ratio) and drought tolerance (e.g. high resistance to embolism, osmotic

154 adjustment) (Ludlow, 1989; De Micco & Aronne, 2012; Brunner *et al.,* 2015). In perennial

155 species, reducing water loss is a priority under drought (Maseda & Fernández, 2006)

156 regardless of whether it occurs through stomatal closure and/or leaf loss. Stomatal closure has

157 a direct cost in terms of carbon assimilation and may be unsustainable in the long-term

158 (McDowell *et al.*, 2008; McDowell, 2011; Poyatos *et al.*, 2013), whereas structural

159 adjustments (e.g. loss of leaves and above-ground woody tissues) are particularly costly in

160 woody plants. Large woody organs are persistent and cannot be discarded during periods of

161 water scarcity without partial or total mortality. Similarly, at the stand level, water

162 availability per individual will depend on the overall water demands of the plants competing

163 for the same water resources. Measures of stand structural development, such as stem

164 density, basal area, or leaf area index (LAI), relative to a long-term baseline, should then be

165 significant contributing factors to the drought susceptibility of forest stands through structural

166 overshoot under fluctuating climate conditions (Ruiz-Benito *et al.*, 2013).

167

168 **Stem density and leaf area influence on tree responses to extreme droughts**

169 According to the above rationale, drought-induced tree mortality should be more pronounced

170 where stem density is the highest, all else being equal. We explored the validity of this

171 hypothesis relative to drought-linked tree mortality across biomes by performing a review of

172 the scientific literature using search terms "drought" and "mortality" and including

173 quantitative, field-based observational research studies performed on adult trees (see

174 Appendix S1 for full details). Of the 75 papers that identified drought-induced tree mortality

175 (DITM), tree density was the most commonly mentioned covariate in DITM events (33% of

176   cases) alongside biotic agents (i.e. insects, pathogens or herbivores, 29% cases) (Fig. 1).

177   While the overall risk of drought-induced forest mortality is consistent across biomes

178   (Greenwood *et al.*, in press), density and biotic agents as co-drivers of DITM were more

179   often reported in more water- or temperature-limited systems such as tropical savanna and

180   temperate forests, respectively (Fig. 1). Tree mortality in tropical systems overall was more

181   frequently related to the sole effects of episodic droughts or drought in combination with fire

182   (Fig. 1). However, the lower frequency of drought when compared to fire may be influenced

183   by the focus and methods of studies in tropical biomes (i.e. generally focussed less on density

184   effects and biotic agents). Overall, we found that 71% of the 28 cases testing density effects

185   reported a positive association between density and mortality (i.e. higher mortality in denser

186   stands), 14% did not report a significant effect, and 14% reported higher mortality in less

187   dense stands. A single study reported mixed positive and negative density dependent effects.

188   Furthermore, the sign of the density effect was relatively independent of the forest type (Fig.

189   2).

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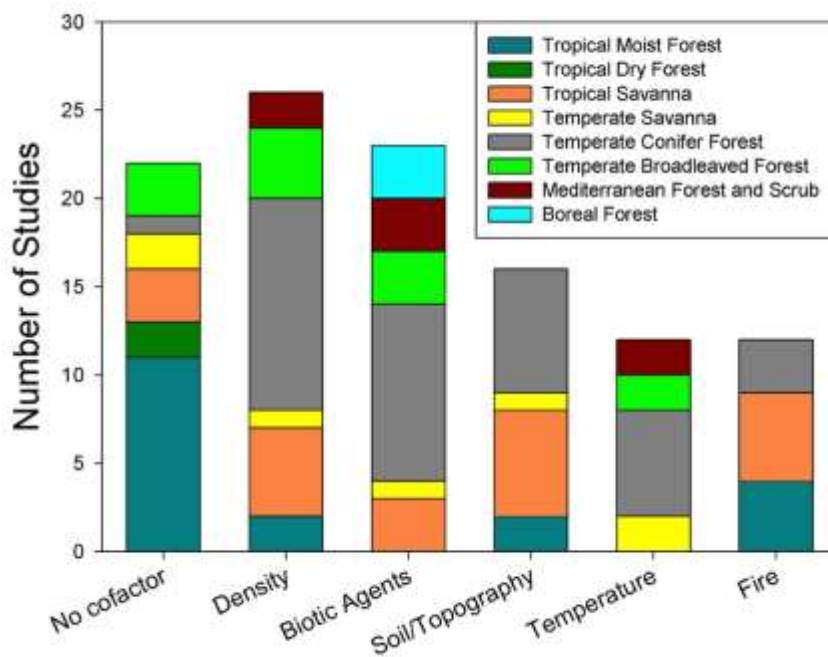
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192 **Figure 1.** Quantitative, field-based observational studies of drought-induced tree mortality

193 that identify as drivers of drought alone (i.e. no cofactor) and co-drivers that interacted with

194 drought in forest types classified following Olson *et al.* (2001) biomes.
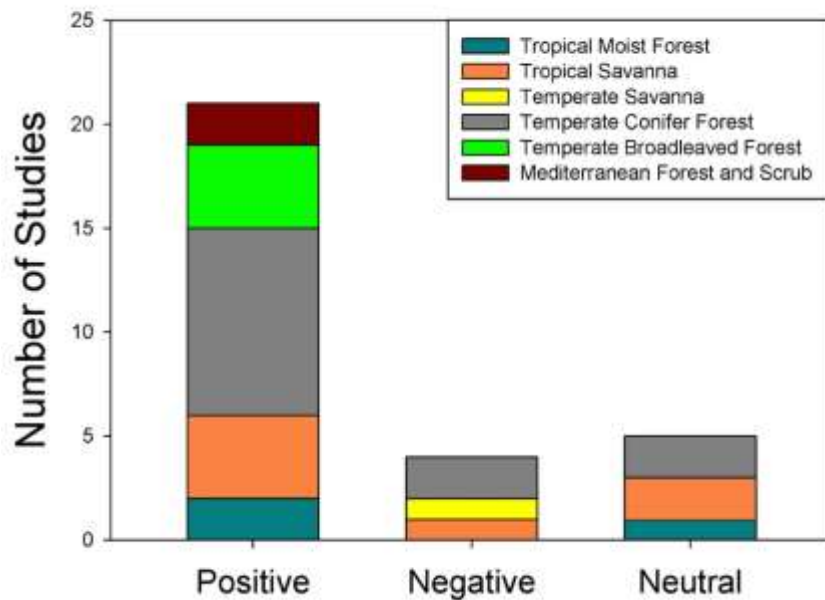
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196 **Figure 2.** Frequency of positive, negative or neutral effect of stand density on drought-

197 induced tree mortality among quantitative, field-based observational studies in forest types

198 classified using Olson *et al.* (2001) biomes.

