



# Hidden collapse is driven by fire and logging in a socioecological forest ecosystem

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**Increasing numbers of ecosystems globally are at risk of collapse. However, most descriptions of terrestrial ecosystem collapse are post hoc with few empirically based examples of ecosystems in the process of collapse. This limits learning about collapse and impedes development of effective early-warning indicators. Based on multidecadal and multifaceted monitoring, we present evidence that the Australian mainland Mountain Ash ecosystem is collapsing. Collapse is indicated by marked changes in ecosystem condition, particularly the rapid decline in populations of keystone ecosystem structures. There also has been significant decline in biodiversity strongly associated with these structures and disruptions of key ecosystem processes. In documenting the decline of the Mountain Ash ecosystem, we uncovered evidence of hidden collapse. This is where an ecosystem superficially appears to be relatively intact, but a prolonged period of decline coupled with long lag times for recovery of dominant ecosystem components mean that collapse is almost inevitable. In ecosystems susceptible to hidden collapse, management interventions will be required decades earlier than currently perceived by policy makers. Responding to hidden collapse is further complicated by our finding that different drivers produce different pathways to collapse, but these drivers can interact in ways that exacerbate and perpetuate collapse. Management must focus not only on reducing the number of critical stressors influencing an ecosystem but also on breaking feedbacks between stressors. We demonstrate the importance of multidecadal monitoring programs in measuring state variables that can inform quantitative predictions of collapse as well as help identify management responses that can avert system-wide collapse.**

ecosystem collapse | multidecadal monitoring programs | early-warning indicators | forest ecosystems

Much has been written about ecosystem collapse (1–4) with the concept now included in the International Union for the Conservation of Nature Red List of Ecosystems classification process (5). A collapsed ecosystem is one in which major changes in ecosystem conditions are widespread and are either irreversible (6) or very time- and energy-consuming to reverse (e.g., ref. 7). The changes in a collapsing ecosystem are often associated with significantly impaired ecosystem processes, eroded provision of ecosystem goods and services, and large losses of biodiversity (2).

Despite the extensive literature on ecosystem collapse, there are very few empirically based descriptions quantifying specific ecosystems undergoing collapse, especially in terrestrial environments (2). Evidence of ecosystem collapse is most often uncovered after it has occurred, meaning there are only retrospective opportunities to describe in detail the changes occurring in the ecosystem during its collapse. This may be one of the reasons why it remains extremely difficult to accurately predict if and when collapse might occur (2, 8). However, the increased likelihood of such problems globally means it is critically important to describe ecosystems in the process of collapse, document the drivers of change and how they manifest, develop more robust early-warning indicators of collapse, and better articulate what might be done to avert collapse.

Here, we use data from a series of multifaceted, long-term empirical studies to describe the process of collapse in the Mountain Ash (*Eucalyptus regnans*) forests of southeastern Australia (Fig. S1) (9–11). This ecosystem supports the tallest flowering plants on Earth with large, old trees approaching 100 m in height (12). The Mountain Ash ecosystem provides habitat for species-rich animal and plant assemblages (including critically endangered taxa), generates most of the water for the ~4.5 million people in Melbourne, stores large amounts of biomass carbon, and supports timber, pulpwood, and tourism industries (13). In particular, we focus our empirical analyses of ecosystem collapse on the current and projected decline in populations of large, old-cavity trees and closely associated cavity-dependent fauna. Changes in populations of these trees are a strong indicator of the condition and status of biodiversity (14) and the ecosystem per se. In addition, large, old-cavity trees are critical to ecosystem function through their influence on patterns of tree germination and seedling recruitment (15) and their disproportionate contribution to carbon storage (16), the water cycle (17), and fire dynamics (18). If collapse were to occur, the dominant overstory Mountain Ash tree species would likely be replaced by *Acacia* spp.-dominated shrubland. There are already areas of *Acacia* without overstory eucalypts within the boundary of the Mountain Ash ecosystem, but they are currently not widespread.

