1 **DROUGHT-INDUCED VEGETATION SHIFTS IN TERRESTRIAL ECOSYSTEMS: THE KEY ROLE OF**

2 **REGENERATION DYNAMICS**

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Abstract

Ongoing climate change is modifying climatic conditions worldwide, with a trend towards drier conditions in most regions. Vegetation will respond to these changes, eventually adjusting to the new climate. It is unclear, however, how close different ecosystems are to climate-related tipping points and, thus, how dramatic these vegetation changes will be in the short- to mid-term, given the existence of strong stabilizing processes. Here, we review the published evidence for recent drought-induced vegetation shifts worldwide, addressing the following questions: (i) what are the necessary conditions for vegetation shifts to occur? (ii) How much evidence of drought-induced vegetation shifts do we have at present and where are they occurring? (iii) What are the main processes that favor / oppose the occurrence of shifts at different ecological scales? (iv) What are the complications in detecting and attributing drought-induced vegetation shifts? (v) What ecological factors can interact with drought to promote shifts or stability? We propose a demographic framework to classify the likely outcome of instances of drought-induced mortality, based upon the survival of adults of potential replacement species and the regeneration of both formerly dominant affected species and potential replacement species. Out of 35 selected case studies only eight were clearly consistent with the occurrence of a vegetation shift (species or biome shift), whereas three corresponded to self-replacements in which the affected, formerly dominant species was able to regenerate after suffering drought-induced mortality. The other 24 cases were classified as uncertain, either due to lack of information or, more commonly, because the initially affected and potential replacement species all showed similar levels of regeneration after the mortality event. Overall, potential vegetation transitions were consistent with more drought-resistant species replacing less resistant ones. However, almost half (44%) of the vegetation trajectories associated to the 35 case studies implied no change in the functional type of vegetation. Of those cases implying a functional type change, the most common one was a transition from tree- to shrub-dominated communities. Overall, evidence for drought-induced vegetation shifts is still limited. In this context, we stress the need for improved, long-term monitoring programs with sufficient temporal resolution. We also highlight the critical importance of regeneration in determining the outcome of drought-induced mortality events, and the crucial role of co-drivers, particularly management. Finally, we illustrate how placing vegetation shifts in a biogeographical and successional context may support progress in our understanding of the underlying processes and the ecosystem-level implications.

64

1. Introduction

66 The distribution of vegetation is largely determined by climate and, in particular, by

67 temperature and water availability (Woodward, 1987). Ongoing climate change is modifying

68 climatic conditions worldwide, with a general trend towards warmer temperatures globally

69 and lower water availability in many regions of the Earth (IPCC 2014). Increased frequency of

70 intense and hotter droughts have already been associated with widespread episodes of

71 vegetation die-off (Allen et al., 2010, 2015) and with increases in background (non-

72 catastrophic) forest mortality rates in some areas (Mantgem et al., 2009; Peng et al., 2011).

73 There is no doubt that widespread plant mortality could result in dramatic modifications in

74 forests and other vegetation types, impacting the ecosystem services they provide to society

75 (Anderegg et al., 2012). It is also clear that ecosystems will eventually adapt to the new

76 climatic conditions. What is less clear, however, is how dramatic these changes will be, given

77 the existence of strong stabilizing processes and the relatively high capacity of vegetation to

78 absorb disturbances avoiding major changes in structure, composition and function (Connell

79 and Ghedini, 2015; Lloret et al., 2012; Reyer et al., 2015). In particular, it remains to be

80 established how close different ecosystem types are to climate-related tipping points and how

81 likely it is that they suffer catastrophic regime shifts (Scheffer et al., 2001) under current and

82 future climate conditions.

83

84 Here, we review the published evidence for recent drought-induced vegetation shifts

85 worldwide, at any spatial scale ranging from local to continental. We first provide some

86 background on the relationship between climate and vegetation distribution from a

87 biogeographical perspective, focusing on drought. We then outline the state of the art in

88 drought-induced mortality research and finally move to the core of the article in which we

89 address the following questions: (i) what are the necessary conditions for vegetation shifts to

90 occur? (ii) How much evidence of drought-induced vegetation shifts do we have at present and

91 where are they occurring? (iii) What are the main processes that favor, and oppose, the

92 occurrence of shifts at different ecological scales? (iv) What are the complications in detecting

93 and attributing drought-induced vegetation shifts? (v) What ecological factors can interact

94 with drought to promote shifts or stability?

95

2. Climate and the distribution of vegetation

97   The influence of climate on vegetation distribution is one of the best-established paradigms in

98   ecology, at least at regional and continental scales (Woodward, 1987). Low temperatures and

99   freezing limit hydraulic conductance and tissue integrity and low water availability reduces

100   water transport capacity and carbon assimilation, potentially leading to hydraulic failure or

101   carbon starvation (McDowell et al., 2011). The combination of high temperature and low

102   rainfall results in a strong conflict between high atmospheric water demands and temperature

103   regulation, on one side, and the need to reduce water use to accommodate low water

104   availability on the other side. Accordingly, models considering the balance between water

105   availability and demand are able to explain vegetation distribution to an important extent

106   (Neilson 1995), illustrating the importance of drought conditions on determining vegetation

107   composition, structure and functioning (Vicente-Serrano et al., 2013; Williams et al., 2013).

108

109   Changes in climate at the global scale are expected to affect general patterns of vegetation.

110   Great effort has been devoted in recent decades to elucidate these modifications by using

111   dynamic global vegetation models. These models are mainly based on the functional response

112   of vegetation types to climate variables (Sitch et al., 2003). This mechanistic approach,

113   together with the need to up-scale from local to continental scales has led to the use of plant

114   functional types, which in fact often correspond to biome types, merging species with similar

115   performance and habitat requirements and moving the modeling focus towards vegetation

116   functional traits. Importantly, plant functional types are also designed to generally describe

117   and quantify vegetation contributions to ecosystem properties and services (Bonan et al.,

118   2002; Quétier et al., 2007). Thus, the distinction between the taxonomic, species-based

119   conception of vegetation and the functional, traits-based one is important when considering

120   vegetation shifts. Overall, these models point to important latitudinal movements of biome

121   ecotones in the near future (Tang and Beckage, 2010). However, a key unresolved issue is the

122   temporal dynamics of the transitions (i.e., gradual versus abrupt changes), which in turn result

123   from the interaction of climate with other drivers, such as land use transformations, biota

124   migrations and changes in fire regimes (Higgins and Scheiter, 2012; Reyer et al., 2015).

125

126   There are also a number of reasons why the accuracy of the predictions derived from

127   vegetation models has been questioned, including methodological shortcomings related with

128   data sources and modeling procedures (e.g., Moorcroft et al., 2001; Thuiller et al., 2008). In

129   addition, difficulties in obtaining reliable predictions at local and landscape scales may be

130   explained by species autoecology (genetic, ecophysiological and population responses to

131 environmental variability), biotic interactions (considering the network of facilitative and

132 antagonist relations between plants) and historical background (including biogeographical

133 legacy, disturbance regime, and changes in forest management and land use). All of these

134 factors are relevant to interpretation of climate-induced vegetation shifts at landscape and

135 stand levels by reinforcing or counterbalancing the theoretical equilibrium between climate

136 and plants (García-Valdés et al., 2015).

137

138 The existence and characteristics of vegetation shifts can be studied from paleohistorical

139 records. There is abundant literature reporting a correspondence between vegetation change

140 and climate, particularly drought, across a variety of biomes (Calò et al., 2013; Clifford and

141 Booth, 2015; Schmieder et al., 2013; Shuman et al., 2009). There are, however, important

142 limitations associated with this type of paleo-studies (cf. Swetnam et al., 1999). First, paleo-

143 records commonly have coarse temporal resolutions from an ecological perspective, as abrupt

144 transitions of woody vegetation may occur at decadal scales. Advances in dating resolution are

145 providing support for the existence of vegetation shifts at centennial scales (Williams et al.,

146 2002), and we expect finer resolution to be available in the future (i.e., Calò et al., 2013).

