DROUGHT-INDUCED VEGETATION ShiftS IN TERRESTRIAL ECOSYSTEMS: THE KEY ROLE OF REGENERATION DYNAMICS

Jordi Martínez-Vilalta¹,²,³ & Francisco Lloret¹,²

¹ CREAF, Cerdanyola del Vallès E-08193 (Barcelona), Spain
² Univ. Autònoma Barcelona, Cerdanyola del Vallès E-08193 (Barcelona), Spain
³ corresponding author

Name and complete mailing address of the author for correspondence:
Jordi Martínez Vilalta
CREAF, Campus UAB, Edifici C,
Bellaterra 08193 (Barcelona), SPAIN
Tel.: + 34 93 5813811;
Fax: + 34 93 5814151;
e-mail: Jordi.Martinez.Vilalta@uab.es

This is the author’s version of a work that was accepted for publication in Global and planetary change (Ed. Elsevier). Changes resulting from the publishing process, such as peer review, editing, corrections, structural formatting, and other quality control mechanisms may not be reflected in this document. Changes may have been made to this work since it was submitted for publication. A definitive version was subsequently published in Martínez-Vilalta, J. and Lloret, F. “Drought-induced vegetation shifts in terrestrial ecosystems: the key role of regeneration dynamics” in Global and planetary change, vol. 144 (Sep. 2016), p. 94-108.

DOI 10.1016/j.gloplacha.2016.07.009
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.

Keywords: Drought; Management; Mortality; Regeneration; Succession; Vegetation shifts
1. Introduction

The distribution of vegetation is largely determined by climate and, in particular, by temperature and water availability (Woodward, 1987). Ongoing climate change is modifying climatic conditions worldwide, with a general trend towards warmer temperatures globally and lower water availability in many regions of the Earth (IPCC 2014). Increased frequency of intense and hotter droughts have already been associated with widespread episodes of vegetation die-off (Allen et al., 2010, 2015) and with increases in background (non-catastrophic) forest mortality rates in some areas (Mantgém et al., 2009; Peng et al., 2011).

There is no doubt that widespread plant mortality could result in dramatic modifications in forests and other vegetation types, impacting the ecosystem services they provide to society (Anderegg et al., 2012). It is also clear that ecosystems will eventually adapt to the new climatic conditions. What is less clear, however, is how dramatic these changes will be, given the existence of strong stabilizing processes and the relatively high capacity of vegetation to absorb disturbances avoiding major changes in structure, composition and function (Connell and Ghedini, 2015; Lloret et al., 2012; Reyer et al., 2015). In particular, it remains to be established how close different ecosystem types are to climate-related tipping points and how likely it is that they suffer catastrophic regime shifts (Scheffer et al., 2001) under current and future climate conditions.

Here, we review the published evidence for recent drought-induced vegetation shifts worldwide, at any spatial scale ranging from local to continental. We first provide some background on the relationship between climate and vegetation distribution from a biogeographical perspective, focusing on drought. We then outline the state of the art in drought-induced mortality research and finally move to the core of the article in which we address 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, and 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?

2. Climate and the distribution of vegetation
The influence of climate on vegetation distribution is one of the best-established paradigms in ecology, at least at regional and continental scales (Woodward, 1987). Low temperatures and freezing limit hydraulic conductance and tissue integrity and low water availability reduces water transport capacity and carbon assimilation, potentially leading to hydraulic failure or carbon starvation (McDowell et al., 2011). The combination of high temperature and low rainfall results in a strong conflict between high atmospheric water demands and temperature regulation, on one side, and the need to reduce water use to accommodate low water availability on the other side. Accordingly, models considering the balance between water availability and demand are able to explain vegetation distribution to an important extent (Neilson 1995), illustrating the importance of drought conditions on determining vegetation composition, structure and functioning (Vicente-Serrano et al., 2013; Williams et al., 2013).

Changes in climate at the global scale are expected to affect general patterns of vegetation. Great effort has been devoted in recent decades to elucidate these modifications by using dynamic global vegetation models. These models are mainly based on the functional response of vegetation types to climate variables (Sitch et al., 2003). This mechanistic approach, together with the need to up-scale from local to continental scales has led to the use of plant functional types, which in fact often correspond to biome types, merging species with similar performance and habitat requirements and moving the modeling focus towards vegetation functional traits. Importantly, plant functional types are also designed to generally describe and quantify vegetation contributions to ecosystem properties and services (Bonan et al., 2002; Quétier et al., 2007). Thus, the distinction between the taxonomic, species-based conception of vegetation and the functional, traits-based one is important when considering vegetation shifts. Overall, these models point to important latitudinal movements of biome ecotones in the near future (Tang and Beckage, 2010). However, a key unresolved issue is the temporal dynamics of the transitions (i.e., gradual versus abrupt changes), which in turn result from the interaction of climate with other drivers, such as land use transformations, biota migrations and changes in fire regimes (Higgins and Scheiter, 2012; Reyer et al., 2015).

There are also a number of reasons why the accuracy of the predictions derived from vegetation models has been questioned, including methodological shortcomings related with data sources and modeling procedures (e.g., Moorcroft et al., 2001; Thuiller et al., 2008). In addition, difficulties in obtaining reliable predictions at local and landscape scales may be explained by species autoecology (genetic, ecophysiological and population responses to
environmental variability), biotic interactions (considering the network of facilitative and antagonist relations between plants) and historical background (including biogeographical legacy, disturbance regime, and changes in forest management and land use). All of these factors are relevant to interpretation of climate-induced vegetation shifts at landscape and stand levels by reinforcing or counterbalancing the theoretical equilibrium between climate and plants (García-Valdés et al., 2015).

The existence and characteristics of vegetation shifts can be studied from paleohistorical records. There is abundant literature reporting a correspondence between vegetation change and climate, particularly drought, across a variety of biomes (Calò et al., 2013; Clifford and Booth, 2015; Schmieder et al., 2013; Shuman et al., 2009). There are, however, important limitations associated with this type of paleo-studies (cf. Swetnam et al., 1999). First, paleo-records commonly have coarse temporal resolutions from an ecological perspective, as abrupt transitions of woody vegetation may occur at decadal scales. Advances in dating resolution are providing support for the existence of vegetation shifts at centennial scales (Williams et al., 2002), and we expect finer resolution to be available in the future (i.e., Calò et al., 2013). Second, the attribution of vegetation changes to the climate’s influence is not always unequivocal because climate changes are inferred from indirect sources, typically sedimentary measures and biological indicators like pollen (i.e., Calò et al., 2013; Schmieder et al., 2013) that should be complemented by other climate proxies, such as stable isotopes (Shuman et al., 2009). Studies in temperate forests in NE North America provide an example of the correspondence between abrupt climatic events involving drought – estimated from hydrogen stable isotopes - and rapid vegetation changes at temporal scales that are reasonably close to ecological processes (500 years) (Shuman et al., 2009). The relationship between climate and vegetation shifts, however, is often complex due to the interaction with other drivers, particularly disturbance regimes, involving insect outbreaks, wildfires and human activity (Calò et al., 2013; Clifford and Booth, 2015; Foster et al., 2006). In short, at relatively long temporal and broad spatial scales the strong overall relationship between climate and vegetation changes is firmly sustained, but higher resolution information that could elucidate the nature and velocity of such relationships at finer scales merits further research.

