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1   **Tree mortality across biomes is promoted by drought intensity, lower wood density and**

2   **higher specific leaf area**

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45   **Abstract**

46

47   Drought events are increasing globally, and reports of consequent forest mortality are

48   widespread. However, due to a lack of a quantitative global synthesis, it is still not clear

49   whether drought-induced mortality rates differ among global biomes and whether functional

50   traits influence the risk of drought-induced mortality. To address these uncertainties, we

51   performed a global meta-analysis of 58 studies of drought-induced forest mortality. Mortality

52   rates were modelled as a function of drought, temperature, biomes, phylogenetic and

53   functional groups, and functional traits. We identified a consistent global-scale response,

54   where mortality increased with drought severity (log mortality (trees trees^{-1} year^{-1}) increased

55   0.46 (95% CI=0.2-0.7) with one SPEI unit drought intensity). We found no significant

56   differences in the magnitude of the response depending on forest biomes or between

57   angiosperms and gymnosperms or evergreen and deciduous tree species. Functional traits

58   explained some of the variation in drought responses between species (i.e. increased from 30

59   to 37% when wood density and specific leaf area were included). Tree species with denser

60   wood and lower specific leaf area showed lower mortality responses. Our results illustrate the

61   value of functional traits for understanding patterns of drought-induced tree mortality and

62   suggest that mortality could become increasingly widespread in the future.

63

64   **INTRODUCTION**

65

66   Increased frequency and intensity of drought events, defined as deviation from local

67   long-term average climate, are predicted to occur throughout the world as a consequence of

68   global climate change (Dai, 2013; Trenberth et al. 2014). Forest mortality related to extreme

69   drought has already been reported worldwide (Allen et al. 2010, 2015), with potentially far-

70   reaching impacts on forest diversity and function (Slik, 2004), human society and economies

71   (Anderegg et al. 2013; Hanewinkel et al. 2013), biogeochemical cycling (Bonan 2008;

72   Adams et al. 2010), and species distribution (Benito-Garzon et al. 2013). Forests play a major

73   role in driving global climate due to their key role in hydrological cycling (Bonan 2008;

74   Frank et al. 2015) and ability to sequester and store large amounts of carbon (Pan et al. 2011).

75   Evidence already exists for a widespread reduction in carbon sequestration during drought in

76   tropical (Gatti et al. 2014; Doughty et al. 2015) and temperate forest ecosystems (Anderegg et

77   al. 2015).

78

79   There are many examples of drought-induced tree mortality, and several reviews and

80   region-specific syntheses (e.g. Fensham et al. 2009; Allen et al. 2010; Phillips et al. 2010).

81   Additionally, the information gleaned from observational studies of drought-induced tree

82   mortality is supplemented by broad-scale experimental work, which usually allows clearer

83   attribution of causes and deeper mechanistic understanding (Estiarte et al. 2016; Meir et al.

84   2015). There is however, a lack of quantitative synthesis at a global scale. Despite recent

85   syntheses addressing size-dependent mortality (Bennett et al. 2015) and the importance of

86   hydraulic traits in global-scale mortality (Anderegg et al. 2016), it is difficult to discern

87   broad-scale patterns or to predict future responses. While differential mortality is often

88   reported between co-existing species (e.g. Mueller et al. 2005; Ruthrof et al. 2015), and

89   studies have increased our understanding of the physiological mechanisms of tree mortality

90   (Mencuccini et al. 2015; Davi and Cailleret, 2017), there is still a lack of knowledge of

91   drought-induced mortality responses of different tree functional strategies at a global scale.

92

93   Examples of recent mortality related to drought and heat stress exist across all

94   forested continents and major forest types (Figure 1). In Northern temperate forests, high

95   mortality rates are reported for *Pinus sylvestris*, associated with droughts in the 1990s and

96   2000s (Dobbertin et al. 2005; Galiano et al. 2010) and for *Populus tremuloides* in western

97   Canada (Hogg et al. 2008) and in the USA (Worrall et al. 2008; Ganey and Vojta, 2011; Kane

98   et al. 2014). Drought impacts are particularly well known in the Southwest USA (Allen et al.

99   2015), with high mortality of numerous tree species, including: *Juniperis monosperma* (Gitlin

100   et al. 2006), *Pinus ponderosa, Pinus edulis, Pseudotsuga menziesii,* and *Abies concolor*

101   (Ganey and Vojta 2011; Kane et al. 2014). Mortality is also well documented in

102   Mediterranean areas, for example in Spain, high mortality is occurring in *Pinus halepensis*

103   plantations (Garciá de la Serrana et al. 2015), in natural forests in the Sierra Nevada (Herrero

104   et al. 2013) and in Scots pine populations in the Pyrenees and the north east (Vilà-Cabrera et

105   al. 2013). In the southern hemisphere, broad-scale tree die-off events are affecting multiple

106   *Eucalyptus* and *Corymbia* species in Australia (Fensham and Holman, 1999; Rice et al. 2004;

107   Fensham et al. 2009; Matusick et al. 2013) and *Nothofagus* and *Austrocedrus* stands in

108   Patagonia (Suarez and Kitzberger 2008). In tropical areas, extreme droughts associated with

4

109   El Niño-Southern Oscillation events have led to increased mortality in species-rich tropical

110   forests in Asia (Aiba and Kitayama, 2002), Central America (Chazdon et al. 2005) and South

111   America (Williamson et al. 2000) while 2005 and 2010 droughts in Amazonia were also

112   associated with mortality increases (Phillips et al. 2009; Feldpausch et al. 2016).

113

114   Some studies suggest that drought and/or increased temperature impacts on

115   demography will be greatest in, or limited to, already arid ecosystems (Ruiz-Benito et al.

116   2014). Indeed, a synthesis by Anderegg et al. (2015) found evidence of stronger reductions in

117   tree growth after drought in dry ecosystems. Conversely, we could expect that the trees in

118   these drier ecosystems may be more adapted to water stress (Arndt et al. 2015), and that the

119   species growing in generally moister conditions could be most sensitive to extreme drought

120   events (Jump et al. in press). Similarly, individuals growing nearer the dry range edge of their

121   species may be more sensitive, but not necessarily, as local adaptation could play a role in

122   counteracting the effects of drier conditions (Lázaro-Nogal et al. 2016). Current uncertainty

123   about which areas are likely to be the most vulnerable to drought is an obstacle for

124   conservation and management planning, while gaps in our understanding of the physiological

125   explanations for drought-induced mortality, and high variation between locations and species

126   make long-term and broad-scale predictions of forest vulnerability and community

127   composition difficult (McDowell et al. 2013; Meir et al. 2015).

128

129   Drought-induced tree mortality can lead to long-term changes in the composition and

130   structure of forests due to species and age-specific sensitivities (Martínez-Vilalta and Lloret,

131   2016). Cailleret et al. (2013) predict future broad-scale mortality of the dominant tree species

132   *Picea abies* and *Abies alba* and their replacement with *Fagus sylvatica* in response to summer

133   droughts in Bavaria, and Ruthrof et al. (2015) show that *Eucalyptus marginata* is more

134 sensitive to drought than *Corymbia calophylla* in southwestern Australia and predict future

135 compositional shifts. Several examples exist where high mortality of dominant tree species

136 suggests a shift in community composition; montane forests of Switzerland and northern

137 Spain may be undergoing a vegetation shift due to increased drought. *Pinus sylvestris* suffers

138 high mortality and poor regeneration and tends to be replaced by the more drought tolerant

139 *Quercus* species (Galiano et al. 2010; Rigling et al. 2013; Aguade et al. 2015). In the

140 Southwest USA *Pinus edulis* suffers high mortality during drought and *Juniperus* spp are

141 becoming dominant (Mueller et al. 2005), or forest die-off leads to a persistent shift of

142 vegetation type from forest to woodland (Allen and Breshears, 1998). In Patagonia, severe

143 drought events have led to a shift in forest composition, with *Nothofagus dombeyi* being

144 replaced with *Austrocedrus chilensis* (Suarez and Kitzberger, 2008). In extreme cases,

145 changes in drought conditions could potentially lead to a biome shift, resulting in, for

146 example, a seasonally dry tropical forest becoming a savanna, especially when other drivers

147 of change, such as deforestation, act in synergy with drought (Staal et al. 2015).