199

200 While stand density is generally a co-driver in drought-induced tree mortality, total leaf area

201 is a major determinant of plant water requirements and, therefore, has the potential to mediate

202 drought impacts from individual organs up through the whole-forest scale (Fig. 3). Stand-

203 level leaf area is normally expressed as the leaf area index (LAI), corresponding to projected

204 canopy leaf area relative to ground area (m^2 m^{-2}), which can be calculated as the product of

205 the projected leaf area of each tree (hereafter, crown leaf area, m^2 $tree^{-1}$) and stand density

206 (tree m^{-2}). LAI can be used as a proxy of functional responses to resource availability, as for

207 example with water availability (Margolis *et al.*, 1995; Pook *et al.*, 1997; Smettem *et al.*,

208 2013; Duursma *et al.*, 2016), and combines a number of ecosystem properties that are

209   dependent on climate, forest management, and legacy effects (Johnstone *et al.*, 2016).

210   Furthermore, LAI is dynamic and changes with stand development and self-thinning

211   processes (Holdaway *et al.*, 2008) and is critical in driving forest productivity (Reich, 2012).

212   LAI also depends on forest type and climate, where temperature limitations on LAI have

213   been identified in cool climates whereas water availability is the main climatic driver in other

214   climates (Iio *et al.*, 2014), with LAI decreasing as water stress increases (Grier & Running,

215   1977; Luo *et al.*, 2004). Since LAI is coupled to the temporal availability of water, including

216   pulsed deficits as drought (Iio *et al.*, 2014), drought is expected to lead to LAI and biomass

217   reductions along a gradient of response running from premature leaf senescence and partial

218   canopy dieback, to whole plant mortality (Fig. 3) such that drought-induced tree dieback and

219   mortality events result from the temporal mismatch between LAI and water availability in a

220   given environment.

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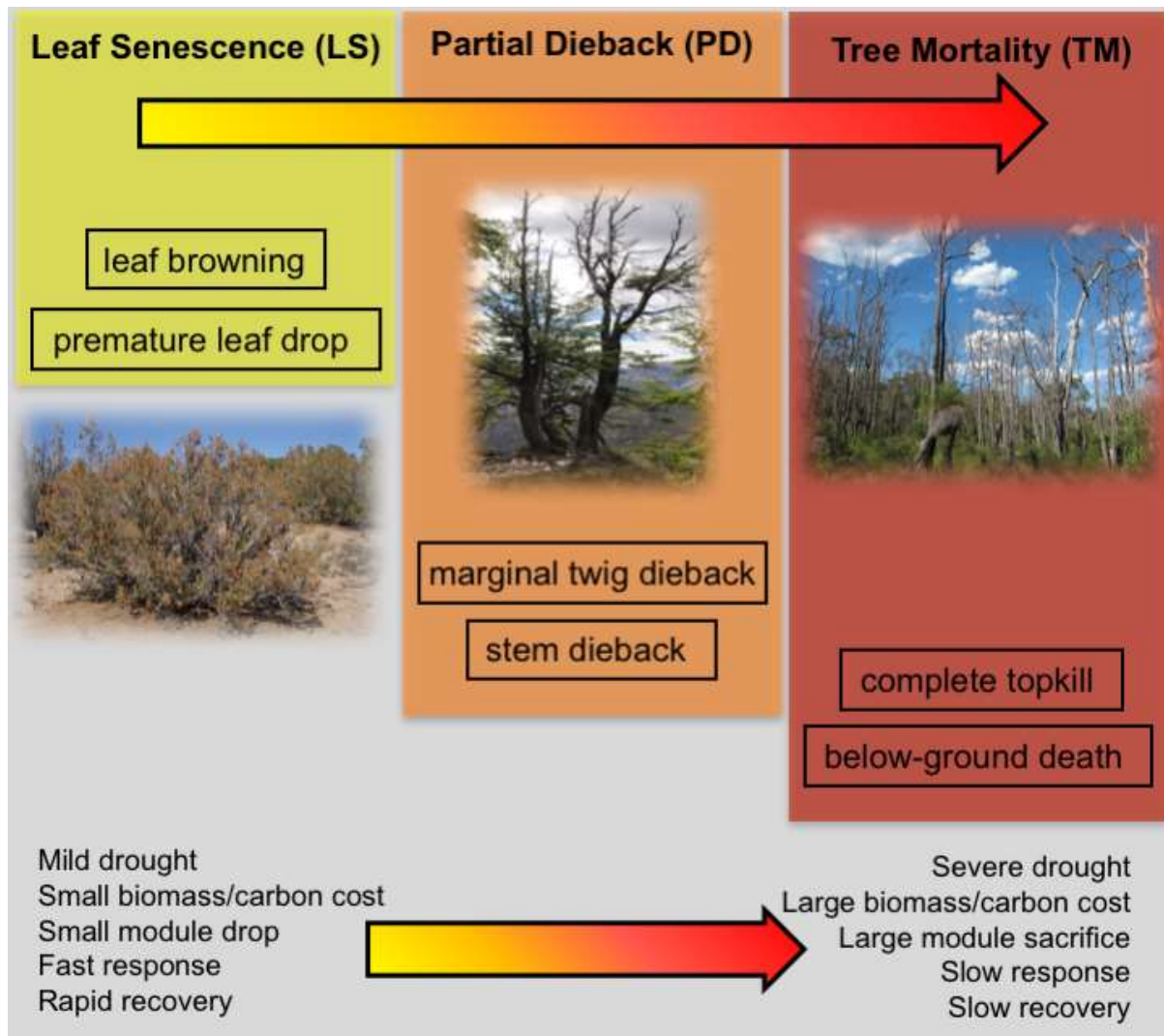
Figure 3. Spectrum of tree or forest structural loss responses to decreases in water availability, or increases in drought stress. Photographs: Extensive premature leaf senescence (LS) of one-seed juniper (*Juniperus monosperma*), northern New Mexico, USA (2013, C.D. Allen), in response to protracted and extreme hotter drought (Allen *et al.*, 2015). Partial dieback (PD) of canopies of evergreen coihue (*Nothofagus dombeyi*), Patagonia, Argentina (2015, T. Kitzberger), from both extreme and chronic drought (Suarez & Kitzberger, 2010). Complete topkill tree mortality (TM) of jarrah (*Eucalyptus marginata*), southern Western Australia (2012, C.D. Allen), triggered by extreme hotter drought in early 2011 and a chronically drying climate (Matusick *et al.*, 2013).