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

Drought-induced vegetation mortality has been reported in many areas worldwide, frequently associated with high temperatures, and the number of reported mortality episodes has
increased dramatically over the last years (Allen et al., 2010; Williams et al., 2013). There is
some concern, however, regarding the extent to which this trend reflects a global increase in
vegetation mortality or the recent increase in detection effort (Martínez-Vilalta et al., 2011;
Steinkamp and Hickler, 2015). In addition, the multiplicity of disturbances affecting forests and
the diversity of factors that may contribute to observed mortality patterns makes the
attribution of causes difficult (cf. Allen et al., 2015; McDowell et al., 2015). In many cases, for
instance, the effects of drought interact with those of rapid successional dynamics associated
to changes in forest management (e.g., Vilà-Cabrera et al., 2010), and disentangling these two
effects remains challenging.

Despite much research effort, the mechanisms underlying drought-induced plant mortality
remain insufficiently understood (McDowell et al., 2008, 2011; Sala et al., 2010), and a
definitive classification of plant physiological strategies to face drought is still lacking (Klein,
2014; Martínez-Vilalta et al., 2014). An important outcome of recent studies on the
mechanism of drought-induced mortality is the realization that water and carbon economy of
plants are tightly linked during extreme drought, so that failures in the water and carbohydrate
transport systems (hydraulic and phloem failure, respectively) and extreme carbohydrate
depletion (carbon starvation) are likely to co-occur (Mencuccini et al., 2015; Parolari et al.,
2014; Sevanto et al., 2014). The contribution of biotic factors and their interaction with the
physiological mechanisms of mortality (Gaylord et al., 2013; Oliva et al., 2014) further
complicates attribution (Anderegg et al., 2015b). The complexity of mortality mechanisms is
problematic because it limits our capacity to assess the causes of a given mortality event, as
well as our capacity to predict when and where these events are likely to occur in the future
(McDowell et al., 2013). In that regard, comparative physiological studies of drought responses
of coexisting species, either in the field or under controlled experimental conditions (e.g.,
Garcia-Forner et al., 2015; Nardini et al., 2015), are likely to be particularly useful.

Many studies have found an association between climate anomalies and drought-induced
mortality at different spatial and temporal scales (e.g., Fensham et al., 2009; Suarez and
Kitzberger, 2010; Mitchell et al., 2014). Spatiotemporal patterns of drought-induced vegetation
mortality, however, tend to be complex. At relatively small spatial scales (stand to catchment),
high mortality rates often are associated with shallow soils (Gitlin et al., 2006; Vilà-Cabrera et
al., 2013), higher exposure to radiation (Gitlin et al., 2006), low topographic soil moisture
(Galiano et al., 2010), dense stands (i.e., higher competition) (Guarín and Taylor, 2005; Vilà-
Cabrera et al., 2013), and biotic agents (Gaylord et al., 2013). However, exceptions are common, and even within a particularly well-documented system such as the piñon-juniper woodlands in SW USA the degree of discrepancy between studies can be remarkable (Meddens et al., 2015), likely reflecting high spatial variability in climate, soils, topography and disturbance history (Romme et al., 2009; Swetnam and Betancourt, 1998). In general, complex interactions between factors leading to mortality are not always easy to capture in statistical models based on ‘opportunistic’ field observations.

At broad spatial scales, additional processes need to be considered. For instance, changes in species dominance along aridity gradients imply that drought resistant species (in absolute terms) tend to occupy drier habitats and may not be necessarily closer to their physiological limits (relative to the local conditions where they live). As a result, predicting what species and populations are more vulnerable to a given precipitation anomaly is not straightforward. This is consistent with observations of drought-induced mortality in wet environments (e.g., tropical rainforests (Phillips et al., 2009)) and with the fact that hydraulic safety margins have been reported to be similar across biomes at the global scale (Choat et al., 2012). Within species, functional and morphological traits vary widely along environmental gradients (e.g., Siefert et al., 2015; Vilà-Cabrera et al., 2015), and the balance between plasticity and local adaptation processes becomes critical (Valladares et al., 2014). Despite all these complications, recent studies show promising avenues. For instance, populations occupying more marginal locations within the species’ bioclimatic niche are more affected by drought-induced die-off in Mediterranean woody communities (Sapés, 2013). In another recent report, climatic water deficit simulated from a hydrologic model was able to predict regional patterns of *Populus tremuloides* mortality with 75% accuracy (Anderegg et al., 2015a). Similarly, a logistic regression using species identity, mean climate and climate anomalies for a given year provided a reasonably good fit to regional patterns of forest decline in NE Spain (Chaparro, 2013).

4. On the necessary conditions for vegetation shifts to occur

Vegetation shifts are a particular case of ecosystem regime shifts, which can be defined as large, relatively rapid and persistent reorganizations of the state of ecosystems (Brook et al., 2013). Regime shifts may result from a large permanent change in environmental conditions, but may also result from relatively small or transient changes in environmental drivers (Scheffer et al., 2001; 2012). This second type of regime shifts implies the presence of tipping
points, and is frequently (but not always) associated with the existence of multiple ‘stable’ states (Petraitis, 2013). Tipping points are associated with positive feedbacks that, once a critical threshold is passed, propel change toward an alternative state (Scheffer et al., 2012). The kind of vegetation shifts we are concerned with here occur when a pulse-type disturbance (i.e., a drought) triggers a reorganization of the ecosystem that is maintained after environmental conditions return to pre-disturbance levels. This definition of drought-induced vegetation shifts is an example of catastrophic regime shift and involves multiple ‘stable’ states and hysteresis (the return path to the original state differs from the original trajectory that led to the current state, making the change difficult to reverse) (Scheffer et al., 2001).

Several studies have documented evidences of catastrophic regime shifts in ecosystems (Folke et al., 2004; Scheffer et al., 2001). Although most of them come from aquatic environments (particularly lakes and marine systems), there are also examples from terrestrial ecosystems. Among those, some of the best characterized cases include desertification in the Sahara region (Foley et al., 2003; Janssen et al., 2008), forest-woodland ecotones (Allen & Breshears, 1998), transitions between forest, savanna and treeless states in tropical systems (Hirota et al., 2011; van Nes et al., 2014), and peatland dynamics (Hilbert et al., 2000) or transitions between forests, treeless tundra and steppe in the boreal biome (Juday et al., 2015; Scheffer et al., 2012). However, detecting multiple ‘stable’ states and catastrophic shifts from temporal and spatial patterns is difficult, mainly due to the difficulty of having proper controls and long-enough time series (Petraitis, 2013; see also Andersen et al., 2009; Scheffer and Carpenter, 2003). The use of spatial patterns is particularly problematic, as shown, for instance, by the controversy around the use of spatial vegetation patterns (in particular, their patch size distribution) as a suitable indicator of catastrophic vegetation shifts in drylands (Kéfi et al., 2007; Maestre and Escudero, 2009; Rietkerk et al., 2004).