147 Second, the attribution of vegetation changes to the climate's influence is not always

148 unequivocal because climate changes are inferred from indirect sources, typically sedimentary

149 measures and biological indicators like pollen (i.e., Calò et al., 2013; Schmieder et al., 2013)

150 that should be complemented by other climate proxies, such as stable isotopes (Shuman et al.,

151 2009). Studies in temperate forests in NE North America provide an example of the

152 correspondence between abrupt climatic events involving drought – estimated from hydrogen

153 stable isotopes - and rapid vegetation changes at temporal scales that are reasonably close to

154 ecological processes (500 years) (Shuman et al., 2009). The relationship between climate and

155 vegetation shifts, however, is often complex due to the interaction with other drivers,

156 particularly disturbance regimes, involving insect outbreaks, wildfires and human activity (Calò

157 et al., 2013; Clifford and Booth, 2015; Foster et al., 2006). In short, at relatively long temporal

158 and broad spatial scales the strong overall relationship between climate and vegetation

159 changes is firmly sustained, but higher resolution information that could elucidate the nature

160 and velocity of such relationships at finer scales merits further research.

161

162 **3. Overview of recent drought-induced vegetation die-off**

163 Drought-induced vegetation mortality has been reported in many areas worldwide, frequently

164 associated with high temperatures, and the number of reported mortality episodes has

165 increased dramatically over the last years (Allen et al., 2010; Williams et al., 2013). There is

166 some concern, however, regarding the extent to which this trend reflects a global increase in

167 vegetation mortality or the recent increase in detection effort (Martínez-Vilalta et al., 2011;

168 Steinkamp and Hickler, 2015). In addition, the multiplicity of disturbances affecting forests and

169 the diversity of factors that may contribute to observed mortality patterns makes the

170 attribution of causes difficult (cf. Allen et al., 2015; McDowell el al., 2015). In many cases, for

171 instance, the effects of drought interact with those of rapid successional dynamics associated

172 to changes in forest management (e.g., Vilà-Cabrera et al., 2010), and disentangling these two

173 effects remains challenging.

174

175 Despite much research effort, the mechanisms underlying drought-induced plant mortality

176 remain insufficiently understood (McDowell et al., 2008, 2011; Sala et al., 2010), and a

177 definitive classification of plant physiological strategies to face drought is still lacking (Klein,

178 2014; Martínez-Vilalta et al., 2014). An important outcome of recent studies on the

179 mechanism of drought-induced mortality is the realization that water and carbon economy of

180 plants are tightly linked during extreme drought, so that failures in the water and carbohydrate

181 transport systems (hydraulic and phloem failure, respectively) and extreme carbohydrate

182 depletion (carbon starvation) are likely to co-occur (Mencuccini et al., 2015; Parolari et al.,

183 2014; Sevanto et al., 2014). The contribution of biotic factors and their interactions with the

184 physiological mechanisms of mortality (Gaylord et al., 2013; Oliva et al., 2014) further

185 complicates attribution (Anderegg et al., 2015b). The complexity of mortality mechanisms is

186 problematic because it limits our capacity to assess the causes of a given mortality event, as

187 well as our capacity to predict when and where these events are likely to occur in the future

188 (McDowell et al., 2013). In that regard, comparative physiological studies of drought responses

189 of coexisting species, either in the field or under controlled experimental conditions (e.g.,

190 Garcia-Forner et al., 2015; Nardini et al., 2015), are likely to be particularly useful.

191

192 Many studies have found an association between climate anomalies and drought-induced

193 mortality at different spatial and temporal scales (e.g., Fensham et al., 2009; Suarez and

194 Kitzberger, 2010; Mitchell et al., 2014). Spatiotemporal patterns of drought-induced vegetation

195 mortality, however, tend to be complex. At relatively small spatial scales (stand to catchment),

196 high mortality rates often are associated with shallow soils (Gitlin et al., 2006; Vilà-Cabrera et

197 al., 2013), higher exposure to radiation (Gitlin et al., 2006), low topographic soil moisture

198 (Galiano et al., 2010), dense stands (i.e., higher competition) (Guarín and Taylor, 2005; Vilà-

199   Cabrera et al., 2013), and biotic agents (Gaylord et al., 2013). However, exceptions are

200   common, and even within a particularly well-documented system such as the piñon-juniper

201   woodlands in SW USA the degree of discrepancy between studies can be remarkable

202   (Meddens et al., 2015), likely reflecting high spatial variability in climate, soils, topography and

203   disturbance history (Romme et al., 2009; Swetnam and Betancourt, 1998). In general, complex

204   interactions between factors leading to mortality are not always easy to capture in statistical

205   models based on 'opportunistic' field observations.

206

207   At broad spatial scales, additional processes need to be considered. For instance, changes in

208   species dominance along aridity gradients imply that drought resistant species (in absolute

209   terms) tend to occupy drier habitats and may not be necessarily closer to their physiological

210   limits (relative to the local conditions where they live). As a result, predicting what species and

211   populations are more vulnerable to a given precipitation anomaly is not straightforward. This

212   is consistent with observations of drought-induced mortality in wet environments (e.g.,

213   tropical rainforests (Phillips et al., 2009)) and with the fact that hydraulic safety margins have

214   been reported to be similar across biomes at the global scale (Choat et al., 2012). Within

215   species, functional and morphological traits vary widely along environmental gradients (e.g.,

216   Siefert et al., 2015; Vilà-Cabrera et al., 2015), and the balance between plasticity and local

217   adaptation processes becomes critical (Valladares et al., 2014). Despite all these complications,

218   recent studies show promising avenues. For instance, populations occupying more marginal

219   locations within the species' bioclimatic niche are more affected by drought-induced die-off in

220   Mediterranean woody communities (Sapés, 2013). In another recent report, climatic water

221   deficit simulated from a hydrologic model was able to predict regional patterns of *Populus*

222   *tremuloides* mortality with 75% accuracy (Anderegg et al., 2015a). Similarly, a logistic

223   regression using species identity, mean climate and climate anomalies for a given year

224   provided a reasonably good fit to regional patterns of forest decline in NE Spain (Chaparro,

225   2013).

226

227   **4. On the necessary conditions for vegetation shifts to occur**

228   Vegetation shifts are a particular case of ecosystem regime shifts, which can be defined as

229   large, relatively rapid and persistent reorganizations of the state of ecosystems (Brook et al.,

230   2013). Regime shifts may result from a large permanent change in environmental conditions,

231   but may also result from relatively small or transient changes in environmental drivers

232   (Scheffer et al., 2001; 2012). This second type of regime shifts implies the presence of tipping

233   points, and is frequently (but not always) associated with the existence of multiple 'stable'

234   states (Petraitis, 2013). Tipping points are associated with positive feedbacks that, once a

235   critical threshold is passed, propel change toward an alternative state (Scheffer et al., 2012).

236   The kind of vegetation shifts we are concerned with here occur when a pulse-type disturbance

237   (i.e., a drought) triggers a reorganization of the ecosystem that is maintained after

238   environmental conditions return to pre-disturbance levels. This definition of drought-induced

239   vegetation shifts is an example of catastrophic regime shift and involves multiple 'stable' states

240   and hysteresis (the return path to the original state differs from the original trajectory that led

241   to the current state, making the change difficult to reverse) (Scheffer et al., 2001).

242

243   Several studies have documented evidences of catastrophic regime shifts in ecosystems (Folke

244   et al., 2004; Scheffer et al., 2001). Although most of them come from aquatic environments

245   (particularly lakes and marine systems), there are also examples from terrestrial ecosystems.

246   Among those, some of the best characterized cases include desertification in the Sahara region

247   (Foley et al., 2003; Janssen et al., 2008), forest-woodland ecotones (Allen & Breshears, 1998),

248   transitions between forest, savanna and treeless states in tropical systems (Hirota et al., 2011;

249   van Nes et al., 2014), and peatland dynamics (Hilbert et al., 2000) or transitions between

250   forests, treeless tundra and steppe in the boreal biome (Juday et al., 2015; Scheffer et al.,

251   2012). However, detecting multiple 'stable' states and catastrophic shifts from temporal and

252   spatial patterns is difficult, mainly due to the difficulty of having proper controls and long-

253   enough time series (Petraitis, 2013; see also Andersen et al., 2009; Scheffer and Carpenter,

254   2003). The use of spatial patterns is particularly problematic, as shown, for instance, by the

255   controversy around the use of spatial vegetation patterns (in particular, their patch size

256   distribution) as a suitable indicator of catastrophic vegetation shifts in drylands (Kéfi et al.,

257   2007; Maestre and Escudero, 2009; Rietkerk et al., 2004).