233

Leaf area index under changing resource availability

Resource limitations are at the base of our understanding of tree growth and forest dynamics. To the extent that forest resource use is determined by the product of tree density and individual tree size, both variables cannot increase at the same time (unless resources are not limiting). This is at the core of self-thinning theory, which predicts a negative relationship between tree density and tree size during forest development over time, at least within a range of tree densities and for even-aged stands (Yoda *et al.*, 1963). This negative relationship is normally described using a power law (linear in log-log scale) independently of the tree size measure used (Westoby *et al.*, 1984; Weller, 1987; Zeide, 1987). Several variables have been used to describe tree size (e.g. biomass, diameter, height, crown size), resulting in different self-thinning slopes. Here, we propose the use of crown leaf area as a measure of tree size when studying resource limitations in the context of drought-induced responses (see Fig. 4), since variables related to crown leaf area are arguably good proxies for individual resource use and physiological responses to specific perturbations, particularly drought. Furthermore, its relationship with crown allometry and growing-space-filling, instead of diameter or biomass, make the corresponding relationship between stem density and crown leaf area highly interpretable for individual and species-specific responses (Morris, 2003; Pretzsch & Schütze, 2005; Charru *et al.*, 2012). For simplicity, we assume that the slope of the log relationship between crown leaf area and tree density is -1, implying constant LAI over time at the stand level (unless resource availability changes), as is traditionally assumed during self-thinning (Long & Smith, 1984; Osawa & Allen, 1993; but see Holdaway *et al.*, 2008; Coomes *et al.*, 2012). However, our application of the proposed framework to forest SO responses to drought does not depend on this particular assumption

257 and would apply regardless of the slope of the relationship as long as it is negative (Coomes

258 *et al.*, 2012).

259

260 The generality of the ideas underlying the self-thinning line (STL) concept makes it a

261 powerful model to understand the impact of changes in resource availability on forest

262 structure since its intercept is frequently dependent on resource availability (sometimes

263 treated as site quality, Appendix S2). Modifications of the STL have been widely studied

264 across different sites and species, whereas studies covering variations over time are scarcer

265 (Appendix S2). The STL intercept increases with higher resource availability or productivity

266 for a given species or, more generally, with release from any previously limiting factor (Bi,

267 2001; Weiskittel *et al.*, 2009; Zhang *et al.*, 2013; and Appendix S2). The slope of the STL

268 relationship can be modified by differences in shade-tolerance (Pretzsch & Biber, 2005;

269 Weiskittel *et al.*, 2009), perturbations (Oliver, 1995; Coomes *et al.*, 2012) and changes in soil

270 fertility (Morris, 2003) and due to inter-site variability (see a complete description in

271 Appendix S2). However, generally, the slope of the STL varies little through time (Pretzsch

272 *et al.*, 2014) and space (Bi *et al.*, 2000; Bégin *et al.*, 2001; Bi, 2001), at least when there is no

273 recruitment limitation and mature forests are experiencing competitive thinning (Duncanson

274 *et al.*, 2015). Furthermore, although lower slopes could occur under increased aridity,

275 intercept variations are much stronger than slope variations (Deng *et al.*, 2006; Dai *et al.*,

276 2009; Bai *et al.*, 2010). Consequently, we base our conceptual framework of drought

277 responses on the expectation that changes in environmental conditions over time should

278 result in a range of approximately parallel relationship between crown leaf area and tree

279 density within a site (Fig. 4a; and references in Appendix S2), as it is generally supported by

280 changes through time (Garcia, 2012; Pretzsch *et al.*, 2014). We note, however, that the

281 general principles presented here would still apply if alternative 'self-thinning lines' were not

282 strictly parallel.

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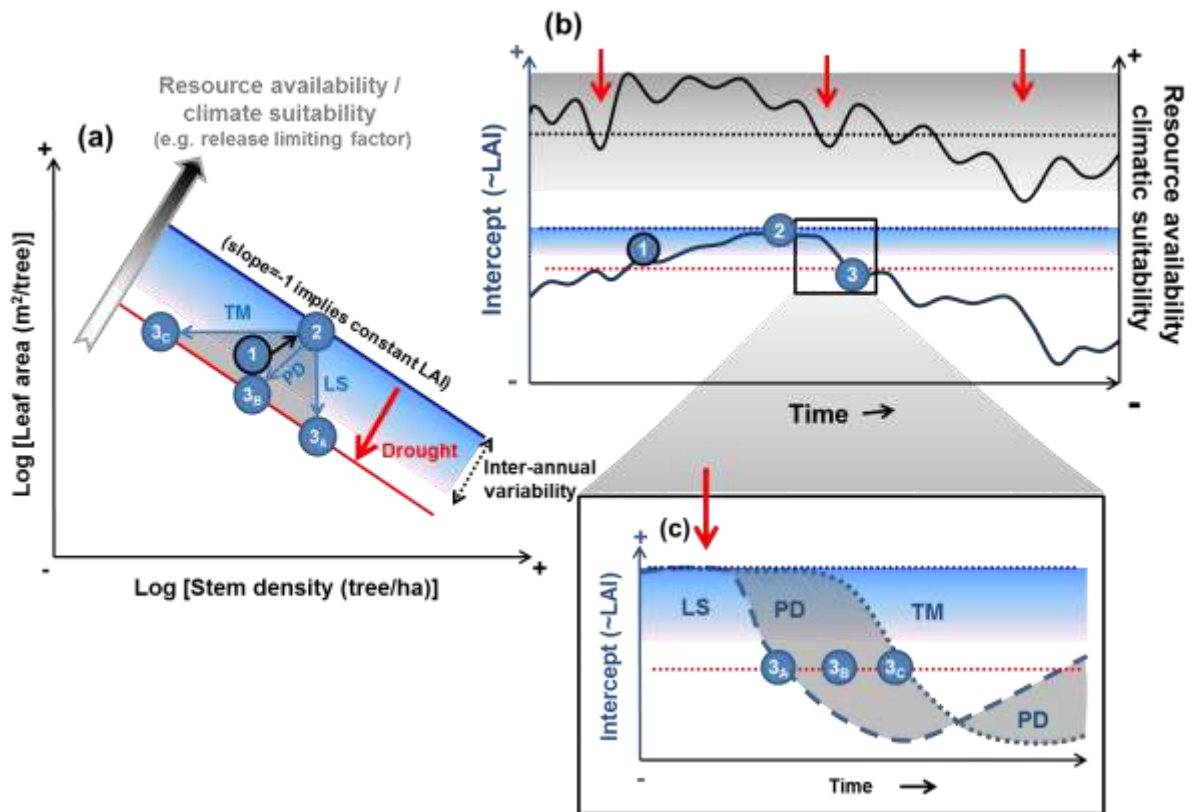
Figure 4. Structural overshoot (SO) framework highlighting temporal mismatches between

resource demand and supply. Resource demand is assumed to be proportional to leaf area

index (LAI) in a concept analogous to self-thinning but using crown leaf area as a measure of

individual tree size. Panel **(a)** shows the theoretical effect of an extreme drought (red arrow)

on the 'self-thinning' intercept (i.e. when stem density=1 tree ha^{-1}), equivalent to the leaf area

index (LAI) of the stand. The situation depicted in the figure illustrates a forest stand located

initially in a position (state 1) from which there is an increase in LAI and stand density over

time (to state 2) due to release from a limiting factor. Under an extreme drought event, there

is a reduction in stand-level LAI, that can occur through: leaf senescence (LS) only, state 3_A;