We argue here that a demographic approach provides a useful framework for detecting and assessing potential vegetation shifts. From a demographic perspective, a vegetation shift implies an abrupt change in the relative abundances of dominant species in a community (composition), and should be reflected in the demographic rates of the species involved (Lloret et al., 2012). In particular, such a change requires that the formerly dominant species are replaced by other potentially dominant ones, which would normally be present in the community before the drought but may also colonize after it. The typical process leading to a drought-induced vegetation shift can be conceptualized in four steps: (i) a drought event
causes high adult mortality rates in (at least) one dominant species; (ii) these adult mortality rates are higher than those experienced by one or more potential replacement species; (iii) these potential replacement species show substantial regeneration; and (iv) regeneration of the initially dominant species is very low or absent. However, other combinations may also lead to a vegetation shift (see Figure 1 for a complete classification).

More generally, and based on the criteria presented in the previous paragraph, we can distinguish several situations (Figure 1):

**Vegetation shift.** Arguably, the most important condition for a vegetation shift to occur is that regeneration of a potential replacement species is successful during a relevant time period after the mortality event. If, in addition to that, there is no regeneration of the formerly dominant species, the evidence for a shift is clear. In principle, the shift will be faster if adults of the potential replacement species have survived (SSf in Figure 1) than if not (SSs).

**No shift.** Vegetation composition will remain unchanged in the mid-term if the formerly dominant species regenerates while the potential replacement species does not. In these cases, we may refer to reversal (RV), when adults of the potential replacement species survive achieving transitory dominance, or to self-replacement (SR), when such survival is not observed.

**Uncertain outcome.** If regeneration of both the formerly dominant and the potential replacement species is observed, the final outcome is uncertain. Obviously, the likelihood of a shift is higher if there is adult survival of the potential replacement species (UNa) than if not (UNC). In addition, if there is no regeneration of the dominant or potential replacement species, but there is survival of adults of this latter species, the outcome is also uncertain (UNb), although a species shift may still take place in the long-term.

**Biome shift.** When there is neither regeneration nor survival of adults of the dominant or potential replacement species, the most likely outcome is colonization by a new species not represented in the original community or, in extreme cases, complete loss of vegetation (i.e., transition to bare soil). We refer to such changes as biome shifts (BS).

Temporal considerations are critical in any framework aiming at classifying potential vegetation shifts. In our case (Figure 1), the reference time frame 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). We assume that observations on mortality and regeneration are taken shortly (up to a few years) after the mortality event, as is usually the case, and are used to assess subsequent community dynamics. In order for vegetation shifts to
be realized, measured demographic rates should be good estimates of per-capita rates of population growth, and should continue at similar rates for long enough to drive the system into a new state (cf. Petraitis, 2013). For instance, enough time without other major disturbances is required for the new community to develop. The opposite case should also be considered, as repeated droughts may lead to disproportionate effects relative to the impact of a single drought of the same intensity, due to legacy effects (Anderegg et al., 2015c). In addition, many vegetation types (particularly forests) are inertial systems where adults can live for hundreds of years and mortality and recruitment may depend on different environmental drivers and be highly decoupled in time (Shugart and Urban, 1989). Under directional climate change, a shift in such systems may occur simply because the original ecosystem cannot develop under the new conditions, even if it could have been maintained in the absence of the disturbance triggering the shift (Dobrowski et al., 2015; Smith et al., 2009).

5. Characterization of recent drought-induced vegetation shifts

We conducted a literature review of papers reporting drought-induced vegetation shifts. We started by searching the Web of Science (accessed 15/05/2015) with the following keywords (topic search): (vegetation OR forest OR woodland OR shrubland OR biome) AND (shift$ OR change$ OR transition$ OR replacement$ OR substitution$ OR succession) AND drought$ AND (mortality OR die-off OR dieoff OR decline OR die-back OR dieback) AND (regeneration OR recruitment). This search resulted in a list of 319 papers. The abstracts of all these papers were checked to select papers fulfilling the following criteria: (i) they were field-based, original research papers (i.e., reviews, studies under experimentally controlled conditions and purely modelling papers were excluded); (ii) they studied ‘natural’ vegetation (e.g., forest plantations were excluded), (iii) they studied the effects of a drought event that occurred at a well-defined point in time (i.e., a pulse event) after 1950; (iv) they measured or made some inference on the vegetation dynamics after the drought event. The list was completed with a few additional case studies from Allen et al. (2010) or other key references that had not been detected in our initial query. Selected papers were organized by case studies, so that articles studying a similar transition within the same broadly defined region were pooled together to avoid giving extra weight to more intensively studied systems, and each case was classified according to the framework presented in Figure 1 (Table 1).

Our final list included 35 case studies (Table 1 and Figure 2). The majority of them (N = 24) were classified as uncertain according to the framework in Figure 1, whereas 7 corresponded
to species shifts, three to self-replacements and one to a biome shift (Figure 2). Uncertain cases were mostly associated to two different situations. The first was lack of information regarding either mortality of the potential replacement species or regeneration of the affected or replacement species (N = 7). Secondly, in 15 instances uncertainty arose from similar levels of regeneration of both the initially affected and the potential replacement species, precluding inferences on the mid-term trajectory of the study system. Finally, in two cases (piñon-juniper woodlands in SW USA and beech in England) uncertainty resulted from inconsistencies in the regeneration patterns (of the affected and potential replacement species, respectively) reported in different studies carried out in the same systems. We note, however, that the piñon-juniper vegetation occurs over a wide range of environmental conditions and includes different pine and juniper species (Romme et al., 2009). Therefore, inconsistencies in regeneration patterns across studies likely reflect different trajectories (including SSf, UNa and probably also BS) in different parts of the range of this vegetation type.

The seven cases corresponding to species shifts occurred in temperate, Mediterranean and tropical climates, whereas the recorded biome shift was reported in a dry climate (Table 1 and Figure 2). The low sample size makes it difficult to reach any strong conclusion on the spatial distribution of these shifts, but they seem to be widely distributed across biomes and climate types. Regarding the spatial scope, reported vegetation shifts went all the way from local to subcontinental scales. In five cases other drivers besides drought were mentioned in the corresponding papers, including biotic agents and land management (e.g., grazing, fire use).