258

259   We argue here that a demographic approach provides a useful framework for detecting and

260   assessing potential vegetation shifts. From a demographic perspective, a vegetation shift

261   implies an abrupt change in the relative abundances of dominant species in a community

262   (composition), and should be reflected in the demographic rates of the species involved (Lloret

263   et al., 2012). In particular, such a change requires that the formerly dominant species are

264   replaced by other potentially dominant ones, which would normally be present in the

265   community before the drought but may also colonize after it. The typical process leading to a

266   drought-induced vegetation shift can be conceptualized in four steps: (i) a drought event

267   causes high adult mortality rates in (at least) one dominant species; (ii) these adult mortality

268   rates are higher than those experienced by one or more potential replacement species; (iii)

269   these potential replacement species show substantial regeneration; and (iv) regeneration of

270   the initially dominant species is very low or absent. However, other combinations may also

271   lead to a vegetation shift (see Figure 1 for a complete classification).

272

273   More generally, and based on the criteria presented in the previous paragraph, we can

274   distinguish several situations (Figure 1):

275   *Vegetation shift.* Arguably, the most important condition for a vegetation shift to occur is that

276   regeneration of a potential replacement species is successful during a relevant time period

277   after the mortality event. If, in addition to that, there is no regeneration of the formerly

278   dominant species, the evidence for a shift is clear. In principle, the shift will be faster if adults

279   of the potential replacement species have survived (SSf in Figure 1) than if not (SSs).

280   *No shift*. Vegetation composition will remain unchanged in the mid-term if the formerly

281   dominant species regenerates while the potential replacement species does not. In these cases,

282   we may refer to reversal (RV), when adults of the potential replacement species survive

283   achieving transitory dominance, or to self-replacement (SR), when such survival is not observed.

284   *Uncertain outcome.* If regeneration of both the formerly dominant and the potential

285   replacement species is observed, the final outcome is uncertain. Obviously, the likelihood of a

286   shift is higher if there is adult survival of the potential replacement species (UNa) than if not

287   (UNc). In addition, if there is no regeneration of the dominant or potential replacement

288   species, but there is survival of adults of this latter species, the outcome is also uncertain

289   (UNb), although a species shift may still take place in the long-term.

290   *Biome shift*. When there is neither regeneration nor survival of adults of the dominant or

291   potential replacement species, the most likely outcome is colonization by a new species not

292   represented in the original community or, in extreme cases, complete loss of vegetation (i.e.,

293   transition to bare soil). We refer to such changes as biome shifts (BS).

294

295   Temporal considerations are critical in any framework aiming at classifying potential

296   vegetation shifts. In our case (Figure 1), the reference time frame is the typical generation time

297   of the dominant species in the community (i.e., a shift will occur if the identity of the dominant

298   species changes after one generation). We assume that observations on mortality and

299   regeneration are taken shortly (up to a few years) after the mortality event, as is usually the

300   case, and are used to assess subsequent community dynamics. In order for vegetation shifts to

9

301   be realized, measured demographic rates should be good estimates of per-capita rates of

302   population growth, and should continue at similar rates for long enough to drive the system

303   into a new state (cf. Petraitis, 2013). For instance, enough time without other major

304   disturbances is required for the new community to develop. The opposite case should also be

305   considered, as repeated droughts may lead to disproportionate effects relative to the impact

306   of a single drought of the same intensity, due to legacy effects (Anderegg et al., 2015c). In

307   addition, many vegetation types (particularly forests) are inertial systems where adults can live

308   for hundreds of years and mortality and recruitment may depend on different environmental

309   drivers and be highly decoupled in time (Shugart and Urban, 1989). Under directional climate

310   change, a shift in such systems may occur simply because the original ecosystem cannot

311   develop under the new conditions, even if it could have been maintained in the absence of the

312   disturbance triggering the shift (Dobrowski et al., 2015; Smith et al., 2009).

313

314   **5. Characterization of recent drought-induced vegetation shifts**

315   We conducted a literature review of papers reporting drought-induced vegetation shifts. We

316   started by searching the Web of Science (accessed 15/05/2015) with the following keywords

317   (topic search): (vegetation OR forest OR woodland OR shrubland OR biome) AND (shift$ OR

318   change$ OR transition$ OR replacement$ OR substitution$ OR succession) AND drought$ AND

319   (mortality OR die-off OR dieoff OR decline OR die-back OR dieback) AND (regeneration OR

320   recruitment). This search resulted in a list of 319 papers. The abstracts of all these papers were

321   checked to select papers fulfilling the following criteria: (i) they were field-based, original

322   research papers (i.e., reviews, studies under experimentally controlled conditions and purely

323   modelling papers were excluded); (ii) they studied 'natural' vegetation (e.g., forest plantations

324   were excluded), (iii) they studied the effects of a drought event that occurred at a well-defined

325   point in time (i.e., a pulse event) after 1950; (iv) they measured or made some inference on

326   the vegetation dynamics after the drought event. The list was completed with a few additional

327   case studies from Allen et al. (2010) or other key references that had not been detected in our

328   initial query. Selected papers were organized by case studies, so that articles studying a similar

329   transition within the same broadly defined region were pooled together to avoid giving extra

330   weight to more intensively studied systems, and each case was classified according to the

331   framework presented in Figure 1 (Table 1).

332

333   Our final list included 35 case studies (Table 1 and Figure 2). The majority of them (*N* = 24)

334   were classified as uncertain according to the framework in Figure 1, whereas 7 corresponded

335   to species shifts, three to self-replacements and one to a biome shift (Figure 2). Uncertain

336   cases were mostly associated to two different situations. The first was lack of information

337   regarding either mortality of the potential replacement species or regeneration of the affected

338   or replacement species (*N* = 7). Secondly, in 15 instances uncertainty arose from similar levels

339   of regeneration of both the initially affected and the potential replacement species, precluding

340   inferences on the mid-term trajectory of the study system. Finally, in two cases (piñon-juniper

341   woodlands in SW USA and beech in England) uncertainty resulted from inconsistencies in the

342   regeneration patterns (of the affected and potential replacement species, respectively)

343   reported in different studies carried out in the same systems. We note, however, that the

344   piñon-juniper vegetation occurs over a wide range of environmental conditions and includes

345   different pine and juniper species (Romme et al., 2009). Therefore, inconsistencies in

346   regeneration patterns across studies likely reflect different trajectories (including SSf, UNa and

347   probably also BS) in different parts of the range of this vegetation type.

348

349   The seven cases corresponding to species shifts occurred in temperate, Mediterranean and

350   tropical climates, whereas the recorded biome shift was reported in a dry climate (Table 1 and

351   Figure 2). The low sample size makes it difficult to reach any strong conclusion on the spatial

352   distribution of these shifts, but they seem to be widely distributed across biomes and climate

353   types. Regarding the spatial scope, reported vegetation shifts went all the way from local to

354   subcontinental scales. In five cases other drivers besides drought were mentioned in the

355   corresponding papers, including biotic agents and land management (e.g., grazing, fire use).

356

357   To explore the functional implications of the potential vegetation shifts described in the

358   different case studies we classified them depending on the functional type of the affected

359   dominant species and the potential replacement one(s) (Table 1). Functional types were

360   defined based on broad plant classification (needleleaf / gymnosperm vs. broadleaf /

361   angiosperm), leaf habit (deciduous vs. evergreen), and growth form (tree, shrub, herb),

362   similarly to Lawrence and Chase (2007). Only six thus defined functional types were

363   represented in our case studies: needleleaf evergreen tree, NET; broadleaf evergreen tree,

364   BET; broadleaf deciduous tree, BDT; broadleaf evergreen shrub, BES; broadleaf deciduous

365   shrub, BDS; and needleleaf evergreen shrub, NES. When there was more than one functional

366   type represented in the affected dominant species or in the potential replacement species

367   within a case study, we considered as many trajectories as combinations of functional types

368   occurred in each case.

369

370   When all cases were considered (39 individual trajectories), there were 17 trajectories (44%)

371   implying no change in functional type even if the vegetation shift was realized (i.e., the

372   affected and potential replacement species belonged to the same functional type) (Figure 3).

373   BET -> BET transitions (a broadleaf evergreen tree being replaced by the same or another

374   species of the same functional type) were the most common situation overall ($N = 11$

375   trajectories). Directional (i.e., non-circular) trajectories originating from NET and BET were

376   more common than directional trajectories ending in these functional types (10 vs. 4 and 6 vs.