148

149   Changes in tree species and functional composition directly affect forest structure and

150 functioning, although today there is still debate on which functional groups are the most

151 sensitive to drought. Functional groups are composed of individuals with shared

152 physiological responses to, and impacts on, the environment (Tilman et al. 1997). Individuals

153 are often classified into groups based on shared values of particular traits, with the aim of

154 aiding the prediction of response to changes in environment (Hooper and Vitousek, 1997).

155 Evidence exists for differential response of species depending on functional traits and groups;

156 e.g. Phillips et al. (2010) found a higher sensitivity to drought in larger trees with lower-

157 density wood in tropical forests. The functional composition of these forests is, therefore,

158 expected to shift in favour of smaller trees with denser wood, which could result in a

159   reduction in carbon storage (Stephenson et al. 2014; Fauset et al. 2015). The study of changes

160   in functional composition, and the differential response of species depending on functional

161   traits or broad functional groups, could offer some scope for generalisation of drought

162   response and the mechanisms involved. Indeed, differences in response have been identified

163   based on broad taxonomic and functional groupings; for example, gymnosperms are

164   generally shown to be more sensitive to drought than angiosperms (Anderegg et al. 2015). In

165   Mediterranean and temperate regions of Europe, angiosperms and gymnosperms show

166   contrasting responses to global change. While drying climate reduces growth in both, an

167   increase in temperature and changes in recent management have been associated with

168   increased dominance of angiosperms at the expense of gymnosperms (Gómez-Aparicio et al.

169   2011; Coll et al. 2013; Rigling et al 2013; Vayreda et al. 2016). Widespread evidence also

170   exists that larger trees generally may be more at risk from drought-induced mortality (Phillips

171   et al. 2010; Bennett et al. 2015; McDowell and Allen, 2015). The importance of tree size has

172   been suggested in both observational studies and broad-scale experiments in tropical forests

173   (Nepstad et al. 2007; Rowland et al. 2015). Other traits implicated in drought responses, such

174   as wood density (Pratt et al. 2007), specific leaf area (Valladares and Sánchez-Gómez 2006)

175   and root depth (Irvine et al. 2002, 2004) also are likely to affect tree sensitivity to drought.

176

177   Given the likely impacts of climate change on ecosystem composition and function,

178   there is an urgent need to synthesise data on tree mortality in order to better understand

179   current patterns and predict the impacts on different forest biomes at a global scale. Here we

180   synthesised data from 58 papers including 398 tree species, from 33 locations and 42 drought

181   events worldwide (Figure 1). We modelled mortality data (proportion of standing dead trees

182   and annual rates) in response to drought and temperature, and we explored differences

183   between biomes and functional groups and investigated the influence of specific functional

184 traits. Specifically, we ask: 1) Is there a consistent broad-scale relationship between drought,

185 temperature and forest mortality, or are there significant differences between biomes? 2) Are

186 there differences in mortality based on major phylogenetic or functional groups such as

187 angiosperms/gymnosperms or deciduous/evergreen species? 3) Do functional traits explain

188 variation in species-level mortality?

189

190 **METHODS**

191

192 **A global dataset of forest mortality in response to drought**

193

194 We sought relevant peer-reviewed publications via Web of Science, Google Scholar and

195 Scopus using combinations of the following search terms: "mortality", "drought", "forest",

196 "tree", "dieback", "die-off", "defoliation", "drying" and "climate change". Additional

197 references from the review of Allen et al. (2010) were also included. We screened papers for

198 relevance based on the abstract and saved them for further consideration if they met the

199 general criteria of reporting drought-induced tree mortality. Papers were selected for final

200 inclusion in the meta-analysis if they met the following criteria: 1) mortality data were

201 provided, as a proportion of trees dead, either as a single value based on one survey or as an

202 annualized rate calculated between two or more survey periods; these two types of data were

203 analysed separately. 2) Surveys were ground-based, from aerial photographs or satellite

204 imagery, or a combination of these methods. 3) Mortality was attributed to drought (either

205 one event or a series of events). Experimental studies were only included when the control

206 plots were subject to natural drought during the experimental period and then only the data

207 from these controls were included. 4) The data were collected at the plot level, with a

208 minimum plot size of 0.01 ha, and a minimum number of trees for each species and plot of

209 five individuals. 5) The survey year(s) and the drought year(s) were clearly reported. 6) Cases

210 where mortality occurred due to fire acting in combination with drought were excluded, but

211 studies where biotic interactions such as attack by bark beetles had occurred were included.

212 Finally, 7) mortality was reported for adult trees (not seedlings or saplings) at the species

213 level. Initially, we studied more than 200 drought and mortality relevant papers in detail, and

214 extracted relevant data. Finally, 58 papers met all the inclusion criteria, 30 of these provide

215 annualized mortality rates, and 28 have single survey proportional values of standing

216 mortality. The case studies cover all forested continents and major forest types (Figure 1).

217 Thirty-three different locations (at the geographic scale of country or state in the case of

218 USA) and 42 drought events (location/time combinations) are covered by our dataset.

219 Selection criteria and particularly the need for quantitative mortality information led to

220 several important and broad-scale studies being excluded (e.g. Phillips et al. 2009).

221

222   From each publication, we extracted information on the standing proportional

223 mortality (% dead trees of all trees of each species) or an annual rate of mortality ($m=1-$

224 $(N_1/N_0)^{1/t}$, where N_0 and N_1 are the number of trees present at the beginning and end of the

225 survey interval, t (Sheil et al. 1995)), at the species-level. We report this species-specific

226 mortality as a proportion: trees trees^{-1} year $^{-1}$. We also recorded species identity, geographic

227 coordinates, year of the drought, plot size (ha) and sample size (No. plots and trees). If the

228 information was available, we recorded site data as stand density (No. trees ha^{-1}), soil

229 descriptions (e.g. order/classification, depth, texture) and management history. While such

230 site-specific differences will introduce additional variation into the response of trees to

231 drought, these factors were rarely reported, and we could not incorporate them into the

232 analysis. We were also unable to account for forest age or successional stage, as this was

233   rarely reported. Full information on all studies and species included in the analysis is

234   available in Supporting Information (Appendix S1 and S2).