## Significance

**Almost all descriptions of ecosystem collapse are made after it has occurred and not during the process of collapse. We describe the process of collapse in the iconic Australian Mountain Ash ecosystem. We uncovered empirical evidence for hidden collapse, which occurs when an ecosystem superficially appears to be intact but a prolonged period of decline coupled with long lag times for recovery mean that collapse is almost inevitable. This is because key ecosystem components continue to decline for long periods even after drivers of collapse are removed. Hidden collapse suggests a need for actions well before managers perceive they are required. Long-term monitoring targeting different classes of state variables can be used to provide early warnings of impending collapse.**

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ecosystems. In addition to the 1939 wildfire that affected 70% of the Mountain Ash ecosystem, a subsequent wildfire in 2009 burned almost half of the Mountain Ash estate, causing a rapid loss of old, large trees (Fig. 1). In addition, ~80% of the Mountain Ash ecosystem is broadly designated for clearcutting (37). Both fire and logging damage or remove remaining old-growth forest (38) and large, old trees (21, 26), cause direct mortality of animals on perturbed sites (39), and impair habitat suitability for animal and plant biota over many decades or centuries during stand recovery (40–42).

Compared with fire and logging, climate change is an emerging slow-acting driver of collapse of the Mountain Ash ecosystem. Notably, the effects of climate change were not included in projections of populations of large, old trees (Fig. 1), given difficulties in parameterizing corresponding Markov chains, but indicate that our forecasts of the future abundance of these trees are likely an overestimate. Indeed, altered climatic regimes may reduce the extent of Mountain Ash forest by up to 80% by 2080 (43). Furthermore, temperature extremes and depressed rainfall associated with changing climates have been implicated in significantly reducing germination rates for Mountain Ash trees (15, 27) as well as increasing mortality of large, old trees to levels approximately 10 times greater than the background rate for the Mountain Ash ecosystem (44). Increased heat stress and mortality of heat-intolerant species such as the Greater Glider (45) may be elevated by climate change. Wood anatomy also may be altered by climate change in ways that increase timber splitting during logging operations.

**Interactions Among Key Drivers of Collapse.** Interactions between the three key drivers discussed above create major challenges for the management in the Mountain Ash ecosystem. This is because interactions between fire, logging, and climate change perpetuate and/or exacerbate the negative independent effects of these drivers (Fig. 3). As an example, two of the best-understood drivers in Mountain Ash ecosystems—logging and fire—can interact in at least four ways. First, burned forests are often subject to post-disturbance clearcutting (42) which removes remaining structures such as large, old trees that wildlife could use as refugia or that could act as protective buffers to altered microclimatic regimes for flora or fauna. Second, young logged and regenerated forests may have an elevated probability of a crown-scorching burn for at least 40 y postlogging (46), exacerbating mortality risk for wildlife returning to these areas (39) and reducing the likelihood of successful Mountain Ash seedling recruitment (15) during this time. Third, an array of young, fire-prone cut-blocks in logged landscapes elevates the risk of spatial contagion in fire across the Mountain Ash ecosystem (47), threatening remaining uncut stands already under pressure from timber-harvesting operations. Fourth, wildfires deplete available timber resources and thereby increase logging pressure on, and the rate of cutting of, unburned forest. In turn, the dwindling supply and unsustainable extraction of timber resources from remaining unburned forests increases the risk of collapse of timber and paper industries dependent on harvesting the Mountain Ash ecosystem (30).