377   3 for NET and BET, respectively). Overall, there were 10 transitions from trees to shrubs,

378   whereas the opposite change was not observed. Transitions between species with different

379   leaf habit were relatively rare, but were more common from evergreen to deciduous ($N = 5$;

380   mostly NET -> BDT) than the opposite ($N = 2$). Only nine trajectories corresponded to species

381   or biome shifts according to our scheme (Figure 1; red arrows in Figure 3). Of these, three

382   corresponded to BET -> BET transitions. Trajectories corresponding to species or biome shifts

383   affected only NET or BET functional types (three in each case).

384

385   Finally, the three cases in which self-replacement was observed affected broadleaf evergreen

386   species (two BET, one BES) and occurred in different climatic regions (tropical, temperate and

387   Mediterranean). More generally, a shift seems unlikely, at least in the short term, whenever

388   regeneration of the affected species is observed, even if potential replacement species are also

389   regenerating. If we add the 15 uncertain cases in which there was regeneration of the affected

390   species (UNa, UNc in Figure 1) to the self-replacement cases, we end up with 18 cases (51% of

391   35 case studies) in which the weight of the evidence seems to be against the occurrence of a

392   vegetation shift.

393

394   **6. Drought-induced vegetation shifts in practice: crucial challenges to understanding and**

395   **prediction**

396   We only found eight case studies that fulfilled our criteria to be considered drought-induced

397   vegetation shifts (species or biome shifts in Figure 1). And even these cases correspond only to

398   situations in which the available evidence, often representing a short time period, is consistent

399   with the occurrence of a shift; and not necessarily to cases in which these shifts are certain or

400   even likely. We acknowledge that our search criteria were biased towards identifying instances

401   of vegetation change that had been placed in a demographic context (see previous section).

402   Although we accept that this might have resulted in missing some convincing cases of drought-

403 induced vegetation shifts, we argue that this effect is likely to be minor, as it is difficult to

404 describe and attribute recent (post-1950) vegetation shifts without assessing demographic

405 rates (mortality and regeneration). Considering the low number of drought-induced vegetation

406 shifts we detected, a reasonable first conclusion would be that these shifts are not yet

407 common or detectable. However, this conclusion needs qualification in some respects (see

408 also Hughes et al., 2013). Firstly, vegetation shifts are likely to be inherently rare events, and

409 their detection by standard vegetation monitoring systems, such as national forest inventories,

410 is inefficient. As a result, most reports of vegetation shifts arise from opportunistic studies

411 initiated by scientists as a response to an observed mortality event. While informative, this

412 approach makes it difficult to assess the spatial representativeness of the event and to

413 evaluate the subsequent community dynamics for a sufficiently long period (cf. White and

414 Jentsch (2001) on the importance of the scale of observation). Secondly, and related to the

415 previous point, regeneration is frequently the key ecological process determining long-term

416 community dynamics. However, it rarely has been assessed in studies of drought-induced

417 mortality. Thirdly, recent climatic impacts on vegetation have occurred in the presence of

418 other important drivers, in most cases directly related to human activities (e.g., changes in

419 land-use, grazing practices, forest management, fire use). These three aspects are addressed in

420 the following sub-sections.

421

422 *6.1. Need for long term monitoring with sufficient temporal resolution*

423 Better vegetation monitoring systems are urgently needed if we are to assess how common

424 drought-induced vegetation shifts currently are and make sound projections of how frequent

425 they are going to be in the future (see Allen et al. (2010) and Hartmann et al. (2015) for similar

426 assertions in the context of drought-induced tree mortality). An adequate monitoring system

427 should have, at least, the following characteristics: (i) it should be able to distinguish different

428 vegetation types (i.e., changes in composition), not only changes in canopy structure and

429 physiological state; (ii) it should cover a spatially representative area and have the potential to

430 become global; (iii) it should have sufficient spatial and temporal resolution to detect the

431 processes of interest; and, critically; (iv) it should be long-term. It seems clear that remote

432 sensing holds the greatest promise for such a system, particularly at broad regional or global

433 scales (Hansen et al., 2013; McDowell et al., 2015). However, ground-based inventories also

434 will be essential, as most remote sensing techniques require extensive ground evaluation and

435 frequently lack the desired spatiotemporal resolution (McDowell et al., 2015; Trumbore et al.,

436 2015; although cf. Asner et al., 2016).

437

438   While standard national forest inventories (NFIs) are well-suited for assessing changes in tree

439   biomass and carbon stocks (e.g., Mohren et al., 2012), they have important limitations for

440   detecting vegetation shifts. Firstly, plot size (<< 1 ha) and distribution are not designed to

441   capture relatively infrequent events, such as drought-related disturbances. Secondly, the time

442   interval between surveys (frequently > 5 years) makes it difficult to attribute changes in

443   structure or composition to a specific cause. Thirdly, forest inventories commonly lack

444   accurate information about regeneration, a key process to obtain projections of forest

445   dynamics (see next section). Finally, NFIs do not sample non-forested areas, which seriously

446   limits their capacity to detect changes between forests and other vegetation types. Many of

447   these limitations are shared by forest health monitoring programs, such as the European ICP-

448   Forests, despite their usefulness for detecting long-term changes in tree condition (e.g.,

449   drought-related leaf loss: Carnicer et al., 2013). Standardized, broad scale plot monitoring

450   networks, such as the recently launched CTFS-ForestGEO (Anderson-Teixeira et al., 2014) offer

451   great promise due to their relatively large plot sizes and global coverage, but they still suffer

452   from relatively infrequent surveys (~5 years) and lack of coverage of non-forested areas.

453

454   **6.2. It is about regeneration, of course!**

455   Recent research on drought-induced vegetation change has focused on plant mortality. While

456   this is normal, as mortality is the most conspicuous and immediate effect of an extreme

457   drought, we argue here that this focus should be complemented with a greater emphasis on

458   the demographic responses following the mortality event. Even after devastating adult

459   mortality, a vegetation shift will only occur if the initially affected species is not able to

460   regenerate and become dominant again (Lloret et al., 2012). It is clear from our review that

461   self-replacement or reversal (cf. Figure 1) may be common outcomes of drought-induced

462   mortality events, at least in the short term. This result is not surprising in the context of other

463   disturbances. For instance, self-replacement (cf. direct regeneration) has been long known to

464   be a common response of Mediterranean communities after fire, which originated the term

465   'autosuccession' (Hanes, 1971; Trabaud and Lepart, 1980). Although we now know that

466   autosuccession does not always occur (Rodrigo et al., 2004), it remains the most common

467   response to wildfire in Mediterranean systems (Pausas et al., 2009) and it has also been

468   reported in many other ecosystem types in response to a variety of disturbances (Johnstone

469   and Chapin, 2006; Zeppenfeld et al., 2015). Of course, the fact that there is regeneration of the

470   affected species soon after a mortality event does not rule out the possibility that a vegetation

471   shift will occur in the mid-term. This is particularly true in the context of strong directional

472   climate change, as sustained temperature raise and associated drivers (biotic agents, wildfires)

473   may result in future failure of seedling recruitment in areas with good regeneration under

474   current conditions (Allen et al., 2015; Brando et al., 2014; McDowell et al., 2016; Williams et

475   al., 2013).

476

477   In order to understand when and where a species or biome shift is likely to occur, as opposed

478   to self-replacement, we need to place the focus on regeneration dynamics at appropriate

479   temporal scales. The distinction between the 'habitat niche', defined by the requirements of

480   mature plants, and the 'regeneration niche', defined as the requirements for a successful

481   replacement of mature individuals (Grubb, 1977), becomes relevant in that context. Self-

482   replacement will be likely to occur after drought-induced mortality when the regeneration

483   niche of the affected species is at least as wide as its habitat niche, particularly with regards to

484   water availability. It is normally assumed that juveniles of a given species have narrower niches

485   than adults (Jackson et al., 2009), and most studies seem to support this view (e.g., Bell et al.,

486   2014; Dobrowski et al., 2015). In the case of water availability, an important reason for that is

487   that seedlings typically have much shallower root systems than adults (the situation may be

488   different for resprouts; see below), limiting their capacity to access deep water sources (Pratt

489   et al., 2008). However, inherent climatic variability, particularly in water-limited systems, may

490   offer pulses of suitable conditions for regeneration (Swetnam and Betancourt, 1998). The local

491   conditions after mortality events may change substantially relative to pre-disturbance

492   conditions, including likely increases in resource availability per capita (particularly light but

493   also water and nutrients), and reductions in the capacity of the canopy to moderate

494   environmental conditions (temperature, vapor pressure deficit). These changes are likely to

495   interact with each other (von Arx et al., 2013) and, collectively, will determine the likelihood of

496   self-replacement and overall community stability (Frelich and Reich, 1999).