235

236   **Drought, temperature and functional trait data at a global scale**

237

238   In order to assess the relationship between climate change and mortality we collected drought

239   and temperature data. We calculated drought with the Standardised Precipitation

240   Evapotranspiration Index (SPEI), using the mean SPEI at a 12-month timescale, obtained

241   from SPEIbase v.2.3 (2014) (http://hdl.handle.net/10261/104742). SPEI is a multi-scalar

242   drought index available as a global gridded dataset at a spatial resolution of $0.5°$ and has

243   advantages over other drought indices as it allows for the identification of drought at different

244   temporal scales, whilst also being sensitive to changes in evaporative demand (Vicente-

245   Serrano et al. 2010). It has weaknesses, in that soil properties are not accounted for so it does

246   not include a measure of water extractability, but we chose it here based on the evidence that

247   it outperforms other traditional indices such as PDSI (Palmer drought severity index) and SPI

248   (standardised precipitation index) (Vicente-Serrano et al. 2010; Bachmair et al. 2015; Blauhut

249   et al. 2016). SPEI is calculated based on the difference (D) between monthly precipitation

250   and potential evapotranspiration ($D=P-PET$), with the D values aggregated at different

251   timescales from 3 to 24 months, following a procedure whereby SPEI is expressed as a

252   standardised index, with negative values indicating drought over the timescale considered,

253   relative to median values for a long-term reference period. SPEI currently covers the period

254   January 1901 to December 2014. We chose a 12-month period, as it should identify

255   prolonged droughts, of significance for trees. For temperature, we used monthly data from

256   CRUTEM4 dataset (HadCRUT4, https://crudata.uea.ac.uk/cru/data/temperature/), a global

257   gridded dataset at $0.5°$ spatial resolution (Osborn and Jones, 2014) developed by the Climatic

258   Research Unit (University of East Anglia) and the Hadley Centre (UK Met Office). For each

259   study the climate data described above were extracted for the reported geographical

260   coordinates for seven temporal windows: each of 1-5 years preceding the final date of

261   mortality data collection reported in the study, the period between surveys (only for annual

262   rate data), and the reported drought periods. Mean and minimum values of SPEI and mean

263   and maximum values for temperature were calculated from monthly data for each of these

264   periods for every study. We considered the SPEI for up to 5 years before the mortality

265   occurred because a lag is often reported between drought and subsequent mortality. Although

266   these climatic datasets are excellent resources for our global analysis, the somewhat coarse

267   spatial resolution at which they are available potentially reduces the variation that we can

268   explain since we are unable to consistently describe climate at a finer site-specific scale.

269

270   Each study was categorised into a broad biome type based on geographic location, species

271   composition, climate conditions and forest type. Biome types are broadly based on the

272   categories described by Whittaker (1975). We categorised each study to one of the following

273   types: temperate gymnosperm (mid-high latitude and/or altitude forests composed mainly of

274   gymnosperm species); temperate angiosperm (mid-high latitude and/or altitude forests

275   composed mainly of angiosperm species); Mediterranean and dry woodlands (Mediterranean

276   systems and dry temperate, subtropical woodlands and woodland savanna ecotones); tropical

277   (wet tropical forests). While these biome categories encompass diverse forest types,

278   alternative groupings did not lead to different results when the effect of biome was modelled.

279   We obtained information on phylogenetic groups depending on angiosperm or gymnosperm

280   classification and functional groups depending on leaf phenology/lifespan

281   (evergreen/deciduous) by searching the literature for species information in peer reviewed

282   publications. We obtained functional trait data from the TRY traits database (wood density

283 (WD), specific leaf area (leaf area per unit dry mass; SLA), maximum tree height (MH)

284 (Kattge et al. 2011; Appendix S2)) and from the Royal Botanic Gardens Kew Seed

285 Information Database (seed mass; SM: Royal Botanic Gardens Kew, 2016)). Full trait data

286 was available for 171 of the 398 species in our dataset (see Appendix S2 for species list and

287 data). The subset of species for which trait data were available was similar in terms of the

288 balance between biomes to the full annual mortality dataset (Appendix S3, Table S3.1). For a

289 small number of species, the trait value was extrapolated from the genus level, by averaging

290 the value for three or more species of the same genus (details in Appendix S2). We selected

291 the traits WD, SLA, MH and SM to achieve a balance between drought relevance and data

292 availability. These traits are widely recognised as key traits of plant function and

293 performance; they are relevant to growth, survival and reproduction and can determine

294 species positions along major axes of ecological strategies of resource acquisition and use

295 (Swenson et al. 2012; Díaz et al. 2016). Traits such as P50 (the xylem pressure inducing 50%

296 loss of conductivity; Choat et al. 2012) may be more directly related to drought but hydraulic

297 traits were not available for most species. We show the relationship between WD and SLA

298 and raw mortality (Fig. S3.1 and S3.2 in Appendix S3) and P50 (Figure S3.3). For the species

299 we modelled, we found a weak positive correlation between P50 and WD ($r = 0.2$), and a

300 stronger positive correlation between P50 and SLA ($r = 0.75$ for a logarithmic fit; Figure

301 S3.3). While the TRY traits database represents an excellent resource, we acknowledge that

302 there are limitations associated with the application of species mean values. Variation in

303 study methods, and differences in sample sizes between species occur for traits deposited in

304 TRY, which could lead to some uncertainty around trait values, and there is no consideration

305 of intraspecific variation. Nevertheless, we do not expect such variability to introduce a

306 systematic bias into our analyses.

307

Statistical analysis

We followed a linear, three-step modelling process whereby we determined the effects on species-specific tree mortality of: 1) different timescales of SPEI and temperature; 2) biome and phylogenetic and functional groups; and 3) functional traits. We fitted linear mixed effect models using a normal error distribution and log link following an Information Theoretic Approach (Burnham and Anderson, 2002), where models are ranked based on AIC (Akaike Information Criterion) values. Models were fitted with the lme4 package (Bates et al. 2015) in R 3.2.2 (R Core Team 2015). Annualised and proportional species-level mortality data were log transformed prior to analysis, and were analysed separately due to the different nature of these data types. Since there were some zero values in the dataset, 0.001 was added to every mortality value before transformation.

To be sure of the representativeness of the timescale selected, we determined the effects of different timescales of SPEI and temperature on species-level mortality rate. Mortality was modelled against mean and minimum SPEI and mean and maximum temperature calculated at the seven timescales defined (each of 1-5 years before final mortality data collection, year(s) of reported drought, the years between surveys). The predictor variables were standardised to z scores prior to modelling using the scale function in R, which subtracts the mean and divides by the standard deviation. Models containing different combinations of the timescales of SPEI and temperature were compared with the best model selected through ranking of AICc values (AIC corrected for small sample size, Burnham and Anderson 2004; Bunnefeld and Phillimore 2012), and the importance of fixed effects was assessed through the magnitude of parameter estimates. We consider a reduction of AICc of 2 or more to indicate a significantly better model (Burnham and Anderson, 2004).

333   Additionally, a likelihood ratio test was performed to test the significance of the best model

334   (as indicated by AICc value) compared to a null model containing only random effects, and

335   the next best model in the AICc ranking. SPEI and temperature variables were included as

336   fixed effects in all models, and a study-specific identifier was included as a random intercept

337   to account for multiple species occurring in one study and for the site-specific information

338   such as tree density and soil information that we were unable to include in the models. The

339   different timescales of drought were investigated first through model comparison

340   parameterised only with SPEI, and then temperature was added as an additional fixed effect

341   to the model including the optimum drought timescale.

342

343   Once the most parsimonious combination of climatic fixed effects was determined,

344   the differences between biomes and due to major phylogenetic and functional groups were

345   investigated (i.e. angiosperms/gymnosperms and deciduous/evergreen, respectively). Biome

346   was included as a fixed main effect and angiosperm/gymnosperm, deciduous/evergreen

347   groups were included as a fixed main effect and an interaction term with climate (SPEI and

348   temperature). Each model was compared to the same model without the inclusion of the

349   respective subgrouping, based on model AICc values and likelihood ratio test.