To explore the functional implications of the potential vegetation shifts described in the different case studies we classified them depending on the functional type of the affected dominant species and the potential replacement one(s) (Table 1). Functional types were defined based on broad plant classification (needleleaf / gymnosperm vs. broadleaf / angiosperm), leaf habit (deciduous vs. evergreen), and growth form (tree, shrub, herb), similarly to Lawrence and Chase (2007). Only six thus defined functional types were represented in our case studies: needleleaf evergreen tree, NET; broadleaf evergreen tree, BET; broadleaf deciduous tree, BDT; broadleaf evergreen shrub, BES; broadleaf deciduous shrub, BDS; and needleleaf evergreen shrub, NES. When there was more than one functional type represented in the affected dominant species or in the potential replacement species within a case study, we considered as many trajectories as combinations of functional types occurred in each case.
When all cases were considered (39 individual trajectories), there were 17 trajectories (44%) implying no change in functional type even if the vegetation shift was realized (i.e., the affected and potential replacement species belonged to the same functional type) (Figure 3). BET -> BET transitions (a broadleaf evergreen tree being replaced by the same or another species of the same functional type) were the most common situation overall (N = 11 trajectories). Directional (i.e., non-circular) trajectories originating from NET and BET were more common than directional trajectories ending in these functional types (10 vs. 4 and 6 vs. 3 for NET and BET, respectively). Overall, there were 10 transitions from trees to shrubs, whereas the opposite change was not observed. Transitions between species with different leaf habit were relatively rare, but were more common from evergreen to deciduous (N = 5; mostly NET -> BDT) than the opposite (N = 2). Only nine trajectories corresponded to species or biome shifts according to our scheme (Figure 1; red arrows in Figure 3). Of these, three corresponded to BET -> BET transitions. Trajectories corresponding to species or biome shifts affected only NET or BET functional types (three in each case).

Finally, the three cases in which self-replacement was observed affected broadleaf evergreen species (two BET, one BES) and occurred in different climatic regions (tropical, temperate and Mediterranean). More generally, a shift seems unlikely, at least in the short term, whenever regeneration of the affected species is observed, even if potential replacement species are also regenerating. If we add the 15 uncertain cases in which there was regeneration of the affected species (UNa, UNc in Figure 1) to the self-replacement cases, we end up with 18 cases (51% of 35 case studies) in which the weight of the evidence seems to be against the occurrence of a vegetation shift.

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

We only found eight case studies that fulfilled our criteria to be considered drought-induced vegetation shifts (species or biome shifts in Figure 1). And even these cases correspond only to situations in which the available evidence, often representing a short time period, is consistent with the occurrence of a shift; and not necessarily to cases in which these shifts are certain or even likely. We acknowledge that our search criteria were biased towards identifying instances of vegetation change that had been placed in a demographic context (see previous section). Although we accept that this might have resulted in missing some convincing cases of drought-
induced vegetation shifts, we argue that this effect is likely to be minor, as it is difficult to
describe and attribute recent (post-1950) vegetation shifts without assessing demographic
rates (mortality and regeneration). Considering the low number of drought-induced vegetation
shifts we detected, a reasonable first conclusion would be that these shifts are not yet
common or detectable. However, this conclusion needs qualification in some respects (see
also Hughes et al., 2013). Firstly, vegetation shifts are likely to be inherently rare events, and
their detection by standard vegetation monitoring systems, such as national forest inventories,
is inefficient. As a result, most reports of vegetation shifts arise from opportunistic studies
initiated by scientists as a response to an observed mortality event. While informative, this
approach makes it difficult to assess the spatial representativeness of the event and to
evaluate the subsequent community dynamics for a sufficiently long period (cf. White and
Jentsch (2001) on the importance of the scale of observation). Secondly, and related to the
previous point, regeneration is frequently the key ecological process determining long-term
community dynamics. However, it rarely has been assessed in studies of drought-induced
mortality. Thirdly, recent climatic impacts on vegetation have occurred in the presence of
other important drivers, in most cases directly related to human activities (e.g., changes in
land-use, grazing practices, forest management, fire use). These three aspects are addressed in
the following sub-sections.

6.1. Need for long term monitoring with sufficient temporal resolution

Better vegetation monitoring systems are urgently needed if we are to assess how common
drought-induced vegetation shifts currently are and make sound projections of how frequent
they are going to be in the future (see Allen et al. (2010) and Hartmann et al. (2015) for similar
assertions in the context of drought-induced tree mortality). An adequate monitoring system
should have, at least, the following characteristics: (i) it should be able to distinguish different
vegetation types (i.e., changes in composition), not only changes in canopy structure and
physiological state; (ii) it should cover a spatially representative area and have the potential to
become global; (iii) it should have sufficient spatial and temporal resolution to detect the
processes of interest; and, critically; (iv) it should be long-term. It seems clear that remote
sensing holds the greatest promise for such a system, particularly at broad regional or global
scales (Hansen et al., 2013; McDowell et al., 2015). However, ground-based inventories also
will be essential, as most remote sensing techniques require extensive ground evaluation and
frequently lack the desired spatiotemporal resolution (McDowell et al., 2015; Trumbore et al.,
2015; although cf. Asner et al., 2016).
While standard national forest inventories (NFIs) are well-suited for assessing changes in tree biomass and carbon stocks (e.g., Mohren et al., 2012), they have important limitations for detecting vegetation shifts. Firstly, plot size (<< 1 ha) and distribution are not designed to capture relatively infrequent events, such as drought-related disturbances. Secondly, the time interval between surveys (frequently > 5 years) makes it difficult to attribute changes in structure or composition to a specific cause. Thirdly, forest inventories commonly lack accurate information about regeneration, a key process to obtain projections of forest dynamics (see next section). Finally, NFIs do not sample non-forested areas, which seriously limits their capacity to detect changes between forests and other vegetation types. Many of these limitations are shared by forest health monitoring programs, such as the European ICP-Forests, despite their usefulness for detecting long-term changes in tree condition (e.g., drought-related leaf loss: Carnicer et al., 2013). Standardized, broad scale plot monitoring networks, such as the recently launched CTFS-ForestGEO (Anderson-Teixeira et al., 2014) offer great promise due to their relatively large plot sizes and global coverage, but they still suffer from relatively infrequent surveys (~5 years) and lack of coverage of non-forested areas.

6.2. It is about regeneration, of course!

Recent research on drought-induced vegetation change has focused on plant mortality. While this is normal, as mortality is the most conspicuous and immediate effect of an extreme drought, we argue here that this focus should be complemented with a greater emphasis on the demographic responses following the mortality event. Even after devastating adult mortality, a vegetation shift will only occur if the initially affected species is not able to regenerate and become dominant again (Lloret et al., 2012). It is clear from our review that self-replacement or reversal (cf. Figure 1) may be common outcomes of drought-induced mortality events, at least in the short term. This result is not surprising in the context of other disturbances. For instance, self-replacement (cf. direct regeneration) has been long known to be a common response of Mediterranean communities after fire, which originated the term ‘autosuccession’ (Hanes, 1971; Trabaud and Lepart, 1980). Although we now know that autosuccession does not always occur (Rodrigo et al., 2004), it remains the most common response to wildfire in Mediterranean systems (Pausas et al., 2009) and it has also been reported in many other ecosystem types in response to a variety of disturbances (Johnstone and Chapin, 2006; Zeppenfeld et al., 2015). Of course, the fact that there is regeneration of the affected species soon after a mortality event does not rule out the possibility that a vegetation
shift will occur in the mid-term. This is particularly true in the context of strong directional climate change, as sustained temperature raise and associated drivers (biotic agents, wildfires) may result in future failure of seedling recruitment in areas with good regeneration under current conditions (Allen et al., 2015; Brando et al., 2014; McDowell et al., 2016; Williams et al., 2013).