497

498   As in other disturbances, gap size distributions and shade tolerance of the species in the

499   community are likely to play an important role, as well as the fact that tradeoffs between

500   shade and drought resistance are common (Niinemets and Valladares, 2006). Gap sizes opened

501   by drought-induced mortality are likely to be smaller than those characteristic of other

502   disturbances (e.g., fire), and may not be enough to shift the balance in favor of the

503   regeneration of shade-intolerant species. In the case of the relatively shade-intolerant Scots

504   pine in Europe, for instance, adult mortality has been shown to have a negligible or even

505 negative effect on its regeneration, while favoring the relatively shade-tolerant oaks (Galiano

506 et al., 2013, 2010; Rigling et al., 2013). The fact that shade tolerance of juveniles and adults is

507 correlated across species, albeit with an important scatter (Valladares and Niinemets, 2008),

508 may help predicting community dynamics after disturbance. There is a clear need, however,

509 for further studies assessing seedling performance relative to adults and comparing it among

510 coexisting species under changing environmental conditions.

511

512 It is also important to recognize and study the implications of different regeneration strategies.

513 The ability to resprout is a key trait, as it enables the survival of individuals and allows rapid

514 recovery of aboveground biomass after disturbance (Bellingham and Sparrow, 2000; Bond and

515 Midgley, 2001; Clarke et al., 2013). Resprouting is common in many ecosystems (Vesk and

516 Westoby, 2004) and, although it has been studied mostly in the context of vegetation

517 responses to fire, wind throw and clipping, recent papers stress the importance of resprouting

518 in the context of drought stress (Pausas et al., 2015; Zeppel et al., 2014). Drought response

519 strategies frequently co-vary with resprouting ability, which makes it difficult to establish clear

520 associations between this latter trait and vulnerability to drought (Pausas et al., 2015; Saura-

521 Mas and Lloret, 2010). In general, the fact that resprouters typically recover faster than non-

522 resprouters after disturbance, including drought (Zeppel et al., 2014), implies that reversals

523 and self-replacements (cf. Table 1) may be more common when resprouting species are

524 affected. This situation, however, may only apply to certain drought regimes (Pausas et al.,

525 2015). In particular, the ability of resprouting species to persist is likely to decline as the

526 frequency of extreme droughts increases. This is mostly due to the fact that repeated

527 resprouting requires sufficient time between disturbances for reserves (particularly

528 carbohydrates) to build up again (Canadell and López-Soria, 1998). In addition, some studies

529 have identified physiological differences between resprouting and undisturbed individuals,

530 suggesting that the former are more sensitive to drought (Pausas et al., 2015).

531

532 **6.3. Key role of interactions with other drivers**

533 A necessary condition for the occurrence of a vegetation shift is the differential performance

534 of species in terms of adult survival or the recruitment of new cohorts (Figure 1). In many

535 cases, these differences reflect species-specific tolerances to the conditions generated by

536 standing vegetation or by mortality-induced gaps. There is general consensus on the relevance

537 of multiple factors other than the attributes of the species involved in determining tree death,

538 even in cases where drought is well documented (e.g., Frey et al., 2004; Galiano et al., 2010). It

539 is more difficult, however, to disentangle the contribution of such factors on species

540 differential responses, particularly because they usually interact to reinforce or stabilize

541 complex feedbacks. These factors typically include pests and pathogens, grazing, pollution,

542 wildfires and microsite conditions, particularly soil characteristics. These co-drivers of

543 vegetation dynamics often operate at fine spatial scales, undermining our capacity to obtain

544 global patterns in the relationship between water availability and tree mortality, except for

545 drier locations (Steinkamp and Hickler, 2015). In our literature compilation, we found that 86%

546 out of 35 selected case studies recognize the influence of co-drivers. The most common factor

547 was the interaction with biotic agents, which mainly involved pests and pathogens (43% of the

548 cases) and grazing (20%). Forest management, including logging, was also considered relevant

549 in 23% of cases; whereas other disturbances, such as wildfires (14%), seem to play a relevant

550 role only in some regions. The number of studies considering the relevance of non-climatic

551 factors as determinants of recruitment following drought-induced mortality was much lower

552 than those addressing the role of these factors on mortality patterns. In addition, most studies

553 only conducted a general assessment of regeneration without formal test of hypotheses, and

554 particularly the interaction between climatic and non-climatic factors was rarely addressed.

555

556 Contributing factors are often a source of uncertainty when assessing vegetation shifts at fine

557 spatial scales given their idiosyncratic variability, but also because we commonly lack

558 information on their historical influence (i.e., land-use, grazing, forest management,

559 disturbance regime). Nevertheless, we can identify different situations according to their

560 potential interaction with drought episodes. First, co-drivers may enhance mortality by

561 establishing synergies with drought conditions. For instance, severe drought induces reserve

562 depletion in trees, increasing their vulnerability to pests and pathogens (Gaylord et al., 2013;

563 Jactel et al., 2011). In turn, these antagonistic attacks could reduce carbon reserves, eventually

564 conducting to a reinforcing feedback between drought and biotic agents (Oliva et al., 2014).

565 The outcome of these interactions may involve time lags, confounding the contribution of

566 different agents and highlighting the importance of considering medium-term tree survival in

567 addition to mortality pulses. For instance, bark beetles may initiate a successful infestation

568 under drought conditions, in some cases eventually reaching a demographic threshold leading

569 to the death of trees that were not severely affected by drought itself (Allen, 2007).

570 Analogously, drought can have strong direct and indirect synergistic effects on wildfires; e.g.,

571 fine and coarse fuel loads can temporarily increase and change in structure with drought-

572 induced tree mortality, which can change the size and severity of fires (along with drought and

573   land-use), which in turn can jeopardize tree survival and regeneration (Allen, 2007). Ongoing

574   climate changes are projected to foster increased wildfire activity in many ecosystems (IPCC,

575   2014). In Mediterranean systems, fire risk may rise until fuel loads become too low due to

576   water limitations on vegetation growth, while the new climate conditions become less

577   favorable to post-fire vegetation recovery (Batllori et al., 2013; Loepfe et al., 2014).

578

579   Other drivers can contribute to vegetation dynamics without being themselves directly

580   promoted by drought conditions. This is the case of disturbances such as windstorms (Bailo et al.,

581   2004) or pollution (Palik et al., 2011) that further diminish adult survival in addition to drought.

582   Both mortality and post-drought regeneration of *Populus tremuloides* in N America have been

583   proposed to be impacted by grazing (Worrall et al., 2008), but the contribution of herbivores to

584   the differential performance of dominant and potential replacement species needs further study.

585   Although browsing itself can hardly be linked directly to drought conditions, regeneration control

586   by grazing often occurs in semi-arid ecosystems (Maza-Villalobos et al., 2013; Twidwell et al.,

587   2014). Potentially, other factors may counterbalance drought impacts, increasing resilience

588   (Lloret et al., 2012). Some of these factors can involve biotic interactions, such as facilitation,

589   which in turn can be influenced by climatic conditions, including drought. However, the

590   contribution of positive biotic interactions on post-drought vegetation dynamics has been rarely

591   assessed (Lloret and Granzow-de la Cerda, 2013).