350

351   Finally, the effects of functional traits on drought-induced mortality rates were

352   determined. The four continuous functional traits (specific leaf area, maximum height, wood

353   density and seed mass) were added to the best model identified through the process described

354   above as both fixed effects and fixed effect interactions with climate. All traits were initially

355   included and were sequentially removed based on parameter estimates, model AICc values

356   and likelihood ratio tests, as described above. Prior to analysis, we checked for correlation

357   and collinearity between traits. No pair of traits was significantly correlated (maximum r of

358   0.15 for WD and SLA) or collinear (maximum variance inflation factor (VIF; Dormann et al.

359   2012) of 1.2). We also used PCA to investigate trait collinearity and to determine if any

360   combination of traits represented a certain functional strategy. No consistent strategies were

361   identified (Table S3.2, Appendix 3). Trait data were standardised to z scores before

362   modelling to allow parameter estimates to be compared. These functional trait models were

363   fitted based on a subset of the data for which the functional trait data were available (171 of

364   398 species), so AICc values are not comparable with the full optimum model.

365

366   To better explore the direction of the important trait interaction effects identified

367   through the above modelling process, predicted values based on models including each trait

368   individually were plotted as 3D surface plots. These 3D plots were created in SigmaPlot

369   (SigmaPlot v. 12.5 Systat software, San Jose); all other plots were created in R 3.2.2. (R Core

370   team 2015).

371

372   **RESULTS**

373

374   The available standing proportional mortality data are based on single surveys and are limited

375   in their value because it is not possible to determine the date of death, since the trees standing

376   dead at one point in time may have died over a wide range of dates. Therefore, only the

377   results from the analysis of annualised data, which could be attributed to specific drought

378   events, are presented here. However, the results of this analysis were largely consistent with

379   those for standing proportional mortality. The results for standing proportional mortality data,

380   which were analysed separately, are available in Appendix S4.

381

382   Annualised mortality data consisted of 30 studies, 308 species and 27 drought events

383   (Figure 1; Appendix S1). Drought intensity of the reported drought event was highest in

384   Arizona in 2000-2004 with a SPEI value of -3.3 (a monthly mean value; Negron et al. 2009)

385   and lowest in Costa Rica at -0.8 in 1997-1998 (Chazdon et al. 2005). Annual mortality rates

386   (species-level) varied between 0.4 trees trees^{-1} yr^{-1} (Negron et al. 2009) and zero (various

387   sources).

388

389   **Relationship between mortality, drought intensity and temperature**

390

391   The observed SPEI values for the studies included in our analysis show some divergence

392   from global values. A comparison of the distribution of SPEI associated with the study areas

393   and mortality events, relative to the global values over the full time period covered by the

394   studies (1977-2014), shows more negative SPEI values for the time periods associated with

395   reported mortality events (the 5 years before final mortality surveys). There is, however, a

396   large degree of overlap in the distributions of SPEI for the study period and the five years

397   preceding the reported mortality event (Appendix S5).

398

399   The mean SPEI of the reported drought years was the best climatic predictor of annual

400   mortality (Table 1). We identified a consistent response to drought that occurred across all

401   biomes, with mortality increasing as values of SPEI decreased, i.e. as drought, defined as

402   deviation from a long term mean, became more intense (Figure 2a, b). There is little support

403   for the inclusion of biome as a fixed interaction with drought (ΔAICc = 3.2) and the

404   parameter estimates for biome comparisons suggests that the difference in mortality between

405   biomes is small (Figure 3).

406

Functional groups, phylogenetic groups and functional trait effects on drought-induced

tree mortality

We detected no significant difference in the response to drought between angiosperms and

gymnosperms or deciduous and evergreen species. The inclusion of these groups as fixed-

effect interaction terms with SPEI did not improve the model (AICc increased by 0.2 and 0.7,

respectively) and parameter estimates suggest no difference in drought mortality response

(Figure 4a, b).

The functional traits WD and SLA influenced the drought-induced mortality response;

the inclusion of these traits improved the model compared to one that included drought

effects alone (Table 2; Figure 5a, b). However, MH and SM did not correlate with drought

responses (Table 2). Drought-induced mortality was higher among species with lower values

of WD (Figure 6a) and higher values of SLA (Figure 6b). We observed that the slope of

interaction with WD was highest at very negative values of SPEI (more severe drought). For

the interaction with SLA it is stronger at higher values of SPEI, (i.e. when drought is less

severe), and the relationship is reversed compared to that seen at more negative values of

SPEI, where mortality is slightly lower when SLA is higher (Figure 6b).

DISCUSSION

Global-scale patterns of drought-induced mortality

We found a consistent response of tree mortality to drought across biomes, indicative of a

global-scale threat to forests from drought, which is consistent with the widespread nature of

432   recent reports of forest mortality (e.g. Allen et al. 2010, 2015). The fact that we find evidence

433   for a linear increase in log (mortality) (Figures 2 and 5a) with increasing drought intensity

434   means that the relationship with SPEI is exponential and, therefore, increases in drought

435   could have critical consequences for forests. This result is indicative of a threshold response,

436   and contrasts with other broad-scale studies that have suggested a linear relationship between

437   mortality and drought (e.g. Phillips et al 2010). Such a response at the species-level seems

438   realistic, given what we know of responses to drought intensity in individual studies (e.g.

439   Meir et al. 2015). Note, however, that the shape of the drought-mortality response is likely to

440   differ depending on the metric used to characterize drought intensity.

441

442   Our study is the first to identify a global-scale effect of drought intensity on tree mortality at

443   the species-level; previous syntheses have either been limited geographically (Fensham et al.

444   2009; Phillips et al. 2010), or have focused on drivers such as size-dependence of mortality

445   (Bennett et al. 2015) and the influence of hydraulic traits (Anderegg et al. 2016), rather than

446   global patterns. It has been suggested that only dry forests are at risk from drought-induced

447   mortality (Steinkamp and Hickler, 2015). Studies of tree growth have shown responses to

448   drought occurring across the northern hemisphere, although with differences in timescale of

449   response depending on long-term average aridity (Vicente-Serrano et al. 2014). Recent work

450   provides a physiological basis for this global-scale vulnerability to drought-induced

451   mortality, indicating that some 70% of forest species operate at narrow hydraulic safety

452   margins irrespective of biome (Choat et al. 2012). Therefore, species in both arid and mesic

453   habitats could be at high risk of embolism and related mortality if drought increases.

454

455   Our synthesis suggests that there is little difference between angiosperms and

456   gymnosperms or between evergreen and deciduous species in the response of mortality to

457 drought, in line with a recent synthesis by Anderegg et al. (2016). Our global-scale analysis

458 complements that of Anderegg et al. (2016) as these authors use a strict meta-analytic

459 approach by comparing species within a study and consider hydraulic traits, while we focus

460 on a range of traits that are more available and have broad applicability because they relate to

461 multiple aspects of plant functioning (Díaz et al. 2016). We also account explicitly for

462 drought intensity through the inclusion of SPEI data in our models. The fact that we obtain

463 some common results, despite the different methods applied, gives increased support to both

464 analyses. Although our selection of traits allowed for a large sample size, given the greater

465 availability of data, there are certain drawbacks to consider, as the traits we study are unlikely

466 to be directly related to drought-mortality responses. The use of traits with a stronger

467 mechanistic basis (e.g., hydraulic traits) for which the relationship with drought-induced

468 mortality is more direct is probably preferable when they are available.