14

296   diverse combinations of partial dieback (PD) affecting canopy branches and whole stems (in

297   multi-stemmed species), state 3_B (shown as a grey zone); or individual tree mortality (TM),

298   state 3_C. Panel **(b)** shows the temporal dynamics of resource availability/climate suitability

299   (upper graph, dotted black line represents average climatic conditions) and the associated

300   changes in the intercept of the self-thinning line (LAI) (lower graph, including the dotted blue

301   and red lines, which show the intercept for the continuous blue and red lines in panel (a),

302   respectively). We highlighted the impact of three severe droughts using red arrows: the first

303   drought event occurs when forest LAI is still relatively low, and hence the impact on the

304   stand is minor; the second drought occurs when LAI is higher and, therefore, the

305   corresponding response in terms of LAI reduction is also larger (a detailed response is

306   depicted in panel (c)); and, the third arrow depicts an hypothetical situation in which forest

307   resilience has been lost due to continuously worsening conditions and thus an additional

308   drought may result in extreme LAI reductions (not depicted in panels (a) or (c)). The location

309   of the states (1) (i.e. initial state), state (2) (i.e. when self-thinning is occurring under high

310   resource availability and/or climatic suitability), and state (3) (i.e. potential state under

311   persistent severe droughts exceeding the inter-annual variability and potentially leading to

312   new self-thinning lines) are also shown. Panel **(c)** shows a more detailed temporal response of

313   the self-thinning intercept to a drought event, illustrating different dynamics depending on

314   whether the response is primarily through leaf senescence (LS), partial dieback of canopy

315   branches and stems (PD, grey zone), or extensive tree mortality (TM).

316

317   **Temporal mismatch between water demand and availability drives the spectrum of tree**

318   **dieback responses to drought.**

319   Following a period with increasing resource availability (or release from previous limiting

320   factors, such as conditions following disturbances), the self-thinning line would move away

321   from the origin (higher intercept), which implies higher LAI (and water use) at the stand level

322   (Fig. 4a,b). There is increasing evidence that leaf area at both the tree and stand levels

323   responds to changes in water availability, but frequently with lagged responses (Bigler *et al.*,

324   2007). These lags arise from the fact that the water status of trees can be buffered from

325   seasonal or even longer-term variations in climatic water availability (due to, e.g. deep

326   rooting) and also from the fact that individual trees have a substantial capacity to

327   accommodate short-term changes in water stress even without leaf loss (Martínez-Vilalta *et*

328   *al.*, 2014). As a result, temporal changes in LAI are frequently smaller than those observed

329   when comparing the mean conditions of different sites along analogous gradients in water

330   availability (Smettem *et al.*, 2013). A frequent consequence of LAI dynamics lagging

331   somewhat behind environmental changes is the temporal mismatch of resource availability

332   and LAI; in particular, when severe stress occurs after a strongly favourable period, the large

333   difference between resource demand (determined by lagged LAI) and resource availability

334   results in a forest structurally maladapted to the current stressful conditions. We hypothesise

335   that the potential for SO dieback dynamics to occur depends upon the particular magnitude,

336   timing, and sequence of climatic fluctuations, which drive the size and duration of the

337   temporal mismatch between legacy LAI levels and resource availability.

338

339   Given that temporal variability in water (or other limiting resources) drives the development

340   of high tree LAI relative to subsequent resource availability, the resulting SO eventually

341   leads to dieback reductions in leaf area. Individual tree responses can be put in a wider

342   context of diverse structural plant adjustments (Fig. 3), ranging from premature leaf

343   senescence (LS) to partial dieback (PD) of canopies and stems to complete tree mortality

344   (TM). We expect that LAI adjustments will occur more rapidly if they occur through leaf

345   senescence, resulting in shorter temporal lags between water availability and demand. At the

346 other extreme, a response through tree mortality, with a much larger cost in terms of biomass,

347 would tend to occur more slowly and result in longer lags (Fig. 4c), although outbreak

348 dynamics of mortality-causing biotic agents such as bark beetles can drive relatively rapid

349 tree mortality (Anderegg et al. 2015). The implications in terms of recovery at tree and stand

350 levels after disturbance are substantial. Recovery after LS occurs primarily through the

351 growth of new foliage once environmental conditions return to a relatively favourable state,

352 which requires the consumption of stored carbohydrates (Galiano *et al.*, 2011). Recovery

353 from PD, if developmentally possible for the species, additionally requires some level of

354 woody tissue resprouting from the crown, stem, or roots, with an associated greater cost to

355 stored carbohydrate resources, implying slower response times (Galiano *et al.*, 2012). Finally,

356 recovery after complete TM depends on new recruitment, implying even longer response

357 times (Fig. 4c). The response spectrum between LS and TM can be seen as a continuum –

358 they may occur simultaneously in co-occurring species or in different trees of a given

359 population, in which more severe levels of resource stress (or disturbance) increase the

360 likelihood of a TM response (Fig. 3). These three types of responses often occur sequentially

361 in time, starting with LS, followed by PD and, if the stress is intense or persistent enough,

362 resulting in TM (e.g. Galiano *et al.*, 2011). However, they also seem to be site- and species-

363 dependent to varying degrees, as we illustrate below.

364

365 **Structural overshoot and the spectrum of drought-induced forest dieback around the**

366 **world**

367 Different tree species show different strategies in their response to chronic and acute drought

368 stress linked to differences in traits, population history, and the temporal patterns of drought

369 occurrence to which they are adapted. Consequently, changes in water availability can result