592

593   Finally, management constitutes one of the major drivers of vegetation dynamics all over the

594   world and it surely affects the likelihood of drought-induced mortality and subsequent

595   vegetation responses. Management history may increase forest vulnerability to drought

596   through several mechanisms, thus enhancing species shifts. First, management may promote

597   expanding populations to (or beyond) the edge of the species historic distribution, close to its

598   physiological limits of tolerance for both adults and juveniles (e.g., Sánchez-Salguero et al.,

599   2012). Second, increased stand density as a result of past logging (Camarero et al., 2011; Slik,

600   2004), abandonment (Linares et al., 2010b) or fire exclusion (Breshears et al., 2005; Guarín and

601   Taylor, 2005) may lead to higher competition for water resources. Remaining adult trees and

602   new recruits also may be damaged during wood harvesting (Aynekulu et al., 2011). In addition,

603   regeneration may be depleted due to overgrazing (Linares et al., 2011). At regional scales in

604   arid regions, overexploitation of standing biomass can exacerbate rainfall decline, leading to a

605   positive feedback between bare soil cover and aridity (Gonzalez, 2001). Alternatively, stand

606   density reductions (Grant et al., 2013) or direct promotion of regeneration can boost self-

607   replacement or vegetation shifts depending on the favoured species. In contrast with drivers

608   that are the result of processes operating at global or regional scales, these more local

609   management actions (grazing control, modification of stand structure, species selection) may

610   be used as tools to delay or modify local trajectories of vegetation dynamics.

611

612   *6.4. Functional and biogeographical context*

613   Altered climatic conditions will eventually lead to changes in vegetation biogeography.

614   Theoretical predictions, niche correlational approaches and process-based models all support

615   future modifications in the distribution of vegetation and biomes (Sitch et al., 2003; Tang and

616   Beckage, 2010). However, in spite of substantial evidence of the occurrence of drought-

617   induced tree mortality, we are not yet observing widespread vegetation shifts in response to

618   increasing drought conditions. An important necessary condition for these shifts to occur is the

619   existence of a species pool providing potential replacement species. In some reported cases,

620   uncertainty arises because there is no clear replacement tree species (Boehmer et al., 2013;

621   Villalba and Veblen, 1998); in other cases, understory shrubs are the immediate candidates to

622   occupy the gaps opened by tree mortality (Palik et al., 2012, 2011; Saura-Mas et al., 2014;

623   Worrall et al., 2010). In these cases, vegetation responses can often be placed within a

624   successional framework of species replacement following disturbance. The same applies to

625   other studies that point to replacements between coexisting trees with different degree of

626   shade tolerance or successional status in temperate (Galiano et al., 2010; Olano and Palmer,

627   2003) and tropical forests (Chazdon et al., 2005; Oatham and Ramnarine, 2006). Self-

628   replacement can also be placed in this successional framework when new cohorts of standing

629   vegetation can tolerate the conditions imposed by drought, as in Mediterranean shrublands

630   (del Cacho and Lloret, 2012; Lloret et al., 2015), or when drought triggers the decay expected

631   to occur in old cohorts (Boehmer et al., 2013). At the other extreme of species pool availability,

632   studies in diverse tropical forests consistently report structural changes leading to shorter

633   species and lower basal area (Zhou et al., 2014, 2013). Although these structural modifications

634   may correlate with compositional changes at the stand level, the existence of directional shifts

635   at the local scale is less clear, given the high spatial turnover of species in these forests

636   (Lingenfelder and Newbery, 2009; Slik 2004; Zhou et al., 2014, 2013) (but see Fauset et al.

637   (2012) for long-term drought). The relevance of the available species pool in determining

638   future vegetation trajectories highlights the vulnerability of many managed, impoverished

639   forests. The enhancement of woody species diversity in forests, particularly if it is based on

640   native species covering a wide range of bioclimatic niches and genetically diverse populations,

641   constitutes an important management opportunity to improve resilience in forests facing

642   future drier conditions (Jump et al., 2009a; Fauset et al., 2012; Morin et al., 2014; but see

643   Grossiord et al., 2014).

644

645   Overall, current evidence does not show generalized shifts in vegetation functional types

646   induced by drought. This is true even where species replacement is likely to occur, supporting

647   the role of species functional redundancy within communities in promoting resilience. This is

648   particularly clear in tropical forests dominated by BET, as stated above (but see Fauset et al.

649   2012). However, in the instances in which changes in the dominant functional type are

650   predicted, trajectories generally agree with expectations of vegetation responding to drier

651   conditions by favouring species with higher drought resistance. Temperate, relatively moist

652   forests dominated by NET tend to be replaced by BET or BDT species distributed at lower

653   latitudes or altitudes (Bailo et al., 2004; Camarero et al., 2011; Galiano et al., 2010; Navarro-

654   Cerrillo et al., 2014; Rigling et al., 2013). Analogously, temperate moist forests of *Nothofagus*

655   *dombeyii* (BET) tend to be replaced by *Austrocedrus chilensis* (NET), a species distributed into

656   the drier steppe biome (Suarez and Kitzberger, 2008). The only shift of BDT replacing BET

657   corresponds to drought-deciduous species in the Sahel (Gonzalez, 2001). Finally, there is

658   documentation in several cases of forest change from drought stress towards lower-statured

659   vegetation, dominated by shrubs or smaller trees (Bennet et al., 2015; McDowell and Allen,

660   2015), while the opposite (transitions to taller vegetation) does not seem to occur.

661

662   Vegetation changes can be interpreted by comparing the biogeography of the former

663   dominant and the potential replacement species. Our preliminary results allow formulating the

664   hypothesis that species with affected populations located at the edge of the species' climatic

665   range – thus, close to their physiological limits of drought tolerance – likely would be

666   replaced by species better adapted to water scarcity, and hence distributed over drier

667   environments. This hypothesis is consistent with reported species range shifts along altitudinal

668   gradients, but less evident along latitudinal ones (Jump et al., 2009b). Thus, drought episodes

669   would trigger changes in species distributions particularly at ecotones (Allen and Breshears,

670   1998). Nevertheless, a proper analysis of the climatic requirements of the species involved and

671   the effect of co-drivers is needed, because populations living at the edge of its climatic

672   distribution may exhibit compensatory demographic mechanisms (Pironon et al., 2015) and

673   may have experienced selective processes enhancing resilience. In spite of the attractiveness

674   of understanding the biogeographical implications of drought-induced vegetation shifts, in

675 most cases our current knowledge does not allow discriminating between alternative

676 processes, preventing us from reaching general conclusions.

677

678 **7. Concluding remarks**

679 Our literature review shows that the available evidence for drought-induced vegetation shifts

680 is still scarce, and suggests that vegetation exhibits a remarkable resilience to extreme

681 drought, both in terms of composition (i.e., self-replacement) and functional properties.

682 Examples of potential vegetation shifts do not seem to be limited to specific climates or

683 vegetation types. In the cases in which the evidence for species replacement is clearer,

684 vegetation transitions seem to favor dominance of species that are: a) more resistant to

685 drought, as inferred by their patterns of distribution or their functional and structural traits; or

686 b) more pioneer in successional status. Given the limited information currently available on

687 drought-induced vegetation shifts from projected changes in climate, specifically including

688 drought conditions, we stress the need for improved, long-term vegetation monitoring

689 programs with sufficient temporal resolution. We also advocate for changes in approaches to

690 the study of drought-induced mortality and its impact on vegetation dynamics. First, we

691 suggest widening the focus to include not only the triggers of vegetation die-off but also the

692 determinants of vegetation responses after mortality, with a particular emphasis on

693 comparative regeneration dynamics among species. Second, we stress the need to account for

694 the roles of non-drought co-drivers of mortality, particularly the historical legacies of

695 management and land use, in order to understand current patterns of vegetation change and

696 improve predictions of future vegetation dynamics. Finally, we suggest that considering

697 vegetation shifts within biogeographical and successional contexts will improve understanding

698 of the underlying processes and the ecosystem-level implications.

699

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709

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Tables and Figures

Table 1. Case studies of 'drought-induced vegetation shifts' included in the literature review. Codes indicating type of change are explained in Figure 1. ID numbers correspond to those indicated in Figure 2.