469

470   While the global scale of our study is valuable for identifying broad-scale patterns, we

471 acknowledge that the range of species and biomes included may have led to a masking of

472 differences between groups, since in some cases the advantages of one functional strategy in

473 one biome may not be applicable in another. For example, to be an evergreen species has

474 different implications in temperate *versus* tropical forests. Furthermore, the small sample size

475 and associated statistical limited power also may have constrained our ability to find

476 differences between biomes and functional and phylogenetic groups. Despite these potential

477 limitations, the global patterns that we identify and their congruence with related work by

478 other authors demonstrates the value of this work for increasing our understanding of forest

479 drought risk worldwide.

480

481 **Functional traits mediate drought response**

482

483   Our results suggest that high wood density can be associated with lower susceptibility to

484   drought. Although wood density is a complex trait that may be associated with many

485   ecological signals (Broderson, 2016; Gleason et al. 2016) this finding is substantially in

486   accordance with reported functionality of this trait. Wood properties correlated with density

487   affect water storage and transport, because the width and length of conduits determines

488   hydraulic conductance (Chave et al. 2009) and wood density affects mechanical stability and

489   is associated with resistance to drought-induced cavitation (Hacke et al. 2001; Pratt et al.

490   2007). In a study of saplings and seedlings from dry tropical forest, Markesteijn et al. (2011)

491   found a lower vulnerability to cavitation (an ability to withstand more negative P50) in

492   species with higher wood density. They also found evidence for a trade-off between

493   cavitation resistance and hydraulic conductivity, suggesting that the ability to withstand

494   drought leads to a competitive disadvantage during times when water is not limiting.

495   However, weak support was found for this trade-off in a global synthesis by Gleason et al.

496   (2016), which showed that many species can have both low hydraulic conductivity and low

497   cavitation resistance, and that high wood density is not necessarily associated with low

498   conductivity and high cavitation resistance. Generally, species with high wood density are

499   associated with lower growth rates and lower background mortality rates (Chave et al. 2009).

500   The results of our study show that this strategy can lead to lower mortality rates when

501   exposed to drought stress. In contrast to our findings, Hoffmann et al. (2011) found that

502   although species with higher density wood had higher cavitation resistance, their mortality

503   under drought was higher, due to an inability to prevent declines in water potential, compared

504   to species with less dense wood. Hoffmann et al. studied the response to an especially severe

505   drought at the community level, whereas we consider a wide range of drought conditions and

506   vegetation types, suggesting that differences in overall drought severity and spatial scale

507   might explain the differences between the results that they report and those presented here. It

508   is notable that despite the complexity of this trait and its relationship with hydraulic

509   performance, we still find a significant, although noisy, global signal.

510

511   Our analyses provide evidence that tree species with high specific leaf area can be

512   more susceptible to drought-induced mortality than species with lower specific leaf area,

513   although the nature of the relationship varied with drought severity. Specific leaf area

514   determines plant response to changing resource availability (i.e. water and light),

515   photosynthetic potential and growth rates (Poorter et al. 2009). Depending on stomatal

516   properties, higher specific leaf area could imply a higher potential for leaf water loss; in

517   contrast, a low specific leaf area is often associated with xeromorphic plants, adapted to high

518   water stress (Bussotti et al. 2015). Furthermore, woody species associated with arid niches

519   are characterised by relatively lower specific leaf area in the Mediterranean (Costa-Saura et

520   al. 2016). An experimental study by Valladares and Sánchez-Gomez (2006) showed within-

521   species lower specific leaf area if seedlings were exposed to drought, although across species,

522   a high specific leaf area was associated with greater drought tolerance. Reducing specific leaf

523   area under prolonged drought conditions seems to be consistent across species and studies

524   (Poorter et al. 2009) and is suggestive of a higher resistance to drought in plants with a lower

525   specific leaf area. Although we identify a global-scale signal in the relationship between

526   drought and SLA, as for wood density, many ecological signals are associated with SLA

527   making this relationship highly complex. In the future, the integration of directly relevant

528   traits such as P50 could improve the approach taken here.

529

530   Several studies have shown that larger trees could have lower resistance to drought

531   (e.g. Bennett et al. 2015). For example, an experimental drought in a Brazilian Amazonian

532   rainforest resulted in much larger increases in the mortality rates of larger trees compared to

533   smaller ones (Nepstad et al. 2007; Rowland et al. 2015) and a pan-tropical analysis also

534   revealed that larger trees tend to suffer most during drought (Phillips et al. 2010). A global-

535   scale synthesis by Bennett et al. (2015) shows that drought-related mortality is generally

536   greater in larger trees; they analysed drought mortality related to DBH, but they hypothesised

537   that the relationship is due to height effects. However, in our global-scale analysis that

538   explicitly included species maximum height, we did not find a strong effect due to tree

539   height. This apparent contrast might be because the importance of the other traits that we

540   considered overwhelmed any effect of height, but it also could be due to the different

541   approach taken in our study compared to that of Bennett et al. Our analysis was based on

542   species-level maximum height, while their study used size classes at the plot level

543   irrespective of species. Future work should seek to incorporate individual-level tree heights

544   and stand age, as this will provide the most direct assessment on the importance of tree size.

545

546   **Implications**

547

548   Our results suggest that at a global scale, trees with lower wood density and higher specific

549   leaf area tend to be more sensitive to drought. Future increases in the intensity and duration

550   of drought events could therefore lead to changes in forest composition and structure, with

551   implications for forest diversity and ecosystem function. Changes in functional diversity due

552   to the drought sensitivity of different species will also affect forest functioning and drought

553   resilience (Laureto et al. 2015). Forests are an important global carbon sink (Pan et al. 2011)

554   and changes in forest energy exchange could have major consequences for global climate

555   (Frank et al. 2015). Wood density and specific leaf area are both traits that are important for

556   carbon sequestration (Prado-Junior et al. 2016) and storage in aboveground biomass (Chave

557   et al. 2014). It is, therefore, important to consider the impacts that the greater vulnerability

558   associated with particular values of these traits under drought conditions could have on

559   broad-scale carbon storage (Finegan et al. 2015). Generally, higher biomass might be

560   expected to be stored in ecosystems rich in species with levels of these traits associated with

561   high growth rates (low wood density and high SLA (Grime 1998)), but this is context

562   dependent. For example, in dry tropical forests, species with high wood density and low

563   specific leaf area are associated with high growth rates and carbon storage, precisely because

564   they can continue to function during drought (Prado-Junior et al. 2016). Our results also have

565   successional implications; early successional tree species are characterised by low wood

566   density and high specific leaf area (Aiba et al. 2016). If disturbance increases due to drought-

567   induced mortality, then these early successional species could dominate forests, making the

568   community more susceptible to future die-off.