370 in a variety of responses at the population level such that seemingly disparate responses in

different systems are linked through the SO concept along a continuum, from leaf drop to whole plant mortality (Fig. 3). The origin of structural overshoot is usually due to the existence of favourable conditions for growth (e.g. wet or drought-free periods) together with certain management actions or omissions that favour tree encroachment (Table 1). On the one hand, historical climatic variability promotes favourable conditions for growth and biomass increments generally at centennial or decadal periods: centennial such as in *Eucalyptus*-dominated savannah from NE Australia (Fensham *et al.*, 2005; Fensham *et al.*, 2012), multi-decadal for conifer forests of SW North America (Williams *et al.*, 2013; Allen *et al.*, 2015; Williams *et al.*, 2015), or decadal such as in austral *Nothofagus* forests in South America (Suarez *et al.*, 2004; Suarez & Kitzberger, 2008; Suarez & Kitzberger, 2010). On the other hand, human legacies have coupled with climatic variation through successional vegetation growth since the last disturbance or exploitation, ranging from settlement fires in Andean Patagonia, and agricultural and timber exploitation cessation in Europe, to logging in tropical forests or ranching in SW North America and Australia (Table 1, Fig. 5). The accumulation of biomass may be further promoted with forest fire protection (as in South American *Nothofagus* forests), increasing stand densities as well as fuel accumulation and the risk of future fires (as in North American *Pinus* forests, Table 1).
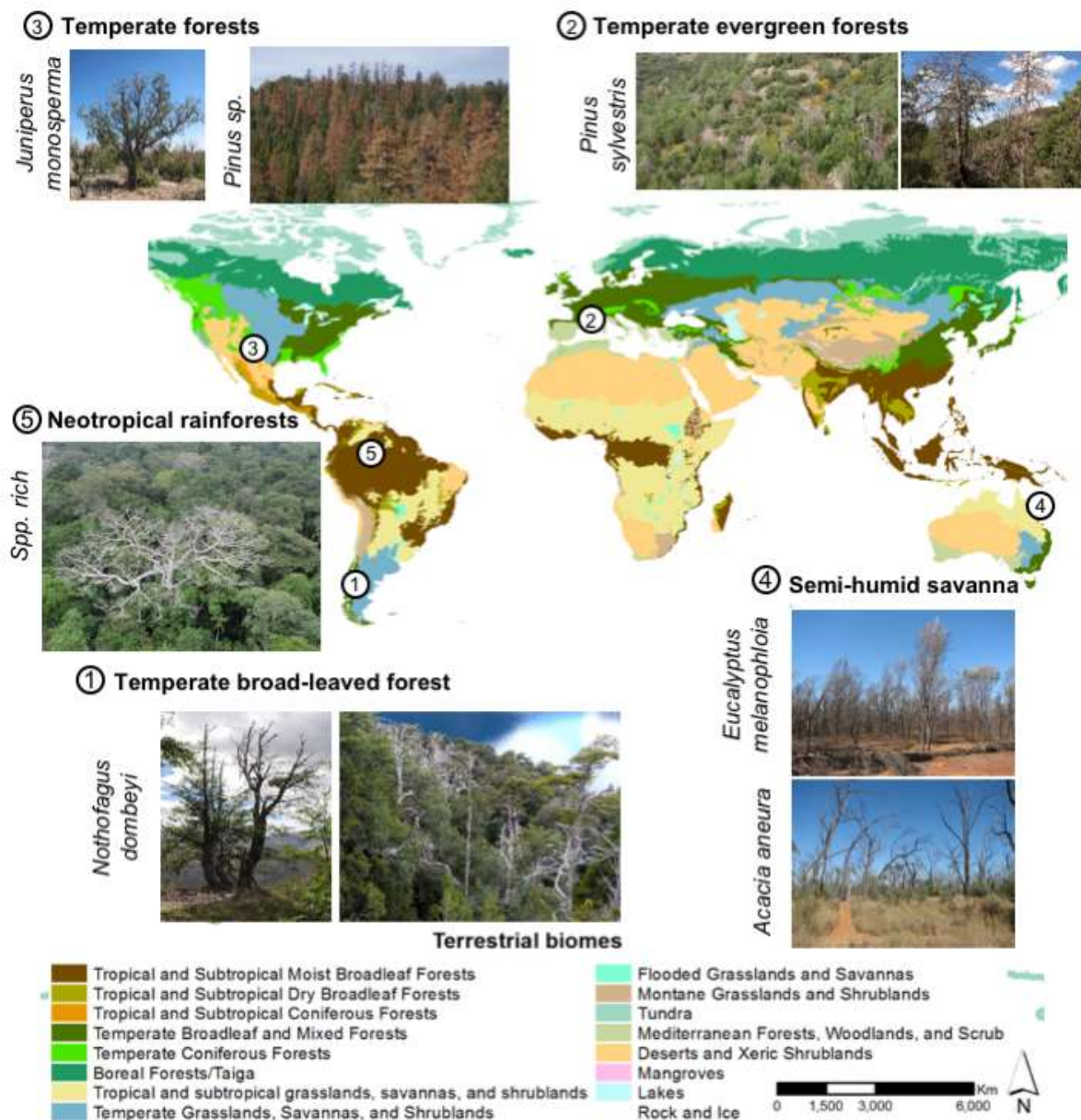
Figure 5. Map location and illustrations of structural overshoot (SO) responses of the case studies summarised in Table 1 and Appendix S3, overlaid on major terrestrial biomes modified from Olson *et al.* (2001). (1): tree mortality of *Nothofagus dombeyi* near Bariloche (Argentina) (photo T. Kitzberger and F. Lloret); (2): tree mortality of *Pinus sylvestris* in Prades (Tarragona, Spain) (photo R. Martin Vidal) and in Teruel (Spain) (F. Lloret); (3): partial dieback of *Juniperus monosperma* in New Mexico (USA) and tree mortality of *Pinus* sp. in Sequoia Natural Park (USA) (photo C. D. Allen); (4): tree mortality of *Eucalyptus*

19

396 *melaniploia* sp. and *Acacia aneura* in Queensland (Australia) (photo R. Fenshman); (5): tree

397 mortality in species rich forests in western Amazonian (Brazil) (photo NASA/JPL-Caltech

398 from Saatchi *et al.* (2013)).

399

400 After periods of biomass accumulation due to both climatic variability and legacy effects,

401 extreme drought events might easily result in SO in a wide variety of forest and tree species

402 (Table 1). Extreme drought may also occur in the context of multiyear climatic oscillations,

403 such as ENSO leading to peaks of drought in the wet season of South American *Nothofagus*

404 forests or extremely low rainfall in the dry season in Amazonian tropical rainforests (see

405 references Table 1). The effects of multiyear droughts can accumulate during several years

406 and eventually result in temporal peaks of extensive mortality (e.g. NE Spain, SW North

407 America and Queensland). Drought effects are commonly reinforced by abiotic and biotic co-

408 drivers, as high temperatures (e.g. SW Argentina, NE Spain, SW North America), soils with

409 low water holding capacity (e.g. S and NE Spain and Queensland), antagonistic biotic

410 interactions (fungal diseases, plant parasites such as mistletoe, insect outbreaks (e.g. NE

411 Spain, SW North America), wildfires (e.g. SW North America and Amazonia), logging

412 and/or habitat disruption (e.g. Amazonia) (Table 1). Some of these co-drivers, in turn may be

413 reinforced by the loss of vigour that usually accompanies SO and tree mortality, such as in

414 the case of biotic antagonists (Franklin *et al.*, 1987), or by the resulting transformation of the

415 environment (Allen, 2007).