ID	Name	Location	Climate	Vegetation type	Drought period	Scale of impact	Affected dominant species or veg. type	Replacing species or vegetation type	Funct. type shift*	Survival replacing species?	Regener. affected species?	Regener. replacing species?	Type of change	Abridged type of change	Other contributing factors	References
1	Afromontane forest Ethiopia	N Ethiopia	Dry	Forest	Late 1980s	Local	*Juniperus procera, Olea europapea*	Early successional shrubs	NET + BET -> BES	Yes	Low	na	UNb / SSf	UN	Management	(1) (2)
2	Atlas Cedar	N Morocco	Medit.	Forest	1993, 1995, 1999	Regional	*Cedrus atlantica*	*Quercus rotundifolia*	NET -> BET	Yes	na (low)	(Yes)	SSf	SS	Management, biotic agents	(3) (4)
3	Sahel woodlands Mali	Gourma, Mali	Dry	Woodland	1983-1984	Regional	*Acacia spp, Combretum glutinosum*	Shrubland	BDT -> BDS	na	Yes	Yes	Una / UNc	UN	Grazing	(5)
4	Sahel woodlands Senegal	NW Senegal	Dry	Woodland	1968-1973	Regional (ecotone)	*Taller trees with larger leaves*	Short, thorny trees	BET -> BDT	na	na	na	BS	BS	Management	(6)
5	Appalachian Forest E USA	North Carolina, USA	Temp.	Forest	1984-1989	Local	*Tilia americana, Fagus grandifolia*	*Acer saccharum, Aesculus flava*	BDT -> BDT	Yes	Yes	Yes	UNa	UN	Succession	(7)
6	Ash NE USA	NE USA	Temp.	Forest	1990s - 2000s	Regional	*Fraxinus nigra*	Shrubland	BDT -> BDS	(Yes)	Low	Low	UNb / BS	UN	Biotic agents, hydrologcal alterations,	(8) (9)

#	Name	Location	Climate	Type	Years	Scale	Species (dominant)	Species (replacing)	Transition						Drivers	Refs
															pollution	
7	Aspen decline N America	Western N America	Temp. / Boreal	Forest	2000s	Subcontinental	*Populus tremuloides*	Conifers / Shrubland	BDT -> NET + BDS	(Yes)	Low	(Low)	UNb / BS	UN	Biotic agents, succession, grazing	(10) – (15)
8	Austrocedrus Patagonia	N Patagonia, Argentina	Dry	Woodland	1950s	Regional (ecotone)	*Austrocedrus chilensis*	na	na	na	(Yes)	na	UN / RV / SR	UN	Wildfires, grazing	(16)
9	Conifers California	Sierra Nevada, California, USA	Medit. montane	Forest	1985-1995, 2000s	Regional	Mixed coniferous forest	na	na	na	Yes	na	UN / RV / SR	UN	Fire suppression, biotic agents	(17) – (20)
10	Evergreen rainforest Trinidad	Trinidad and Tobago	Tropical	Forest	1987-1988, 1994-1995	Local	Primary species	Pioneers	BET -> BET	Yes	Yes	Yes	UNa	UN	Succession, logging	(21)
11	Hemlock NE USA	Massacgusetts, USA	Temp.	Forest	1963-1975	Regional	*Tsuga canadensis*	*Pinus strobus, Acer rubrum*	NET -> NET + BDT	Yes	Yes	Yes	UNa	UN	Biotic agents, windstorms	(22)
12	Metrosideros Hawaii	Hawaii, USA	Tropical	Forest	1954-1985	Regional	*Metrosideros polymorpha*	*na*	BET -> BET	na	Yes	na	SR	SR	Cohort senescence	(23)
13	Nothofagus Patagonia	N Patagonia, Argentina	Temp.	Forest	1998-1999	Regional (ecotone)	*Nothofagus dombeyi*	*Austrocedrus chilensis*	BET -> NET	Yes	Low	Yes	SSf	SS	na	(24) – (27)
14	Oak-Juniper S USA	Texas, USA	Dry	Woodland	1951-1957, 2000s	Local	*Quercus virginiana, Quercus pungens*	*Juniperus ashei*	BET -> NET	Yes	Yes	Yes	UNa	UN	Grazing	(28)
15	Piñon-Juniper SW USA	SW USA	Dry	Woodland	1996, 2002-2005	Regional	*Pinus edulis*	*Juniperus monosperma / J.*	NET -> NES	Yes	Yes / No	Yes	SSf / UNa	UN	Biotic agents, wildfires	(29) – (33)

#	Name	Location	Climate	Biome	Year	Scale	Winner	Loser	Transition							Ref
							osteosperma									
16	Rainforests Costa Rica	NE Costa Rica	Tropical	Forest	1997-1998	Local	Secondary lowland rainforest	na	BES -> BES	na	(Yes)	(Yes)	Una / UNc	UN	Grazing, succession	(34)
17	Tropical Dry Forests Mexico	Jalisco, Mexico	Tropical	Forest	2005	Local	Trees	Shrubs	BDT -> BDS	Low	Yes	Yes	Unc	UN	Succession, biotic agents, grazing	(35)
18	Tropical forest Amazonia	Amazonia	Tropical	Forest	1990s	Subcontinental	Wet-affiliates	Dry-affiliates	BET -> BET	Yes	Yes	Yes	UNa	UN	Other disturbances, succession	(36)
19	Tropical Forests Panama	Barro Colorado Island, Panama	Tropical	Forest	1983	Local	Wet-affiliates	Dry-affiliates	BET -> BET	(Yes)	(Low)	(Yes)	SSf	SS	na	(37) – (39)
20	Beijing China	Beijing, China	Temp.	Forest	1986-2006	Regional	*Quercus* sp.	*Pinus tabuliformis*	BDT -> NET	Yes	na	na	UN / RV / SSf	UN	Air pollution	(40)
21	Tropical and subtropical China	S China	Tropical	Forest	1990s-2000s	Subcontinental	Tall and intermediate trees	Shrubs and small trees	BET -> BES	Yes	Low	Yes	SSf	SS	na	(41) (42)
22	Tropical forest Sarawak	Sarawak, Malaysia	Tropical	Forest	1997-1998	Local	Dipterocarpaceae	na	na	Yes	(Yes)	(Yes)	UN / RV / SSf	UN	na	(43)
23	Tropical rainforest Borneo	Sabah and East Kalimantan, Borneo	Tropical	Forest	1997-1998	Regional	Large trees	Small trees	BET -> BET	Yes	Yes	Yes	UNa	UN	Logging, succession	(44) – (46)
2	Coastal	S Victoria,	Temp.	Woodland	1997-	Local	*Eucalyptus*	*Allocasuarin*	BET ->	Low	No	Low	SSf	SS	Fire	(47)

No	Name	Location	Climate	Veg. type	Period	Scale	Declining species	Replacement species	PFT						Drivers	Ref
4	woodland Australia	Australia			2009		*spp.*	*a littoralis, A. verticillata*	BET						exclusion, succession	
2 5	Eucalyptus Queensland	Queensland, Australia	Dry	Woodland	1990s - 2000s	Regional	*Eucalyptus crebra, E. xanthoclada, E. melanophloia, E. populnea*	*Corymbia spp.*	BET -> BET	Yes	Yes	Yes	UNa	UN	Grazing, wildfires	(48) – (50)
2 6	Eucalyptus Tasmania	Central Plateau, Tasmania, Australia	Temp.	Forest	1990s - 2000s	Local	*Eucalyptus gunnii ssp. divaricata*	*Eucalyptus pauciflora*	BET -> BET	Yes	Low	Yes	SSf	SS	Grazing	(51) – (53)
2 7	Eucalyptus Western Australia	Western Australia	Medit.	Woodland	2010- 2011	Regional	*Eucalyptus marginata*	*Corymbia calophylla*	BET -> BET	Yes	Yes	Yes	UNa	UN	Biotic agents	(54)
2 8	Nothofagus New Zealand	S Island, New Zealand	Temp.	Forest	1970s	Local	*Nothofagus fusca*	*Nothofagus menziesii*	BET -> BET	Yes	Yes	Yes	UNa	UN	Biotic agents	(55)
2 9	Nothofagus New Zealand	N Island, New Zealand	Temp.	Forest	1970s	Local	*Nothofagus solandri*	na	BET -> BET	na	Yes	na	SR	SR	Biotic agents, succession	(56)
3 0	Beech England	S England	Temp.	Forest	1976, 1980s	Local	*Fagus sylvatica*	*Fraxinus excelsior / Quercus robur*	BDT -> BDT	Yes	No	Yes / No	SSf / UNb	UN	Biotic agents, windthrow	(57) (58)
3 1	Evergreen oaks Spain	Spain	Medit.	Forest / Woodland	1990s, 2000s	Regional	*Quercus ilex, Quercus suber*	Shrubs	BET -> BES	Yes	Yes	Yes	UNa	UN	Biotic agents	(58) – (63)
3 2	Fir S Europe	S Europe	Medit. montane	Forest	1980s - 2000s	Regional	*Abies alba*	*Pinus sylvestris,*	NET -> NET +	na	na	na	UN	UN	Biotic agents, logging	(64) – (66)