569

570   Our synthesis identifies global-scale drought-induced tree mortality responses, and our

571   analyses of species-specific mortality rates with climate and functional trait data provide

572   quantitative insights into global-scale patterns. However, our best model only explained 37%

573   of the variation in mortality rate. To reliably assess the impact of drought events, and to

574   predict the consequences for forests in the future, effective long-term monitoring across a

575   wide range of forest types is required. In addition, detailed reporting of site conditions would

576   allow future syntheses to consider the importance of factors such as tree density in drought-

577   induced mortality at a global scale (Jump et al. in press). Here, we identified drought-induced

578   mortality responses worldwide that are species-specific, but further analysis depending on

579   stand and tree level characteristics are critical to adequately identify and manage vulnerable

580   forests. Additionally, the consideration of intra-specific variation in functional traits could

581   significantly improve our ability to predict the responses of forests to future drought. The

582   traits we have identified as critical for drought resistance at a global scale are known to vary

583   within species across environmental gradients (Fajardo and Piper, 2011), thus trait variation

584   across environmental gradients (e.g. Vilà-Cabrera et al. 2015) should be incorporated in

585   future models to better predict climate change impacts in forests worldwide. Although our

586   results do not have high predictive power in themselves, they provide an advance, since our

587   current ability to predict drought-induced mortality is limited (Meir, Mencuccini and Dewar,

588   2015) and this prediction needs global assessment. Our study highlights the global

589   vulnerability of forests to drought-induced tree mortality and shows that widely available

590   functional traits, such as wood density and specific leaf area, can improve explanatory power.

591

592   **Conclusion**

593

594   Based on a synthesis of studies of drought-induced tree mortality events at a global scale we

595   find evidence of greater forest mortality risk from more severe droughts, consistent across

596   biomes and major functional groups. Using functional traits, we could explain an additional

597   fraction of the variation in drought-induced tree mortality. Trees with less dense wood and

598   high specific leaf area may be most at risk. These results further illustrate the value of

599   species-level trait data for understanding general trends in species responses. Overall, our

600   findings indicate that, with increasingly severe future droughts projected, associated drought-

601   induced tree mortality could become increasingly widespread, with significant implications

602   for forest diversity, ecosystem function and climate feedbacks.

603

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1220 **SUPPORTING INFORMATION**

1221 **Appendix S1:** Information on the studies and species included in the meta-analysis

1222 **Appendix S2:** Species list, mean trait values, A/G and D/E classification and sources of trait

1223 data, including citations and details of the species for which data was extrapolated from the

1224 genus level.

1225 **Appendix S3:** Trait data information: biome representation, raw mortality against traits,

1226 relationship between wood density and specific leaf area and P50, TRY trait reference list.

1227 **Appendix S4**: Model results from single survey proportional mortality data analysis.

1228　**Appendix S5**: SPEI distribution of study areas compared to global values over the same

1229　period.

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1232　**TABLES**

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1234　Table 1: Model comparison using AICc values (AIC corrected for small sample size) and

1235　parameter estimates for sets of models used to identify the optimum model(s). The 95%

1236　confidence intervals associated with the parameter estimates are shown for the fixed effects

1237　in the best model, highlighted in bold. SPEIm represents mean SPEI and TEMPm mean

1238　temperature. Confidence intervals were calculated with boot strapped resampling. The

1239　random effect included in these models was a study specific identifier. Results of likelihood

1240　ratio tests (P-values) are shown for the best models compared to the null model (one

1241　including only random effects) and the next best model, as indicated by AICc values.

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Fixed effect(s)	Parameter estimate(s) (95% CI)	AICc	ΔAICc	R^2 marginal/ conditional	P-value
SPEIm drought years	**-0.46 (-0.7 to -0.2)**	**1876.7**	**0.0**	**0.06/0.29**	**0.0005; <0.0001**
SPEIm between survey years	-0.43	1880.1	3.4	0.05/0.32	
SPEIm drought + TEMPm 3 years pre survey end	-0.46; -0.01	1880.3	3.6	0.06/0.30	
SPEIm drought + TEMPm 5 years pre survey end	-0.46; 0.002	1880.3	3.6	0.06/0.30	

SPEIm drought + TEMPm 2 years pre survey end	-0.46; -0.007	1880.3	3.6	0.06/0.30
SPEIm drought + TEMPm 4 years pre survey end	-0.46; 0.0009	1880.3	3.6	0.06/0.30
SPEIm drought + TEMPm between survey years	-0.46; 0.01	1880.4	3.7	0.06/0.30
Min SPEI drought years	-0.45	1880.5	3.8	0.06/0.34
Min SPEI 2 years pre survey end	-0.54	1880.8	4.1	0.03/0.33
SPEIm + maximum temperature 2 years pre survey end	-0.46; -0.04	1880.8	4.1	0.06/0.30
SPEIm + maximum temperature 3 years pre survey end	-0.46; -0.01	1880.9	4.2	0.06/0.30
SPEIm + maximum temperature 4 years pre survey end	-0.45; 0.01	1880.9	4.2	0.06/0.30
SPEIm + maximum temperature 5 years pre survey end	-0.45; 0.01	1880.9	4.2	0.06/0.30
SPEIm drought + maximum temperature between survey years	-0.45; 0.009	1880.9	4.2	0.06/0.30
Minimum SPEI between	-0.39	1881.5	4.8	0.04/0.34

survey years				
Min SPEI 3 years pre survey end	-0.32	1883.0	6.3	0.03/0.33
Min SPEI 4 years pre survey end	-0.30	1883.3	6.6	0.03/0.32
Min SPEI 5 years pre survey end	-0.31	1883.3	6.6	0.03/0.33
SPEIm 2 years pre survey end	-0.24	1883.8	7.1	0.02/0.31
SPEIm 3 years pre survey end	-0.27	1884.3	7.6	0.02/0.30
SPEIm 5 years pre survey end	-0.19	1885.8	9.1	0.01/0.31
SPEIm 4 years pre survey end	-0.15	1887.0	10.3	0.006/0.31

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1257 Table 2: Model comparison and selection when considering functional traits and drought

1258 response. AICc values (AIC corrected for small sample size) and parameter estimates for sets

1259 of models used to identify the optimum model. SPEIm represents mean SPEI. The model

1260 containing the best combination of fixed effects is shown in bold. The traits considered are

1261 wood density (WD), specific leaf area (SLA), maximum height (MH) and seed mass (SM).

1262 The results of likelihood ratio tests are shown for the best model (P-value), compared to a

1263 null and the next best model. Here the null model for comparison contains random effects and

1264 the fixed effect of mean SPEI of the drought.

1265

Fixed effect(s)	Parameter estimate(s)	AICc	ΔAICc	R^2 marginal/conditional	P-value
SPEIm drought + SPEIm drought x WD + SPEIm Drought x SLA	**-1.28 (-2.04 to -0.52)** **0.38 (-0.2 to 0.97)** **-0.41 (-0.95 to 0.13)**	**1013.5**	**0.0**	**0.14/0.37**	**0.001; 0.01**
SPEIm drought + SPEIm drought x WD	-1.19; 0.39	1014.8	1.3	0.10/0.33	
SPEIm drought + SPEIm drought x SLA	-1.22; -0.38	1015.7	2.2	0.09/0.34	
SPEIm drought	-1.14	1016.6	3.1	0.06/0.30	

SPEIm drought + SPEIm drought x WD + SPEIm drought x MH	-1.26; 0.26; -0.63	1016.6	3.1	
SPEIm drought + SPEIm drought x WD + SPEIm drought x SLA + SPEIm drought x MH	-1.28; 0.27; -0.26; -0.53	1016.8	3.3	0.15/0.37
SPEIm drought + SPEIm drought x SLA + SPEIm drought x MH	-1.24; -0.22; -0.56	1019.7	6.2	0.10/0.33
SPEIm drought + SPEIm drought x (WD, SLA, MH, SM)	-1.28; 0.37; -0.27; -0.5; -0.21	1022.8	9.3	0.16/0.38
SPEIm drought + SPEIm drought x SM	-1.17; -0.12; 0.02	1022.9	9.4	0.07/0.31