In order to understand when and where a species or biome shift is likely to occur, as opposed to self-replacement, we need to place the focus on regeneration dynamics at appropriate temporal scales. The distinction between the ‘habitat niche’, defined by the requirements of mature plants, and the ‘regeneration niche’, defined as the requirements for a successful replacement of mature individuals (Grubb, 1977), becomes relevant in that context. Self-replacement will be likely to occur after drought-induced mortality when the regeneration niche of the affected species is at least as wide as its habitat niche, particularly with regards to water availability. It is normally assumed that juveniles of a given species have narrower niches than adults (Jackson et al., 2009), and most studies seem to support this view (e.g., Bell et al., 2014; Dobrowski et al., 2015). In the case of water availability, an important reason for that is that seedlings typically have much shallower root systems than adults (the situation may be different for resprouts; see below), limiting their capacity to access deep water sources (Pratt et al., 2008). However, inherent climatic variability, particularly in water-limited systems, may offer pulses of suitable conditions for regeneration (Swetnam and Betancourt, 1998). The local conditions after mortality events may change substantially relative to pre-disturbance conditions, including likely increases in resource availability per capita (particularly light but also water and nutrients), and reductions in the capacity of the canopy to moderate environmental conditions (temperature, vapor pressure deficit). These changes are likely to interact with each other (von Arx et al., 2013) and, collectively, will determine the likelihood of self-replacement and overall community stability (Frelich and Reich, 1999).

As in other disturbances, gap size distributions and shade tolerance of the species in the community are likely to play an important role, as well as the fact that tradeoffs between shade and drought resistance are common (Niinemets and Valladares, 2006). Gap sizes opened by drought-induced mortality are likely to be smaller than those characteristic of other disturbances (e.g., fire), and may not be enough to shift the balance in favor of the regeneration of shade-intolerant species. In the case of the relatively shade-intolerant Scots pine in Europe, for instance, adult mortality has been shown to have a negligible or even
negative effect on its regeneration, while favoring the relatively shade-tolerant oaks (Galiano et al., 2013, 2010; Rigling et al., 2013). The fact that shade tolerance of juveniles and adults is correlated across species, albeit with an important scatter (Valladares and Niinemets, 2008), may help predicting community dynamics after disturbance. There is a clear need, however, for further studies assessing seedling performance relative to adults and comparing it among coexisting species under changing environmental conditions. It is also important to recognize and study the implications of different regeneration strategies. The ability to resprout is a key trait, as it enables the survival of individuals and allows rapid recovery of aboveground biomass after disturbance (Bellingham and Sparrow, 2000; Bond and Midgley, 2001; Clarke et al., 2013). Resprouting is common in many ecosystems (Vesk and Westoby, 2004) and, although it has been studied mostly in the context of vegetation responses to fire, wind throw and clipping, recent papers stress the importance of resprouting in the context of drought stress (Pausas et al., 2015; Zeppel et al., 2014). Drought response strategies frequently co-vary with resprouting ability, which makes it difficult to establish clear associations between this latter trait and vulnerability to drought (Pausas et al., 2015; Saura-Mas and Lloret, 2010). In general, the fact that resprouters typically recover faster than non-resprouters after disturbance, including drought (Zeppel et al., 2014), implies that reversals and self-replacements (cf. Table 1) may be more common when resprouting species are affected. This situation, however, may only apply to certain drought regimes (Pausas et al., 2015). In particular, the ability of resprouting species to persist is likely to decline as the frequency of extreme droughts increases. This is mostly due to the fact that repeated resprouting requires sufficient time between disturbances for reserves (particularly carbohydrates) to build up again (Canadell and López-Soria, 1998). In addition, some studies have identified physiological differences between resprouting and undisturbed individuals, suggesting that the former are more sensitive to drought (Pausas et al., 2015).

6.3. Key role of interactions with other drivers

A necessary condition for the occurrence of a vegetation shift is the differential performance of species in terms of adult survival or the recruitment of new cohorts (Figure 1). In many cases, these differences reflect species-specific tolerances to the conditions generated by standing vegetation or by mortality-induced gaps. There is general consensus on the relevance of multiple factors other than the attributes of the species involved in determining tree death, even in cases where drought is well documented (e.g., Frey et al., 2004; Galiano et al., 2010). It
is more difficult, however, to disentangle the contribution of such factors on species differential responses, particularly because they usually interact to reinforce or stabilize complex feedbacks. These factors typically include pests and pathogens, grazing, pollution, wildfires and microsite conditions, particularly soil characteristics. These co-drivers of vegetation dynamics often operate at fine spatial scales, undermining our capacity to obtain global patterns in the relationship between water availability and tree mortality, except for drier locations (Steinkamp and Hickler, 2015). In our literature compilation, we found that 86% out of 35 selected case studies recognize the influence of co-drivers. The most common factor was the interaction with biotic agents, which mainly involved pests and pathogens (43% of the cases) and grazing (20%). Forest management, including logging, was also considered relevant in 23% of cases; whereas other disturbances, such as wildfires (14%), seem to play a relevant role only in some regions. The number of studies considering the relevance of non-climatic factors as determinants of recruitment following drought-induced mortality was much lower than those addressing the role of these factors on mortality patterns. In addition, most studies only conducted a general assessment of regeneration without formal test of hypotheses, and particularly the interaction between climatic and non-climatic factors was rarely addressed.

Contributing factors are often a source of uncertainty when assessing vegetation shifts at fine spatial scales given their idiosyncratic variability, but also because we commonly lack information on their historical influence (i.e., land-use, grazing, forest management, disturbance regime). Nevertheless, we can identify different situations according to their potential interaction with drought episodes. First, co-drivers may enhance mortality by establishing synergies with drought conditions. For instance, severe drought induces reserve depletion in trees, increasing their vulnerability to pests and pathogens (Gaylord et al., 2013; Jactel et al., 2011). In turn, these antagonistic attacks could reduce carbon reserves, eventually conducting to a reinforcing feedback between drought and biotic agents (Oliva et al., 2014). The outcome of these interactions may involve time lags, confounding the contribution of different agents and highlighting the importance of considering medium-term tree survival in addition to mortality pulses. For instance, bark beetles may initiate a successful infestation under drought conditions, in some cases eventually reaching a demographic threshold leading to the death of trees that were not severely affected by drought itself (Allen, 2007).

Analogously, drought can have strong direct and indirect synergistic effects on wildfires; e.g., fine and coarse fuel loads can temporarily increase and change in structure with drought-induced tree mortality, which can change the size and severity of fires (along with drought and
land-use), which in turn can jeopardize tree survival and regeneration (Allen, 2007). Ongoing climate changes are projected to foster increased wildfire activity in many ecosystems (IPCC, 2014). In Mediterranean systems, fire risk may rise until fuel loads become too low due to water limitations on vegetation growth, while the new climate conditions become less favorable to post-fire vegetation recovery (Batllori et al., 2013; Loepfe et al., 2014).

