Global and Planetary Change 144 (2016) 94–108

Contents lists available at ScienceDirect

Global and Planetary Change

journal homepage: www.elsevier.com/locate/gloplacha

Invited review article

Drought-induced vegetation shifts in terrestrial ecosystems: The key role of regeneration dynamics

Jordi Martínez-Vilalta *, Francisco Lloret

[a] CREAF, Cerdanyola del Vallès, E-08193 Barcelona, Spain
[b] Univ. Autònoma Barcelona, Cerdanyola del Vallès, E-08193 Barcelona, Spain

A R T I C L E I N F O

Article history:
Received 2 December 2015
Received in revised form 20 June 2016
Accepted 20 July 2016
Available online 21 July 2016

Keywords:
Drought
Management
Mortality
Regeneration
Succession
Vegetation shifts

A B S T R A C T

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.

Contents

1. Introduction . . . 95
2. Climate and the distribution of vegetation . . . 95
3. Overview of recent drought-induced vegetation die-off . . . 96
4. On the necessary conditions for vegetation shifts to occur . . . 96
5. Characterization of recent drought-induced vegetation shifts . . . 97
6. Drought-induced vegetation shifts in practice: crucial challenges to understanding and prediction . . . 100
   6.1. Need for long term monitoring with sufficient temporal resolution . . . 101

* Corresponding author at: CREAF, Campus UAB, Edifici C, Bellaterra, 08193 Barcelona, Spain.
E-mail address: Jordi.Martinez.Vilalta@uab.es (J. Martínez-Vilalta).

http://dx.doi.org/10.1016/j.gloplacha.2016.07.009
0921-8181/

6.2. It is about regeneration, of course! . . . 101
6.3. Key role of interactions with other drivers . . . 103
6.4. Functional and biogeographical context . . . 103
7. Concluding remarks. . . . 104
Acknowledgements . . . 104
References . . . 104

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 (Mantgem 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