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FIGURES

Figure 1: Locations of the studies included in the analysis. Dark grey shading indicates studies
providing annual rates of mortality based on two or more surveys and light grey standing proportional
mortality values based on a single survey (these are analysed separately with annual mortality rate
analyses presented in the main text and single survey proportions presented in supporting
information). The biome category of each study is indicated by shape. Temperate gymnosperms:
diamonds, temperate angiosperms: triangles, Mediterranean and dry woodlands: circles and tropical:
squares. Annual mortality studies: Aiba and Kitayama, 2002; Chazdon et al. 2005; Condit et al 1995;
da Costa et al. 2010; Dobbertin et al. 2005; Faber-Langendeon and Tester 1993; Fan et al 2012;
Ganey and Vojta 2011; Granzow de la Cerda et al. 2012; Gu et al 2015; Hogg et al. 2008; Huang et al.
2010; Itoh et al. 2012; Kane et al. 2014; Kardol et al. 2010; Klos et al. 2009; Kukowski et al. 2013;
Mueller et al. 2005; Nakagawa et al. 2000; Negron et al. 2009; Newbery and Lingenfelder 2008;
Olano and Palmer, 2003; Potts, 2003; Poulos, 2014; Smith et al. 2015; Tafangenyasha, 1997;
Tsopelas, 2001; Tsopelas et al. 2004; van Nieuwstadt and Shiel, 2005; Worall et al. 2008. Single
survey proportional mortality studies: Aakala et al. 2011; Becker et al. 1998; Bowker et al. 2012;
Cailleret et al. 2013; Fensham, 1998; Fensham and Holman, 1999; Floyd et al. 2009; Foden et al.
2007; Garcia de la Serrana et al. 2015; Gitlin et al. 2006; Heitzman et al. 2007; Khan et al. 1994;
Koepke et al. 2010; Linares et al. 2011; Lwanga, 2003; Markalas, 1992; Martínez Vilalta and Pinol,
2002; Matusick et al. 2013; Millar et al. 2012; Mokria et al. 2015; Rice et al. 2004; Savage, 1997;
Slik, 2004; Suarez and Kitzberger, 2008; Twidwell et al. 2014; Viljoen, 1995; Vincke et al. 2010;
Zegler et a. 2012.

Figure 2: Annual observed mortality data at species-level plotted against mean SPEI for the

reported drought years (a), and log-scale annual observed mortality against mean SPEI for the

reported drought year, including the model prediction using the parameter estimate for the

best model with 95% confidence intervals (b). More negative values of SPEI indicate more

severe drought.

Figure 3: Parameter estimates for the model including mean SPEI of the reported drought

years and biome as fixed effects to test if drought induced mortality varies by biome. The

parameter estimates show the difference in the mortality response to drought of each biome

with 95% confidence intervals, calculated using bootstrapped resampling. Sample sizes

(number of studies) by biome are as follows: temperate gymnosperms: five, temperate

angiosperms: eight, Mediterranean and dry woodlands: seven and tropical: ten.

1303   Figure 4: Parameter estimates for the models including mean SPEI of the reported drought

1304   years and the groups angiosperms/gymnosperms (a) and evergreen/ deciduous (b) as fixed

1305   effect interactions with mean SPEI. 95% confidence intervals are shown, calculated using

1306   bootstrapped resampling.

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1308   Figure 5: Relationship between predicted annual mortality and drought (solid line) with 95 %

1309   confidence (dotted lines) based on the best model including the effect of climate and its

1310   interaction with species-level functional trait data (WD and SLA). This is based on a subset

1311   of the mortality data, for which trait information was available (a). Parameter estimates for

1312   each of the fixed effects included in the best trait model, with 95% confidence intervals,

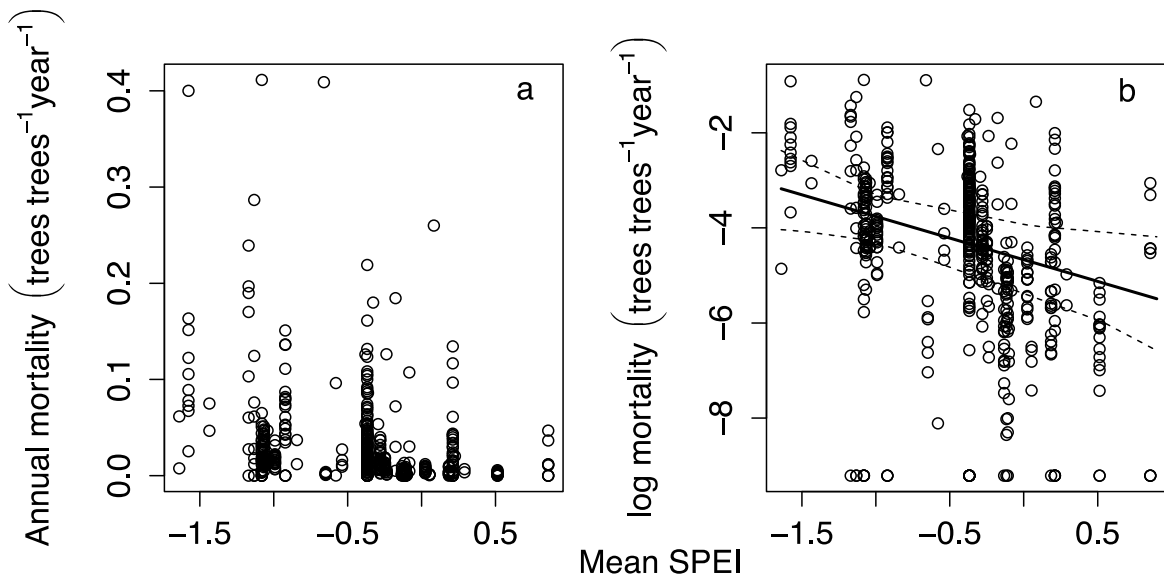1313   calculated using bootstrapped resampling (b).

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1315   Figure 6: The effect of the interaction of mean SPEI of the reported drought years with wood

1316   density (WD) (a) and specific leaf area (SLA) (b) on log drought-induced tree mortality (trees

1317   trees $^{-1}$ year $^{-1}$).

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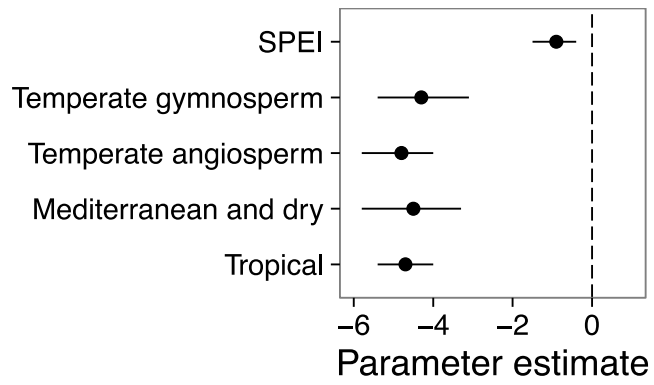1319