Other drivers can contribute to vegetation dynamics without being themselves directly promoted by drought conditions. This is the case of disturbances such as windstorms (Bailo et al., 2004) or pollution (Palik et al., 2011) that further diminish adult survival in addition to drought. Both mortality and post-drought regeneration of Populus tremuloides in N America have been proposed to be impacted by grazing (Worrall et al., 2008), but the contribution of herbivores to the differential performance of dominant and potential replacement species needs further study. Although browsing itself can hardly be linked directly to drought conditions, regeneration control by grazing often occurs in semi-arid ecosystems (Maza-Villalobos et al., 2013; Twidwell et al., 2014). Potentially, other factors may counterbalance drought impacts, increasing resilience (Lloret et al., 2012). Some of these factors can involve biotic interactions, such as facilitation, which in turn can be influenced by climatic conditions, including drought. However, the contribution of positive biotic interactions on post-drought vegetation dynamics has been rarely assessed (Lloret and Granzow-de la Cerda, 2013).

Finally, management constitutes one of the major drivers of vegetation dynamics all over the world and it surely affects the likelihood of drought-induced mortality and subsequent vegetation responses. Management history may increase forest vulnerability to drought through several mechanisms, thus enhancing species shifts. First, management may promote expanding populations to (or beyond) the edge of the species historic distribution, close to its physiological limits of tolerance for both adults and juveniles (e.g., Sánchez-Salguero et al., 2012). Second, increased stand density as a result of past logging (Camarero et al., 2011; Slik, 2004), abandonment (Linares et al., 2010b) or fire exclusion (Breshears et al., 2005; Guarín and Taylor, 2005) may lead to higher competition for water resources. Remaining adult trees and new recruits also may be damaged during wood harvesting (Aynekulu et al., 2011). In addition, regeneration may be depleted due to overgrazing (Linares et al., 2011). At regional scales in arid regions, overexploitation of standing biomass can exacerbate rainfall decline, leading to a positive feedback between bare soil cover and aridity (Gonzalez, 2001). Alternatively, stand density reductions (Grant et al., 2013) or direct promotion of regeneration can boost self-
replacement or vegetation shifts depending on the favoured species. In contrast with drivers that are the result of processes operating at global or regional scales, these more local management actions (grazing control, modification of stand structure, species selection) may be used as tools to delay or modify local trajectories of vegetation dynamics.

6.4. Functional and biogeographical context

Altered climatic conditions will eventually lead to changes in vegetation biogeography. Theoretical predictions, niche correlative methods and process-based models all support future modifications in the distribution of vegetation and biomes (Sitch et al., 2003; Tang and Beckage, 2010). However, in spite of substantial evidence of the occurrence of drought-induced tree mortality, we are not yet observing widespread vegetation shifts in response to increasing drought conditions. An important necessary condition for these shifts to occur is the existence of a species pool providing potential replacement species. In some reported cases, uncertainty arises because there is no clear replacement tree species (Boehmer et al., 2013; Villalba and Veblen, 1998); in other cases, understory shrubs are the immediate candidates to occupy the gaps opened by tree mortality (Palik et al., 2012, 2011; Saura-Mas et al., 2014; Worrall et al., 2010). In these cases, vegetation responses can often be placed within a successional framework of species replacement following disturbance. The same applies to other studies that point to replacements between coexisting trees with different degree of shade tolerance or successional status in temperate (Galiano et al., 2010; Olano and Palmer, 2003) and tropical forests (Chazdon et al., 2005; Oatham and Rammarine, 2006). Self-replacement can also be placed in this successional framework when new cohorts of standing vegetation can tolerate the conditions imposed by drought, as in Mediterranean shrublands (del Cacho and Lloret, 2012; Lloret et al., 2015), or when drought triggers the decay expected to occur in old cohorts (Boehmer et al., 2013). At the other extreme of species pool availability, studies in diverse tropical forests consistently report structural changes leading to shorter species and lower basal area (Zhou et al., 2014, 2013). Although these structural modifications may correlate with compositional changes at the stand level, the existence of directional shifts at the local scale is less clear, given the high spatial turnover of species in these forests (Lingenfelder and Newbery, 2009; Slik 2004; Zhou et al., 2014, 2013) (but see Fauset et al. 2012) for long-term drought. The relevance of the available species pool in determining future vegetation trajectories highlights the vulnerability of many managed, impoverished forests. The enhancement of woody species diversity in forests, particularly if it is based on native species covering a wide range of bioclimatic niches and genetically diverse populations,
constitutes an important management opportunity to improve resilience in forests facing future drier conditions (Jump et al., 2009a; Fauset et al., 2012; Morin et al., 2014; but see Grossiord et al., 2014).

Overall, current evidence does not show generalized shifts in vegetation functional types induced by drought. This is true even where species replacement is likely to occur, supporting the role of species functional redundancy within communities in promoting resilience. This is particularly clear in tropical forests dominated by BET, as stated above (but see Fauset et al. 2012). However, in the instances in which changes in the dominant functional type are predicted, trajectories generally agree with expectations of vegetation responding to drier conditions by favouring species with higher drought resistance. Temperate, relatively moist forests dominated by NET tend to be replaced by BET or BDT species distributed at lower latitudes or altitudes (Bailo et al., 2004; Camarero et al., 2011; Galiano et al., 2010; Navarro-Cerrillo et al., 2014; Rigling et al., 2013). Analogously, temperate moist forests of Nothofagus dombeyii (BET) tend to be replaced by Austrocedrus chilensis (NET), a species distributed into the drier steppe biome (Suarez and Kitzberger, 2008). The only shift of BDT replacing BET corresponds to drought-deciduous species in the Sahel (Gonzalez, 2001). Finally, there is documentation in several cases of forest change from drought stress towards lower-statured vegetation, dominated by shrubs or smaller trees (Bennet et al., 2015; McDowell and Allen, 2015), while the opposite (transitions to taller vegetation) does not seem to occur.

Vegetation changes can be interpreted by comparing the biogeography of the former dominant and the potential replacement species. Our preliminary results allow formulating the hypothesis that species with affected populations located at the edge of the species’ climatic range – thus, close to their physiological limits of drought tolerance – likely would be replaced by species better adapted to water scarcity, and hence distributed over drier environments. This hypothesis is consistent with reported species range shifts along altitudinal gradients, but less evident along latitudinal ones (Jump et al., 2009b). Thus, drought episodes would trigger changes in species distributions particularly at ecotones (Allen and Breshears, 1998). Nevertheless, a proper analysis of the climatic requirements of the species involved and the effect of co-drivers is needed, because populations living at the edge of its climatic distribution may exhibit compensatory demographic mechanisms (Pironon et al., 2015) and may have experienced selective processes enhancing resilience. In spite of the attractiveness of understanding the biogeographical implications of drought-induced vegetation shifts, in
most cases our current knowledge does not allow discriminating between alternative processes, preventing us from reaching general conclusions.

