Journal of Vegetation Science **26** (2015) 4–6

COMMENTARY

# Alternative fire-driven vegetation states

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## Abstract

There is increasing evidence that alternative stable vegetation types exist for a given climate that are maintained by distinct fire regimes. Paritsis et al. (2015, this issue) provide an example in a temperate ecosystem. Here I briefly review cases of bi-stability in various climates, and present a simple model for the transition between states in their system.

Traditionally, most vegetation patterns were thought to be driven by environmental conditions (Holdridge 1947; Whittaker 1975). The role of animals in determining patterns of vegetation has also long been recognized (Hairston et al. 1960; Terborgh et al. 2006), given that herbivores consume vegetation and, in turn, are controlled by carnivores and parasites. There is an increasing volume of literature suggesting that fire also plays an important role in determining vegetation patterns in many ecosystems (Bond et al. 2005; Keeley et al. 2012). This is because fire can consume large amounts of plant biomass (Bond & Keeley 2005; Pausas & Keeley 2014a), affect vast areas in short periods and thus play an overwhelming role in some ecosystems (fire-prone ecosystems).

One of the clearest pieces of evidence for the role of fire in shaping vegetation is the occurrence of alternative vegetation types maintained by different fire regimes in a given climate. The different flammability of alternative communities generates different fire feedback processes that maintain contrasted vegetation types with clear boundaries in a given environment; and fire exclusion blurs this structure. This has been well documented in tropical landscapes (Bond et al. 2005) that are often mosaics of two alternative stable states – savannas and forests – with distinct structures and functions and sharp boundaries. While savannas are subject to frequent grass-fuelled fires (fire-prone, flammable or pyrophilic ecosystems), forests rarely burn (fire-free, non-flammable or pyrophobic ecosystems). This strong contrast is because savannas are open ecosystems dominated by highly flammable grasses, while closed forests inhibit grass fuels and generate microclimatic conditions less conducive to fire. Topography may also determine different vegetation types, but topographic differences are not necessary because micro-scale spatial differences, or temporal windows with longer fire intervals at local scales, may enhance the growth of trees and start the negative feedback process of inhibiting fire conditions – and thus abruptly cause a switch from an open to a closed system. Similarly, some rare events can favour a light fire in a forest and feed back to increase flammability and causes a switch to a savanna (Hoffmann et al. 2012; Murphy & Bowman 2012; Dantas et al. 2013).

Alternative stable vegetation states with sharp boundaries driven by different fire regimes can be observed in other warm ecosystems (App. S1). In this issue, Paritsis et al. (2015) document the existence of alternative stable vegetation states in a cold temperate ecosystem – the beech (*Nothofagus*) forests of southern Patagonia. After studying community composition, stands, fuel structures and micro-environmental conditions in burned and unburned Patagonian forests and shrublands, Paritsis et al. suggest that these two plant communities behave as alternative stable states maintained by distinct fire regimes. Forests are dominated by the non-resprouting, thin-barked tree *Nothofagus pumilo* and rarely burn because this deciduous, broad-leaved tree generates a shady, cool and moist environment that inhibits the growth of light-demanding flammable plants and so reduces fire spread conditions. In contrast, nearby shrublands burn more frequently and are dominated by resprouting shrubs (including the congeneric *N. antartica*); these communities have more continuous fine fuel (Paritsis et al. 2015) and generate microclimatic conditions more conducive to fire than forests (namely, high insolation and thus higher temperatures, lower humidity and greater exposure to wind). In addition, recurrent fires, as well as livestock grazing, increase plant flammability (Blackhall et al. 2015) and thus enhance vegetation–fire feedback processes. Note that the post-fire regeneration strategy of *N. pumilo* is better described as non-resprouter (compared with the resprouter *N. antartica*) rather than obligate seeder (as termed by Paritsis et al. 2015) because the species does not accumulate a persistent seed bank (see Pausas & Keeley 2014b for definitions). Also, Paritsis et al. named *N. pumilo* forests as


Journal of Vegetation Science
Doi: 10.1111/jvs.12237 © 2014 International Association for Vegetation Science

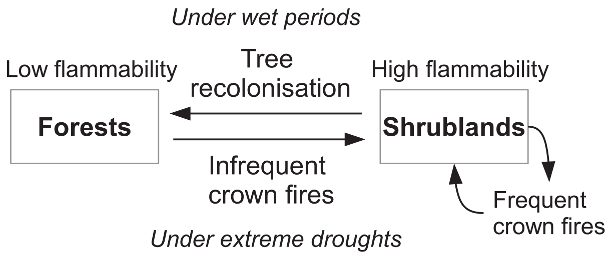


**Fig. 1.** Factors determining the transition between two alternative vegetation states (fire-sensitive forest and fire-resilient shrubland) in a temperate landscape. Human factors (global warming, increased ignitions and livestock grazing) favour transition to shrublands.

fire-resistant communities because of their low flammability – and not because *N. pumilo* possesses fire-resistant traits; in fact, the lack of these traits suggests that this species is sensitive to crown fires (Fig. 1).

The transition from pyrophobic forest to pyrophilic shrublands could be driven by relatively rare droughts that increase the flammability of forests (Fig. 1). In such conditions, natural ignitions (lightning) could generate high-intensity crown fires. Because these forests are sensitive to such fires (non-resprouting trees), the system may abruptly shift to flammable shrubland. Such shrublands are stable as they are more flammable than forests and dominated by resprouting species – and are thus maintained by fire (a fire-resilient community). These shrublands could only revert to pyrophobic forest during a period of wet conditions with no fires as such conditions may provide a competitive advantage to the broad-, non-resprouting *N. pumilo*. The relatively good dispersal and establishment ability of this species, as suggested by the high recolonization at edges of fires (BuFo/Fo in Paritsis et al. 2015), would facilitate recolonization if conditions are appropriate.

These transitions can be driven by natural climatic oscillations (e.g., ENSO events). The fact that *N. antartica* has a lignotuber, i.e., a specialized post-fire resprouting structure (Keeley et al. 2012), suggests that fires are by no means novel in such ecosystems, and thus the bi-stability model (Fig. 1) may be maintained in natural conditions. However, anthropogenic impact tends to generate more frequent transitions towards shrublands than forests. This is because humans have increased ignitions, warmed the climate and introduced livestock that limits tree regeneration. In fact, recolonization by *N. pumilo* is mainly observed in mesic sites that are protected from livestock (Paritsis et al. 2015). Logging also reduces the inhibitory effect of trees on light-demanding flammable plants (e.g., *Chusquea* species) and thus increases flammability; similarly, invasion by alien grasses can enhance flammability (Pausas & Keeley 2014a).

In conclusion, recent advances in fire ecology suggest that the existence of alternative fire-driven vegetation states may be more frequent than previously thought, although human activities may favour one of the states and mask the original bi-stability. Understanding threshold switching from one state to another is crucial in a changing world.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Examples of alternative stable fire-driven vegetation states in different climates.



Doi: 10.1111/jvs.12237 © 2014 International Association for Vegetation Science