Figure 1

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Figure 2

Parameter estimate

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Figure 3

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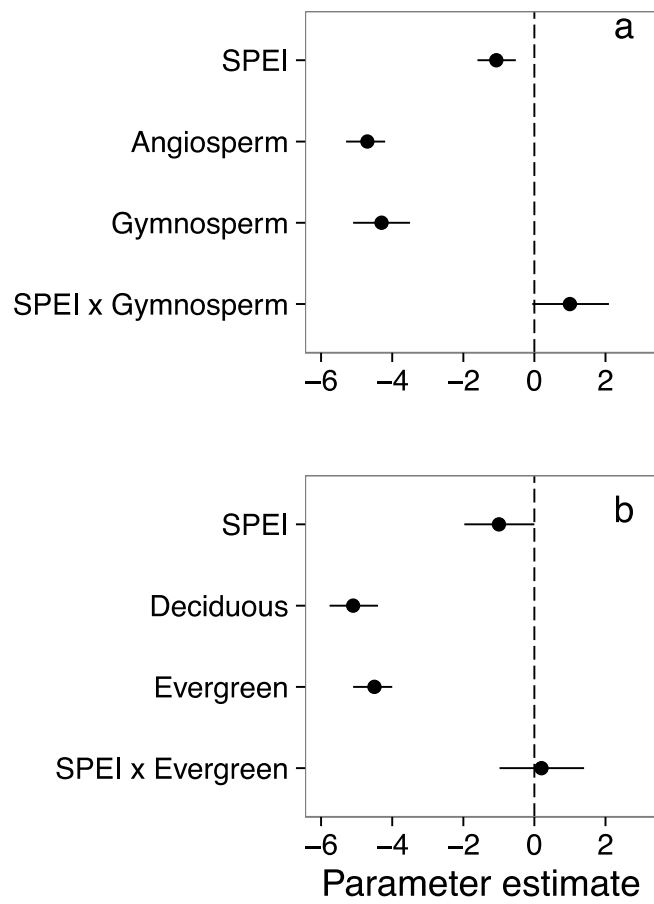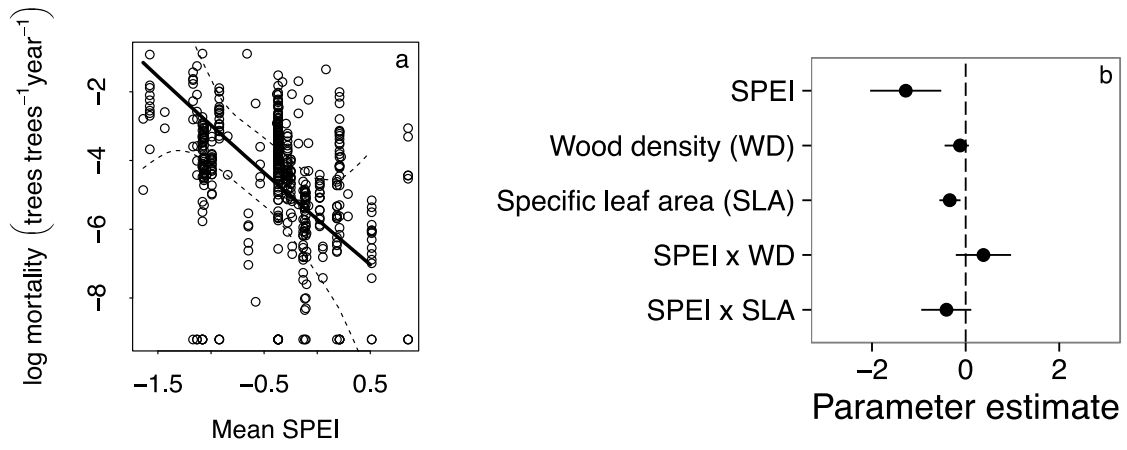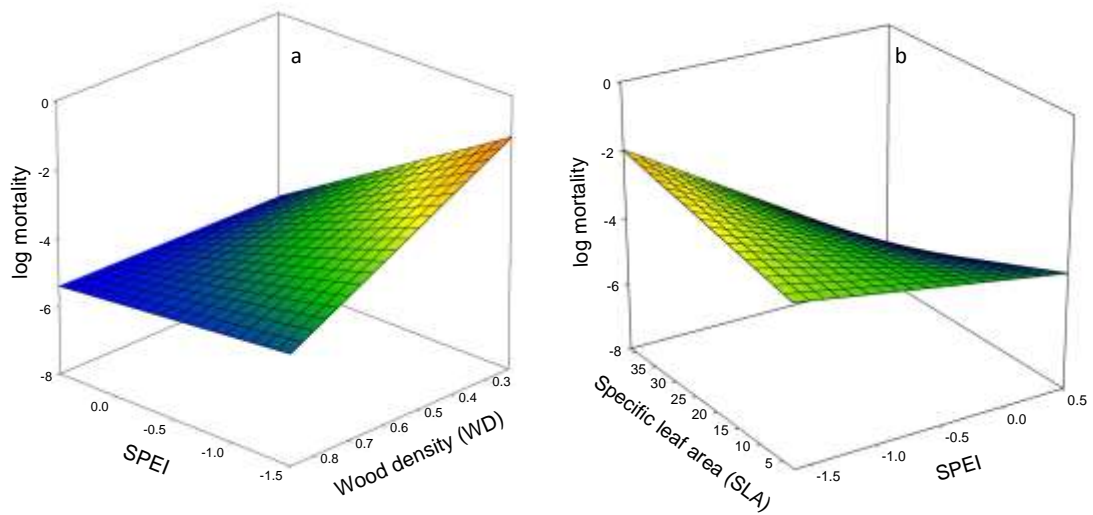Parameter estimate
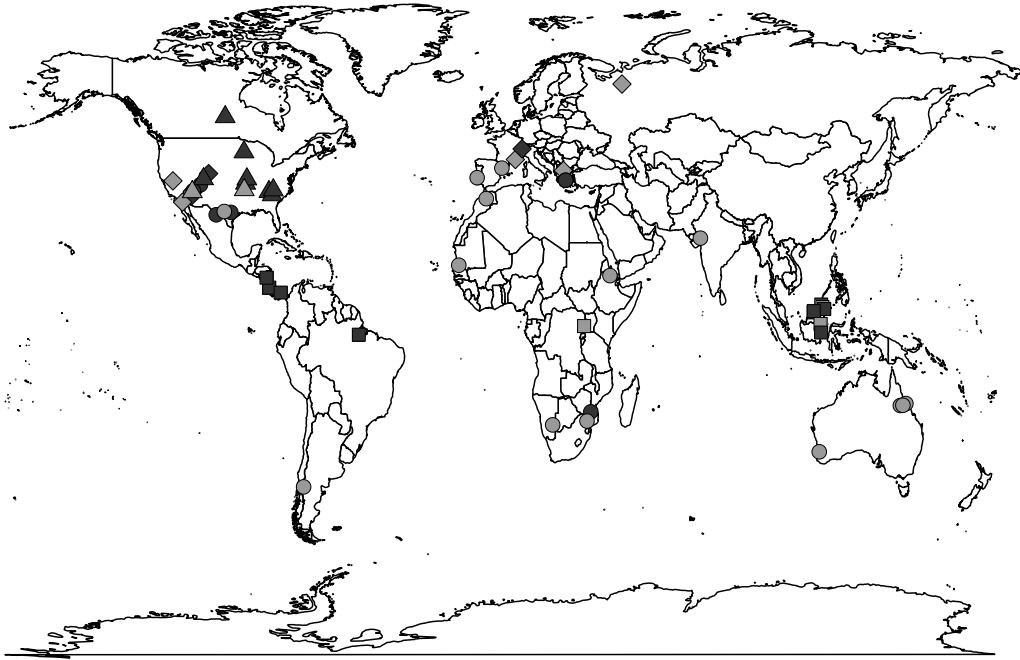
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Figure 4

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1330 **Figure 5**

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