ECOLOGY

Fire, climate and changing forests

Vegetation-type conversions driven by fire and climate change in the western United States forests are altering landscapes.

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A changing climate implies potential transformations in plant demography, communities and disturbances, such as wildfire and insect outbreaks. How do these dynamics play out in terrestrial ecosystems across scales of space and time? 'Type conversion' is a term used to describe abrupt and long-lasting changes in vegetation structure and composition due to various kinds of perturbations. For example, it has long been observed that fire-adapted ecosystems, such as the California chaparral shrublands, are readily replaced by non-native annual grasses when humans increase fire frequency[1,2]. Similar effects are being observed in Sonoran Desert plant communities, where invasion by non-native buffelgrass (*Cenchrus ciliare*) exposes a fire-sensitive plant community to high-intensity fires, which are lethal to the long-lived iconic Sonoran flora such as Saguaro cactus (*Carnegiea gigantea*)[3,4]. While type conversions following severe disturbance have been observed for some time, the mechanisms that underlie such changes are only recently coming to light. Threshold behaviour is of particular concern: as various climate indices pass critical values, some ecosystems may be reaching points of no return, where recovery to the earlier state is no longer possible. A recent publication in the *Proceedings of the National Academy of Sciences USA*[5] has now revealed that increased fire severity impairs post-fire forest regeneration, setting the stage for potential large-scale type conversion of western conifer forests.

There is growing evidence supporting the view that climate change increases the risk of forest fires by enhancing fuel aridity and lengthening the fire season[6,7]. Many interacting factors, such as land-use decisions and the presence of invasive vegetation, influence the process of vegetation type conversions (VTC), but fire severity and pre- and post-fire climate appear to be key. Davis et al.[5], however, are the first to tie specific thresholds in seasonal climate to post-fire regeneration of widespread conifer species over broad areas of the western United States. Seedling recruitment and survival is identified as the key limiting life stage; many older trees can tolerate several years of stressful conditions, but seedlings and young saplings do not have the resources or physiology to survive. Where seedlings fail to establish, the population is eventually fated to disappear.

Fig. 1 | Tree mortality and severe soil damage in Cochiti Canyon, Jemez Mountains, NM, USA, following the Las Conchas Fire in 2011. Credit: Don Falk, University of Arizona

Davis and colleagues[5] examined 33 fires across four regions in the west during the period of 1988– 2007. In the field, they collected seedlings and saplings, and they used tree-ring analysis in the lab to determine which years had successful post-fire regeneration of ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*). They then built statistical models to identify the key climate variables that limited successful tree regeneration and survivorship. For the two species they studied, climatic thresholds for seedling establishment and survival were most affected by seasonal soil moisture, vapour pressure deficit and surface temperatures, with some differences between the two species. Over the past 20 years, climates in much of their study area have crossed critical thresholds in these variables, making conditions increasingly unsuitable for seedling germination and survival. Although the retrospective analysis used in this study has limitations (for example, missing observations of regeneration from mortality) and the full complement of conditions required for forest regeneration is yet to be determined, these findings[5] portend future forest recovery failures.

Recent changes in fire activity are variable across the globe[6], but it appears that warmer conditions are contributing to increases in wildfire area and severity[7]. In many regions, wildland fire is affecting increasingly large areas, leaving a cumulative footprint of substantial ecological effects. For example, over a period of just three decades (1984 to present), wildfires >100 ha have occurred over a large proportion of forested area in the western US. Not all of these fires caused significant tree mortality or soil damage — historically, high-severity areas represent about one-third of the total area burned — but more areas are burning repeatedly, leading to increased tree mortality and soil damage[7].

Under historical climate regimes, forests would recover following episodes of tree mortality, primarily through recruitment of new trees by seed dispersal and seedling establishment. However, landscape patches of high-severity fire are increasing in size — sometimes more than 10,000 ha — putting them beyond the reach of seed dispersal from remnant forest patches or refugia. However, equally important, as Davis and colleagues demonstrate, is that the climate of growing seasons is increasingly unfavourable for seedling survival, as air temperature, vapour pressure deficit and soil moisture exceed thresholds that seedlings can tolerate[5]. The net result is potentially widespread failure of forests to regenerate under the current and emerging climate following wildfire[8]. In this way, wildfire augments the pervasive effects of climate warming, acting as an accelerant and multiplier of tree mortality and forest loss[9].

If fire compromises the regeneration potential of existing vegetation, ecosystems can follow a range of trajectories. Perhaps the key relies on whether a forest is dominated by conifers, such as pines (or most other gymnosperms), or hardwoods (angiosperms), such as oaks, in the northern hemisphere, or eucalyptus in the southern hemisphere. The vast majority of gymnosperm species lack the capacity to regenerate by resprouting from burned stems (with some notable exceptions[10]). Angiosperms have a remarkable capacity to regenerate vegetatively from the burned stems and thus can re-establish the forest in situ without seedling recruitment[11]. Most conifer forests, such as those studied by Davis et al.[5], will not likely return to the pre-fire state without successful seedling recruitment. In the absence of conifer reestablishment, these forests are set on a trajectory of type conversion. In other words, nature abhors a vacuum and species will fill the void left by these conifers. These previously forested landscapes often transition to shrub- or grass-dominated systems and become locked into their new state by the climate and ongoing disturbance.

Loss of forests is often viewed as a management failure, potentially negatively affecting native biodiversity, ecosystem functionality and services, and cultural values. For example, the mostly shrub or grass plant communities established after vegetation-type conversions sequester considerably less carbon than the original forest. On the other hand, in some cases these types of converted communities may be better adapted to the current and emerging climate. For example, Guiterman et al.[12] found that some large patches of Gambel oak (*Quercus gambellii*), a highly drought-tolerant, post-fire colonizer in the Jemez Mountains of New Mexico (Fig. 1), persisted for more than a century. Far from representing an ephemeral successional stage, these alternative ecological communities may be well-adapted to the climate and fire regimes in the coming century, and may signal a need for forest managers to accommodate these changes. ❐

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Competing interests

The authors declare no competing interests.