7. Concluding remarks

Our literature review shows that the available evidence for drought-induced vegetation shifts is still scarce, and suggests that vegetation exhibits a remarkable resilience to extreme drought, both in terms of composition (i.e., self-replacement) and functional properties. Examples of potential vegetation shifts do not seem to be limited to specific climates or vegetation types. In the cases in which the evidence for species replacement is clearer, vegetation transitions seem to favor dominance of species that are: a) more resistant to drought, as inferred by their patterns of distribution or their functional and structural traits; or b) more pioneer in successional status. Given the limited information currently available on drought-induced vegetation shifts from projected changes in climate, specifically including drought conditions, we stress the need for improved, long-term vegetation monitoring programs with sufficient temporal resolution. We also advocate for changes in approaches to the study of drought-induced mortality and its impact on vegetation dynamics. First, we suggest widening the focus to include not only the triggers of vegetation die-off but also the determinants of vegetation responses after mortality, with a particular emphasis on comparative regeneration dynamics among species. Second, we stress the need to account for the roles of non-drought co-drivers of mortality, particularly the historical legacies of management and land use, in order to understand current patterns of vegetation change and improve predictions of future vegetation dynamics. Finally, we suggest that considering vegetation shifts within biogeographical and successional contexts will improve understanding of the underlying processes and the ecosystem-level implications.

Acknowledgements

This research has been supported by the Spanish government through grants FUN2FUN (CGL2013-46808-R), SECADIN (CGL2012-3296) and BIOCLIM (CGL2015-67419-R), and by the Catalan government (2014 SGR 453). The discussions facilitated by the grant ‘Assessing ecosystem recovery after extreme drought-related dieback events worldwide’, funded by the Leverhulme Trust (UK), and by the Ecometas excellence network (CGL2014-53840-REDT), funded by the Spanish government, helped the authors in developing some of the ideas.
presented here. We thank José Luis Ordóñez for his help in crafting Figure 3 and Craig Allen for his kind comments that helped improve a previous version of the manuscript.

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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.