							Fagus sylvatica	BDT								
33	Pinsapo Spain	S Spain	Medit. montane	Forest	1990s - 2000s	Local	*Abies pinsapo*	*Quercus ilex, Q. faginea, Juniperus oxycedrus*	NET -> BET+BDT+NES	Yes	Yes	Yes	UNa	UN	Management, biotic agents	(67) – (69)
34	Scots pine Europe	Central & S Europe	Medit. montane / Temp.	Forest	1990s - 2000s	Regional	*Pinus sylvestris*	*Quercus spp.*	NET -> BET+BDT	Yes	Low	Yes	SSf	SS	Management, successional, biotic agents	(70) – (75)
35	Shrublands SW Spain	Doñana, S Spain	Medit.	Shrubland	2005	Local	*Halimium halimifolium, Rosmarinus officinalis, Cistus libanotis*	na	BES -> BES	na	Yes	na	SR	SR	na	(76) (77)

* Note: NET, needleleaf evergreen tree; BET, broadleaf evergreen tree; BDT, broadleaf deciduous tree; BES, broadleaf evergreen shrub; BDS, broadleaf deciduous shrub; NES, needleleaf evergreen shrub. References: (1) Aynekulu et al., 2011, (2) Mokria et al., 2015, (3) Bentouati, 2008, (4) Linares et al., 2011, (5) Hiernaux et al., 2009, (6) Gonzalez, 2001, (7) Olano and Palmer, 2003, (8) Palik et al., 2011, (9) Palik et al., 2012, (10) Frey et al., 2004, (11) Hogg et al., 2008, (12) Worrall et al., 2008, (13) Worrall et al., 2010, (14) Anderegg et al., 2013, (15) Coop et al., 2014, (16) Villalba and Veblen, 1998, (17) Savage 1997, (18) Guarín and Taylor, 2005, (19) Millar et al., 2007, (20) Van Mantgem and Stephenson, 2007, (21) Oatham and Ramnarine, 2006, (22) Bailo et al., 2004, (23) Boehmer et al., 2013, (24) Suarez et al., 2004, (25) Suarez and Kitzberger, 2008, (26) Suarez and Kitzberger, 2010, (27) Suarez and Sasal, 2012, (28) Twidwell et al., 2014, (29) Breshears et al., 2005, (30) Mueller et al., 2005, (31) Redmond and Barger, 2013, (32) Floyd et al., 2015, (33) Redmond et al., 2015, (34) Chazdon et al., 2005, (35) Maza-Villalobos et al., 2013, (36) Butt et al., 2014, (37) Condit et al., 1995, (38) Condit et al., 1996a, (39) Condit et al., 1996b, (40) Zhang et al., 2014, (41) Zhou et al., 2013, (42) Zhou et al., 2014, (43) Nakagawa et al., 2000, (44) Slik, 2004, (45) Newbery and Lingenfelder, 2008,

(46) Lingenfelder and Newbery, 2009, (47) Zeeman et al., 2014, (48) Fensham and Holman, 1999, (49) Rice et al., 2004, (50) Fensham et al., 2007, (51) Potts et al., 2001, (52) Calder and Kirkpatrick, 2008, (53) Sanger et al., 2011, (54) Matusick et al., 2013, (55) Hosking and Kershaw, 1985, (56) Hosking and Hutcheson, 1988, (57) Peterken and Jones, 1987, (58) Mountford et al., 1999, (59) Lloret et al., 2004b, (60) Lloret et al., 2004a, (61) Galiano et al., 2012, (62) Ibáñez et al., 2015, (63) Saura-Mas et al., 2014, (64) Camarero et al., 2011, (65) Cailleret et al., 2013, (66) Sangüesa-Barreda et al., 2015, (67) Linares et al., 2010b, (68) Linares et al., 2010a, (69) Navarro-Cerrillo et al., 2014, (70) Bigler et al., 2006, (71) Gimmi et al., 2010, (72) Galiano et al., 2010, (73) Galiano et al., 2013, (74) Vilà-Cabrera et al., 2013, (75) Rigling et al., 2013, (76) del Cacho and Lloret, 2012, (77) Lloret et al., 2015.

Figure 1. A framework to classify potential community dynamics after drought-induced mortality. The reference time frame for this classification is the typical generation time of the dominant species in the community (i.e., a shift will occur if the identity of the dominant species changes after one generation).
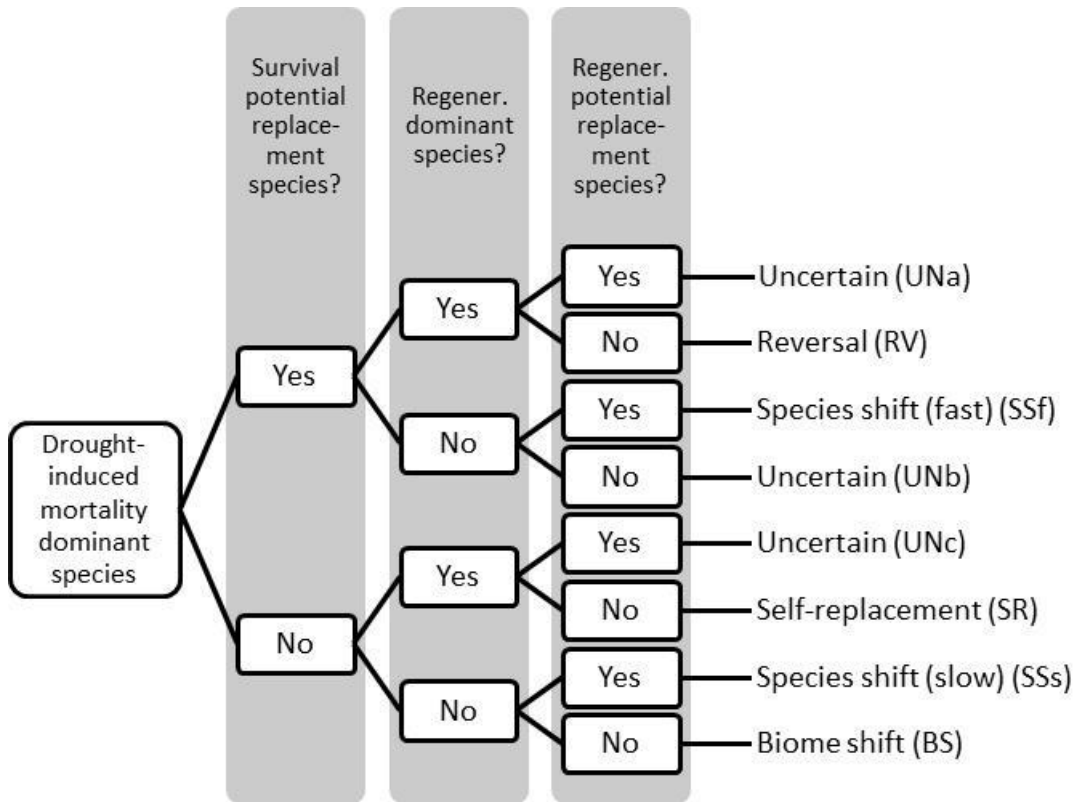
Figure 2. Approximate locations of case studies of possible vegetation shifts considered in this study. Individual case studies are classified according to the framework presented in Figure 1 (abridged as in Table 1: UN, uncertain; SR, self-replacement; SS, species shift; BS, biome shift). Case numbers correspond to ID numbers in Table 1. Note that all symbols have the same size irrespective of the spatial extent of the mortality event they represent.

Figure 3. Frequency of transitions between and within functional types reported in the case studies of possible vegetation shifts considered in this study. Arrows connect the functional type corresponding to the affected dominant species and the functional type of the potentially potential replacement species. Red arrows correspond to cases classified as species or biome shift (SSf, SSs or BS in Figure 1) and black arrows to the rest of cases (all other categories in Figure 1). Arrow thickness is proportional to the number of cases (also numerically noted with each arrow). NET, needleleaf evergreen tree; BET, broadleaf evergreen tree; BDT, broadleaf deciduous tree; BES, broadleaf evergreen shrub; BDS, broadleaf deciduous shrub; NES, needleleaf evergreen shrub.