416

417 The variety of tree-level responses, from LS to PD and individual TM, seems to obey on the

418 one hand the intensity and frequency of droughts (Figure 3) and on the other hand the

419 anatomical and structural differences between species. For example, PD seems to be

420 particularly common in *Fagaceae* and *Nothofagaceae* (Suarez *et al.*, 2004; Galiano *et al.*,

2012), while *Pinaceae* show a more continuous pattern of LS until eventual TM (Galiano *et al.*, 2010; Galiano *et al.*, 2011; Poyatos *et al.*, 2013). Leaf area reductions predicted by the SO framework can eventually translate to changes in the dominant species, particularly when TM is the more conspicuous response (e.g. Allen and Breshears, 1998). Considering the dominant structural responses of the forests (Table 1) while species self-replacement may occur in some cases (Hosking & Hutcheson, 1988), shifts, when they occur, tend to favour more drought-tolerant species, for example, *Austrocedrus chilensis* in *Nothofagus dombeyi* forests (Suarez & Kitzberger, 2008), and *Quercus ilex* or *Q. pubescens* in *Pinus sylvestris* forests (Galiano *et al.*, 2010; Rigling *et al.*, 2013). When the phenomenon extends over large areas, such in SW North America, vegetation shifts can be strongly evident at ecotones (Allen & Breshears, 1998). However, we do not have enough information to identify clear, general trends of species replacement and vegetation shifts, substantially because of large uncertainties in the mid-term fate of the regeneration of the different species (Martínez-Vilalta & Lloret, 2016). At the ecosystem level, tree mortality events have led to an important loss of forest area and stored carbon (Table 1). The reduction of live standing biomass by mortality can in turn increase dead fuel loads, thereby increasing fire risk rapidly (e.g. *Nothofagus* in SW Argentina and tropical rainforest).

Table 1. Summary of five diverse case studies illustrating the SO framework Summary of structural overshoot examples from five continents, including SO legacy causes (both climatic and management legacies), SO response drivers (i.e. climatic drivers and other co-drivers), affected stand conditions and landscape settings, and predominant structural responses. The main affected tree species of each case study are (1): *Nothofagus dombeyi*; (2): *Pinus sylvestris, Quercus ilex*; (3): *Abies* spp., *Pseudotsuga menziesii, Populus* spp., *Pinus ponderosa, Quercus* spp., *Pinus edulis*, and *Juniperus monosperma*; (4): *Eucalyptus* spp. and *Acacia* spp.; and (5): species-rich forest. See Appendix S3 for additional text description of each case study.

Case study (region)	SO legacy cause		SO response drivers		Affected conditions (stand level, functional group, biogeographical location)	Predominant structural responses
	Climatic legacy	Management legacy	Climatic driver	Other co-drivers		
1. Temperate broadleaved forest (N Patagonia, SW Argentina)	Wet or drought-free growth periods	Fire suppression after settlement	Extreme droughts in the wet season; failure of deep soil water recharge	Summer temperatures	High density stands. Trees with declining growth. Dry edge of species range	Massive partial dieback, tree mortality
2. Temperate evergreen forest (Spain)	Wet or drought-free growth periods	Agricultural and timber exploitation abandonment	Extreme droughts over the baseline trend	Shallow and stony soils, mistletoe, fungal pathogens	High density stands. Dry edge of species range	Premature leaf senescence, delayed tree mortality

3.Temperate forests (SW USA)	Wet or drought-free growth periods	Fire exclusion due to ranching and suppression	Episodic extreme droughts, increasing background drought stress	Temperature, insect outbreaks, fungal diseases, amplified fire	High-density stands and some low density. Trees with declining growth. Large and tall trees. Dry edge of species range	From premature leaf senescence and partial dieback to extensive tree mortality
4. Sub-humid savanna (Queensland, Australia)	Biomass load growth during wet periods of the 1950s and 1970s	Difficult to discern	Intense multiyear droughts	Geology, soils	High density stands. Fast growing dominant species, tall trees, high shoot to root. Core of species range	Massive tree mortality
5. Neotropical rainforests (Amazonia & Central America)	Increased biomass growth during drought-free periods	Increased recruitment when canopies are opened by logging	ENSO-related droughts and low dry season rainfall	Fire, logging, fragmentation	Fast growing dominant trees, tall emergent trees, species with low wood density, non-sprouters	Premature leaf senescence, branch dieback, pulses of tree mortality.

444   Key references used in the case studies **(1)**: Suarez *et al.* (2004), Suarez & Kitzberger (2008, 2010); **(2)**: Galiano *et al.* (2010), Hereş *et al.*

445   (2012), Vilá-Cabrera *et al.* (2013), Aguadé *et al.* (2015); **(3)**: Gitlin *et al.* (2006), Williams *et al.* (2013), Griffin & Anchukaitis (2014), Anderegg

446   *et al.* (2015), Meddens *et al.* (2015), Allen (2016); **(4)**: Fensham & Holman (1999), Fensham *et al.* (2005, 2010), Dwyer *et al.* (2010); and **(5)**:

447   Condit *et al.* (1995), Chazdon *et al.* (2005), Rolim *et al.* (2005), Nepstad *et al.* (2007), Costa *et al.* (2010), Saatchi *et al.* (2013).

Implications for forest prediction, monitoring and management under environmental change

The structural overshoot framework is based upon a straightforward premise: that in plant water economy, resource demand cannot outstrip resource supply for an extended period. When such temporal mismatch occurs, the result is a spectrum of tree dieback and mortality (Fig. 3). The generality of the framework is emphasised by its applicability from tree to forest scales. At the whole-tree scale, tree mortality represents the most extreme response that reduces water demand below the available water supply, resulting in landscape-scale declines in demand through widespread reduction in tree density –analogous to self-thinning at the forest scale (Fig. 4).

Given that current rising mean temperatures are projected to be accompanied by increases in the frequency, magnitude and duration of extreme climatic events, forests across the globe will be exposed episodically to greater drought stress (Adams *et al.*, 2009; Allen *et al.*, 2010; Williams et al. 2015; Allen *et al.*, 2015; Frank *et al.*, 2015). An important implication of projected increases in climatic variability in many regions of the world (IPCC, 2014) is that increased fluctuations in water availability may amplify the degree of structural overshoot. As a consequence, large areas of forest may become at risk of dieback effects, even in cases in which LAI remains approximately constant over time. SO may also be exacerbated by transient increases in productivity due to fertilization effects (CO_2, nitrogen), which likely will contribute to divergences between current and sustainable LAI. Indeed, already-witnessed mortality events are not limited to the hotter and drier margins of species distributions (e.g. Fensham *et al.*, 2015) because tree biomass and/or leaf area is expected to adjust to the maximum supportable by the available resources in any given area (Bonan

473   2002). More variable, hotter drought may then result in water availability becoming either a

474   chronic or acute limiting factor for growth, even in regions of a species' distribution where

475   this was not previously the case (Chapin *et al.*, 1987). Consequently, any reduction in the

476   availability of this critical resource can induce a parallel reduction in live biomass, and

477   specifically in LAI. The SO framework, therefore, provides a clear rationale for why forest

478   mortality episodes are spatially variable and can be sudden – since the mechanism for SO is

479   derived from thresholds of water resource demand and availability (Fig. 4). While the

480   framework allows for a clear qualitative understanding of expected forest-drought responses,

481   additional data are required to move to quantitative predictions of spatiotemporal

482   vulnerability, as we outline below.