**Interactions Elevate Collapse Risk and Require Targeted Management Intervention.** We suggest that multiple interacting drivers of change, coupled with the long recovery times of the key ecosystem components that these drivers affect, may be masking collapse, delaying management intervention, and subsequently rendering collapse inevitable. It is possible that altered feedback processes will result from these interactions. Altered feedback processes in ecosystems often characterize shifts to new ecosystem states (48) and, without considerable investment in intensive intervention, can prevent the return of an ecosystem to its original state (49). The limited availability of research on interacting drivers may mean that land managers and policy makers are unaware of (i) the elevated risk of collapse in ecosystems affected by interacting drivers, (ii) the slow recovery times in affected ecosystems, and (iii) the consequent requirement for more drastic interventions to avert ecosystem collapse (compared with a system with a single driver or with multiple

drivers that do not interact). Hence, we argue that it is important for research, policy, and management to focus not only on reducing the number of critical stressors influencing an ecosystem but also on breaking the feedback processes between these multiple stressors.

For the Mountain Ash ecosystem, addressing changes associated with climate change will be challenging and likely will require global collective action. However, given that the effects and synergies of local stressors—wildfire and logging—are understood, policies and management that target these stressors may aid in managing climate change effects as well (3). In particular, as with the Amazon Rainforest in Brazil (see ref. 3), strategies that reduce the opening of the forest canopy will help break interactive feedback processes among fire, logging, and climate change. To do this, the amount of forest being logged must be limited, levels of sustained timber yield must be reduced, and the size of protected areas increased. Expanding the size of protected areas has the benefits of (i) increasing populations of large, old trees, (ii) promoting biodiversity [e.g., animals such as the Greater Glider which are strongly associated with old-growth forest (50)], and (iii) eventually expanding the old-growth estate [where the risk of high-severity of fire is reduced (46)].

**State Variables Informing Early Warnings of Ecosystem Collapse.** Developing robust methods to predict (and then avert) ecosystem collapse remains difficult, in part because so few studies have documented collapse while it is occurring (rather than after it has occurred) (2). A fundamental step in enhanced prediction is the identification (and subsequent monitoring) of appropriate state variables that can be used to provide warnings of collapse sufficiently in advance to avoid collapse (51). Based on insights from this study and extensive previous research and monitoring in Mountain Ash forests, we suggest four classes of state variables that can be used in early-warning analyses in terrestrial socioecological systems. These are (i) rates of decline of key ecosystem structures (e.g., large, old trees), (ii) rates of decline of shorter-lived species dependent on key ecosystem structures (e.g., arboreal marsupials; see Fig. S3), (iii) levels of production of important ecosystem goods and services associated with key ecosystem structures (e.g., water and timber), and (iv) spatial extent of key ecosystem structures (e.g., stands of old growth). The first three classes of variables are suitable for temporal early-warning analyses, while the final class of variable is suitable for spatial early-warning analyses.

The rate of decline in key ecosystem structures is a class of state variable that can be used not only to conduct early-warning analyses but also to better understand the functional condition of an ecosystem. In forested systems, an example of such a state variable is the status of populations of large, old trees. Large, old trees are key attributes of stand structural complexity in almost all forested ecosystems globally (44) and are critical habitat elements for many species of conservation concern (e.g., ref. 52). These trees are readily lost (through logging, clearing, fire, and other processes) but can take many centuries to be recruited (44) and so can show monotonic declines in response to disturbance (Fig. 1). Without recruitment, a threshold likely exists at which the remaining trees are unable to provide services and resources in a way that maintains ecosystem identity (e.g., the loss of large, old-cavity trees is accompanied by losses in fauna associated with these features and that are characteristic of the ecosystem; see Fig. 2), and key processes such as germination are undermined, resulting in ecosystem collapse. As such, monitoring of large, old trees should be complemented with monitoring of tree recruitment (see ref. 27) to better quantify the functionality of the ecosystem as well as the assessment of collapse risk. If recruitment is limited or absent, then the collapse of the system is a certainty without immediate and drastic intervention.

A disadvantage of using large, old trees as a state variable for quantifying collapse risk is the longevity of these ecosystem attributes; when extensively depleted, large, old trees recover slowly (if at all) (Fig. 1). This slow recovery time means that



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