<table>
<thead>
<tr>
<th>ID</th>
<th>Name</th>
<th>Location</th>
<th>Climate</th>
<th>Vegetation type</th>
<th>Drought period</th>
<th>Scale of impact</th>
<th>Affected dominant species or veg. type</th>
<th>Replacing species or vegetation type</th>
<th>Funct. type shift*</th>
<th>Survival replacing species?</th>
<th>Regener. affected species?</th>
<th>Regener. replacing species?</th>
<th>Type of change</th>
<th>Abridged type of change</th>
<th>Other contributing factors</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Afromontane forest Ethiopia</td>
<td>N Ethiopia</td>
<td>Dry</td>
<td>Forest</td>
<td>Late 1980s</td>
<td>Local</td>
<td>Juniperus procera, Olea europaea</td>
<td>Early successional shrubs</td>
<td>NET + BET -&gt; BES</td>
<td>Yes</td>
<td>Low</td>
<td>na</td>
<td>(NET + BET)</td>
<td>Management</td>
<td>(1) (2)</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Sahel woodland, Mali</td>
<td>Gourma, Mali</td>
<td>Dry</td>
<td>Woodland</td>
<td>1983-1984</td>
<td>Regional</td>
<td>Acacia spp, Combretum glutinosum</td>
<td>Shrubland</td>
<td>BDT -&gt; BDS</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>(Un)</td>
<td>Grazing</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Sahel woodlands, Senegal</td>
<td>NW Senegal</td>
<td>Dry</td>
<td>Woodland</td>
<td>1968-1973</td>
<td>Regional (ecotone)</td>
<td>Tall trees with larger leaves, Short,</td>
<td>BET -&gt; BDS</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>(BS)</td>
<td>BS</td>
<td>Management</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Appalachian Forest, E USA</td>
<td>North Carolina, USA</td>
<td>Temp.</td>
<td>Forest</td>
<td>1984-1989</td>
<td>Local</td>
<td>Tilia americana, Fagus grandifolia,</td>
<td>Acer saccharum, Aesculus flava</td>
<td>BDT -&gt; BDS</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>(UNa)</td>
<td>Succession</td>
<td>(7)</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Ash NE USA</td>
<td>NE USA</td>
<td>Temp.</td>
<td>Forest</td>
<td>1990s-2000s</td>
<td>Regional</td>
<td>Fraxinus nigra</td>
<td>Shrubland</td>
<td>BDT -&gt; BDS</td>
<td>(Yes)</td>
<td>Low</td>
<td>Low</td>
<td>UNb / BS</td>
<td>Biotic agents, hydrological alterations, (8) (9)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No.</td>
<td>Region</td>
<td>Subregion</td>
<td>Type</td>
<td>Period</td>
<td>Scale</td>
<td>Species</td>
<td>Biotic agents</td>
<td>Succession, logging</td>
<td>Fire suppression, biotic agents</td>
<td>Biotic agents, wildfires</td>
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<td>Aspen decline</td>
<td>Western N America</td>
<td>Temp. / Boreal Forest</td>
<td>2000s</td>
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<td><em>Populus tremuloides</em></td>
<td>Conifers / Shrubland</td>
<td>BDT -&gt; NET + BDS</td>
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<td>(Low)</td>
<td>UNb / BS</td>
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<td>Biotic agents, succession, grazing</td>
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<td>8</td>
<td>Austrocedrus</td>
<td>N Patagonia, Argentina</td>
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<td>1950s</td>
<td>Regional (ecotone)</td>
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<td>(17) – (20)</td>
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<td>Trinidad and Tobago</td>
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<td>1987–1988, 1994–1995</td>
<td>Local</td>
<td>Primary species</td>
<td>Pioneers</td>
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<td>Succession, logging</td>
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<td>Temp. Forest</td>
<td>1963–1975</td>
<td>Regional</td>
<td><em>Tsuga canadensis</em></td>
<td><em>Pinus strobus, Acer rubrum</em></td>
<td>NET -&gt; NET + BDT</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>UNa</td>
<td>UN</td>
<td>Biotic agents, windstorms</td>
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<td>Hawaii, USA</td>
<td>Tropical Forest</td>
<td>1954–1985</td>
<td>Regional</td>
<td><em>Metrosideros polymorpha</em></td>
<td>na</td>
<td>BET -&gt; BET</td>
<td>na</td>
<td>Yes</td>
<td>na</td>
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<td><em>Quercus virginiana, Quercus pungens</em></td>
<td><em>Juniperus ashei</em></td>
<td>BET -&gt; NET</td>
<td>Yes</td>
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<td>1996, 2002–2005</td>
<td>Regional</td>
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<td><em>Juniperus monosperma / J.</em></td>
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<td>Yes</td>
<td>Yes / No</td>
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<td>Local</td>
<td>Secondary</td>
<td>lowland</td>
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<td>na</td>
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<td>(Yes)</td>
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<td>Tropical Dry Forests</td>
<td>Jalisco, Mexico</td>
<td>Tropical</td>
<td>Forest</td>
<td>2005</td>
<td>Local</td>
<td>Trees</td>
<td>Shubs</td>
<td>BDT -&gt; BDS</td>
<td>Low</td>
<td>Yes</td>
<td>Yes</td>
<td>Unc</td>
<td>UN</td>
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<td>Forest</td>
<td>1990s</td>
<td>Subcontinental</td>
<td>Wet-graduates</td>
<td>Dry-graduates</td>
<td>BET -&gt; BET</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>UNa</td>
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<td>Panama</td>
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<td>1983</td>
<td>Local</td>
<td>Wet-graduates</td>
<td>Dry-graduates</td>
<td>BET -&gt; BET</td>
<td>(Yes)</td>
<td>(Low)</td>
<td>(Yes)</td>
<td>SSf</td>
<td>SS</td>
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<td>Beijing, China</td>
<td>Temp.</td>
<td>Forest</td>
<td>1986-2006</td>
<td>Regional</td>
<td>Quercus sp.</td>
<td>Pinus tabuliformis</td>
<td>BDT -&gt; NET</td>
<td>Yes</td>
<td>na</td>
<td>na</td>
<td>UN / RV / SSf</td>
<td>UN</td>
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<td>Tropical and subtropical China</td>
<td>S China</td>
<td>Tropical</td>
<td>Forest</td>
<td>1990s-2000s</td>
<td>Subcontinental</td>
<td>Tall and intermediate trees</td>
<td>Shrubs and small trees</td>
<td>BET -&gt; BES</td>
<td>Yes</td>
<td>Low</td>
<td>Yes</td>
<td>SSf</td>
<td>SS</td>
<td>na</td>
<td>(41) (42)</td>
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<td>9</td>
<td>Tropical forest</td>
<td>Sarawak</td>
<td>Tropical</td>
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<td>1997-1998</td>
<td>Local</td>
<td>Dipterocarpaceae</td>
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<td>na</td>
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<td>(Yes)</td>
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<td>Tropical rainforest</td>
<td>Sabah and East Kalimantan, Borneo</td>
<td>Tropical</td>
<td>Forest</td>
<td>1997-1998</td>
<td>Regional</td>
<td>Large trees</td>
<td>Small trees</td>
<td>BET -&gt; BET</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>UNa</td>
<td>UN</td>
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<td>(44) – (46)</td>
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<td>13</td>
<td>Coastal</td>
<td>S Victoria,</td>
<td>Temp.</td>
<td>Woodland</td>
<td>1997-1998</td>
<td>Local</td>
<td>Eucalyptus</td>
<td>Allocasuarina</td>
<td>BET -&gt; Low</td>
<td>Low</td>
<td>No</td>
<td>Low</td>
<td>SSf</td>
<td>SS</td>
<td>Fire</td>
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<td>woodland</td>
<td>Australia</td>
<td>2009</td>
<td>spp.</td>
<td>a littoralis, A. verticillata</td>
<td>BET</td>
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<td>2</td>
<td>Eucalyptus</td>
<td>Queensland, Australia</td>
<td>Dry</td>
<td>Woodland</td>
<td>1990s - 2000s</td>
<td>Regional</td>
<td>Eucalyptus crebra, E. xanthoclada, E. melanophloia, E. populnea</td>
<td>Corymbia spp.</td>
<td>BET -&gt; BET</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>UNa</td>
<td>UN</td>
<td>Grazing, wildfires</td>
<td>(48) – (50)</td>
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<td>Central Plateau, Tasmania, Australia</td>
<td>Temp.</td>
<td>Forest</td>
<td>1990s - 2000s</td>
<td>Local</td>
<td>Eucalyptus gunnii ssp. divaricata</td>
<td>Eucalyptus pauciflora</td>
<td>BET -&gt; BET</td>
<td>Yes</td>
<td>Low</td>
<td>Yes</td>
<td>SSf</td>
<td>SS</td>
<td>Grazing</td>
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<td>Western Australia</td>
<td>Medit.</td>
<td>Woodland</td>
<td>2010-2011</td>
<td>Regional</td>
<td>Eucalyptus marginata</td>
<td>Corymbia calophylla</td>
<td>BET -&gt; BET</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
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<td>UN</td>
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<td>S Island, New Zealand</td>
<td>Temp.</td>
<td>Forest</td>
<td>1970s</td>
<td>Local</td>
<td>Nothofagus fusca</td>
<td>Nothofagus menziesii</td>
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<td>Yes</td>
<td>UNa</td>
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<td>Biotic agents</td>
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<td>Temp.</td>
<td>Forest</td>
<td>1970s</td>
<td>Local</td>
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<td>Yes</td>
<td>na</td>
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<td>England</td>
<td>Temp.</td>
<td>Forest</td>
<td>1976, 1980s</td>
<td>Local</td>
<td>Fagus sylvatica</td>
<td>Fraxinus excelsior / Quercus robur</td>
<td>BDT -&gt; BDT</td>
<td>Yes</td>
<td>No</td>
<td>Yes / No</td>
<td>SSf / UNb</td>
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<td>Spain</td>
<td>Medit.</td>
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<td>1990s, 2000s</td>
<td>Regional</td>
<td>Quercus ilex, Quercus suber</td>
<td>Shrubs</td>
<td>BET -&gt; BES</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>UNa</td>
<td>UN</td>
<td>Biotic agents</td>
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<td>S Europe</td>
<td>Medit. montane</td>
<td>Forest</td>
<td>1980s - 2000s</td>
<td>Regional</td>
<td>Abies alba</td>
<td>Pinus sylvestris,</td>
<td>NET -&gt; NET +</td>
<td>na</td>
<td>na</td>
<td>na</td>
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<td>Biotic agents, logging</td>
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<td>S Spain</td>
<td>Medit. montane</td>
<td>Forest</td>
<td>1990s - 2000s</td>
<td>Local</td>
<td>Abies pinsapo</td>
<td>Quercus ilex, Q. faginea, Juniperus oxycedrus</td>
<td>NET -&gt; BET+B DT+NE</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>UNa</td>
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<td>Management, biotic agents</td>
<td>(67) – (69)</td>
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<td>Central &amp; S Europe</td>
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<td>1990s - 2000s</td>
<td>Regional</td>
<td>Pinus sylvestris</td>
<td>Quercus spp.</td>
<td>NET -&gt; BET+B DT</td>
<td>Yes</td>
<td>Low</td>
<td>Yes</td>
<td>SSf</td>
<td>SS</td>
<td>Management, successional, biotic agents</td>
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<td>Doñana, Spain</td>
<td>Medit.</td>
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<td>2005</td>
<td>Local</td>
<td>Halimium halimifolium, Rosmarinus officinalis, Cistus ladanotis</td>
<td>na</td>
<td>BES -&gt; BES</td>
<td>na</td>
<td>Yes</td>
<td>na</td>
<td>SR</td>
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Invited review for Global and Planetary Change

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.