483

484   Our SO framework is based on several assumptions. Firstl, we assume that competition for

485   resources is an important determinant of forest demography, ultimately determined by the

486   balance between resource supply and demand. There is overwhelming evidence showing that

487   stand structure, including land-use and management legacies, is a key driver of forest

488   demography (Vilá-Cabrera *et al.*, 2011; Canham, 2014). Second, leaf area index (LAI) and

489   crown leaf area are good proxies for water demand and, therefore, respond to soil water

490   availability and atmospheric water demand (Grier & Running, 1977; Eagleson, 1982;

491   Margolis *et al.*, 1995), with LAI dynamics frequently lagging behind fluctuations in water

492   availability over time (Gholz, 1982; Nemani & Running, 1989; Hoff & Rambal, 2003).

493   Finally, a corollary of the previous points is that temporal mismatches between LAI and

494   water availability (periods in which current LAI is higher than the long-term sustainable

495   value) are associated with increased dieback risk. Although some temporal variation in LAI

496   due to water availability is well-supported by evidence (as we discuss above), to validate our

497   framework the increased dieback risk needs to be empirically tested. This hypothesis can be

498   addressed experimentally by locally modifying the water balance and monitoring the stand-

499   level responses in terms of LAI and tree mortality for a long-enough period of time (e.g.

500   Martin-StPaul *et al.*, 2013). In addition, long-term time series of LAI dynamics from remote

501   sensing may relate increases in LAI to mortality or dieback risk (Van Gunst *et al.*, 2016).

502

503   To realize the predictive potential of our framework, we need to better understand the

504   dynamics and determine locally relevant thresholds of LAI (e.g. Osem & O'Hara, 2016).

505   Most vegetation models use spatially-explicit estimates of LAI as a key input that determines

506   canopy processes and, indirectly, the water balance (e.g. Running & Coughlan, 1988; Cáceres

507   *et al.*, 2015) and some account for feedbacks on LAI dynamics (e.g. Landsberg & Waring,

508   1997). However, inadequate knowledge of LAI drivers and dynamics (including the specific

509   process drivers of premature leaf drop) currently constrains the ability of vegetation models

510   to realistically simulate temporal mismatches between LAI and water availability with

511   sufficient (at least annual) temporal resolution. New developments in remote sensing of LAI

512   (cf. Zheng & Moskal, 2009) will provide opportunities to better link observed spatial and

513   temporal changes in landscape-scale LAI with time-series data of climate drivers (e.g.,

514   precipitation and temperature), thereby supporting development and parameterization of

515   improved empirical and mechanistic models relating changes in LAI with temporal variation

516   in the local water balance, particularly including temporal mismatches and lags (cf. Young et

517   al. 2017). A potential mismatch between LAI values predicted from these models with

518   equilibrium estimates of maximum LAI predicted under different climate scenarios would

519   then enable us to assess the potential for dieback at the stand scale.

520

521   While the potential for our approach to improve spatial predictions of decline risk appears

522   reasonably straightforward, it currently seems difficult to predict the timing of SO responses,

523   as this depends on our ability to precisely quantify LAI thresholds. In any case, the SO

524   framework provides an operative means of complementing studies assessing forest

525   vulnerability from species-level traits (e.g. Anderegg *et al.*, 2016a) by allowing spatially

526   explicit risk assessments within species ranges (cf. Bradford and Bell 2017). Although

527   physiological safety margins should, in principle, provide the best vulnerability estimates

528   (e.g. hydraulic safety margins, Choat *et al.*, 2012; Anderegg *et al.*, 2015), currently we are

529   very far from being able to determine this information at relevant spatial scales and

530   resolutions.

531

532   Nonetheless, it is increasingly being recognised that to adequately determine the status,

533   trends, and magnitude of changes in forests worldwide, there is an urgent need to develop

534   adequate techniques to detect and assess drivers of forest stress and mortality at broad spatial

535   scales (e.g. global forest monitoring, Allen *et al.*, 2010; McDowell *et al.*, 2015; Trumbore *et*

536   *al.*, 2015). Effective monitoring requires continental and global acquisition of data on tree

537   condition and biomass allocation. Furthermore, such data should be available at an

538   appropriate spatial resolution and intervals short enough to allow detection of the full range

539   of forest dieback responses from premature leaf senescence to whole-tree mortality. Given

540   this combined challenge of scale, resolution and frequency of observation, remote sensing

541   must play the major role in such assessments (Jump *et al*., 2010). Increased capabilities for

542   high-resolution mapping and monitoring through time of forest dieback and tree mortality

543   events at landscape and regional scales are emerging rapidly (Hansen *et al.*, 2013; Mascaro *et*

544   *al.*, 2014; Asner *et al.*, 2016; Cohen *et al.*, 2016; Franklin *et al.*, 2016; Mildrexler *et al.*, 2016;

545   Schwantes *et al.*, 2016). Similarly, recent progress in the capabilities for monitoring forest

546   structural characteristics (e.g. Crowther *et al.*, 2015; Zhang *et al.*, 2015; Asner *et al.*, 2016)

547   now provide potential opportunities to better identify current forest vulnerabilities to the

548 spectrum of SO responses to climate variability and change. These new methods offer

549 opportunities to better assess and attribute the processes and drivers of particular forest

550 dieback episodes, which would then provide valuable inputs for empirical models of tree

551 mortality vulnerability at varying spatial resolutions (e.g. De Keersmaecker *et al.*, 2015;

552 Mitchell *et al.*, 2016).

553

554 However, despite the rapid development of remote-sensing products to provide greater spatial

555 resolution, data availability remains problematic owing to the high cost of many products

556 when applied over large areas. Furthermore, we must be able to better estimate LAI and

557 determine LAI dynamics, and to differentiate between different patterns of individual

558 biomass allocation (Zheng & Moskal, 2009). Remotely-sensed data collected over broad

559 spatial scales are generally of too coarse a resolution to allow an understanding of how leaf

560 area of the system is partitioned at the individual, population and community level or what

561 post-drought changes in LAI mean - for example, leaf flushing, epicormic sprouting, or the

562 re-establishment of the same or different species. In principle, fine resolution synthetic

563 aperture radar (SAR) and LIDAR can allow effective monitoring of forest structure, however,

564 the challenge of collecting and analysing such data at an appropriate assessment interval and

565 spatial scale remains.

566

567 Remote sensing must be paired with effective ground-based monitoring through integration

568 of existing national forest inventory data with global monitoring efforts, such as ICP forests.

569 Moreover, plot-level monitoring must be developed to consistently allow assessment of

570 management impacts and tree allometric relationships, together with reporting of premature

571 leaf senescence and partial dieback. Such data would allow us to better forecast changes in

572 forest structure and function related to human intervention, as well as more effectively

573 calibrate remote sensing methods and better interpret the data that result (Jump *et al.*, 2010).

574 Practically, however, ground-based plot-level monitoring will be limited by observation

575 frequency given the intensive effort required for their collection. Nonetheless, the challenges

576 associated with quantity of data needed at appropriate scale, resolution and monitoring

577 interval can be overcome. First, we must develop a better understanding of the spatiotemporal

578 dynamics of LAI and the relative importance of rainfall deficit, increased temperatures and

579 their combination in driving mortality. Less frequent and less intensive monitoring could then

580 be paired with targeted and responsive frequent and high-resolution monitoring of 'at risk'

581 areas determined based on this improved understanding of SO drivers.

582

583 A corollary of the scope for improved forest monitoring is that without such efforts, the

584 occurrence of SO also can complicate determination of the proximate causes of any particular

585 observed pattern of tree structural dieback responses, since the same pattern of risk can be

586 arrived at via differing routes. Lack of adequate monitoring data can, therefore, make it

587 difficult to differentiate the contribution of historical factors (i.e. development of high total

588 canopy leaf area during a preceding wet period) from the main proximate driver of resource

589 stress (e.g. dry moisture conditions). This issue is in addition to the general challenges of

590 interpreting the diverse array of patterns and processes associated with drought-related forest

591 dieback episodes, which emerge from the interactions among a variety of additional tree

592 stressors, in concert with numerous compensatory factors that reduce vulnerability (e.g.

593 Lloret *et al.*, 2012; Allen *et al.*, 2015; Martínez-Vilalta & Lloret, 2016).

594

595 Where monitoring and/or model projections identify forests as vulnerable to the SO spectrum

596 of dieback responses to anticipated climate variability or climate change, management

597 actions can be considered in order to lessen the risk and magnitude of dieback and mortality

598   (Millar *et al.*, 2007; Keenan & Nitschke, 2016). Potential forest management actions to

599   moderate SO include treatments to directly reduce canopy leaf area, tree density, basal area,

600   or even mean tree height by means of mechanical treatments like pre-commercial thinning or

601   commercial timber harvest (D'Amato *et al.*, 2013; Elkin *et al.*, 2015; Giuggiola *et al.*, 2015;

602   Sohn *et al.*, 2016; Bottero et al. 2017; Bradford and Bell 2017). Clearly, SO management

603   should account for the specific benefits (i.e. wood production, catchment water supply, etc.)

604   obtained for a particular forest by paying special attention to LAI changes coupled with

605   climate fluctuations. The addition of prescribed fire to mechanical thinning treatments can

606   sometimes be used to reduce SO stresses (Tarancón *et al.*, 2014). It is interesting to note that

607   frequent-fire-adapted forests can become over-built in ways analogous to SO through human

608   fire suppression, which can increase the risk of high-severity fire in these forests (Enright *et*

609   *al.*, 2015; Allen 2016). In these cases, combinations of mechanical thinning and burning

610   treatments can also increase the persistence and long-term carbon storage of such forests by

611   lowering risks of stand-replacing fires (Allen *et al.*, 2002; Hurteau *et al.*, 2016).

612

613   It is essential to recognise, however, that thinning by mechanical or fire means is not

614   desirable or appropriate in many forest settings for diverse reasons, including ecological,

615   ethical, aesthetic, economic, scientific, conservation, or logistical considerations (McDowell

616   & Allen, 2015). Other management options to lessen forest vulnerabilities to SO-induced

617   dieback range from actions to maintain more water on-site (Grant *et al.*, 2013; Sun & Vose,

618   2016) to possibly modifying the genetic and/or tree species composition of forest stands

619   toward more drought-resistant genotypes or species (e.g. Aitken & Whitlock, 2014; Fares *et*

620   *al.*, 2015). However, any such management options will inevitably be costly and thus even

621   where practical can only be implemented in high-priority stands or locations that should be

622   adequately evaluated at regional and landscape levels (Jump *et al*., 2010).

624 **Conclusions**

625 While we have made substantial progress in understanding the proximate causes of tree

626 mortality in recent decades, our ability to predict drought-induced mortality in space and time

627 remains restricted. The present-day water resource requirements of woody species in any

628 given area are strongly determined by historical factors including past climatic, disturbance

629 and management legacies acting over decades to centuries. Current rapid environmental

630 changes can, therefore, result in structural overshoot through the temporal mismatch of

631 resource requirements from resource availability at local to regional scales. Improved

632 understanding of structural overshoot drivers and processes ultimately will allow more

633 refined model projections of potential dieback responses of Earth's forest ecosystems when

634 combined with climate change and land use projections. Current climate projections of

635 substantially warming temperatures and increased occurrence of extreme drought events and

636 heatwaves (Cai *et al.*, 2015; Duffy *et al.*, 2015; Tebaldi & Wehner, 2016) suggest strong

637 possibilities that current forests, adapted to historic climate regimes, could soon become

638 structurally "overbuilt" for more stressful future climate episodes (Allen *et al.*, 2015;

639 McDowell & Allen, 2015). Given the resulting potential occurrence of substantial overshoot-

640 induced structural dieback responses, ranging from reductions in canopy leaf area and

641 reduced tree heights to turnover of large trees (and even tree species) through mortality of

642 dominant species, better projections of forest structural overshoot responses are essential for

643 predicting changes to ecosystem functions from regional to global scales (Wei *et al.*, 2014;

644 Frank *et al.*, 2015; Anderegg *et al.*, 2016b; Brouwers & Coops, 2016; Mascorro *et al.*, 2016).

645

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652

653 **SUPPORTING INFORMATION**

654 **Appendix S1**. Methods used for the literature review of co-drivers of drought-induced tree

655 mortality.

656 **Appendix S2**. Studies reporting a temporal or spatial modification in the intercept and/or

657 slope of self-thinning lines.

658 **Appendix S3.** Detailed description of case studies documenting drought-induced tree dieback

659 responses relevant to the structural overshoot framework.

660

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