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.

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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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Data deposition: The arboreal marsupial (stagwatch) data reported in this paper are available at Long Term Ecological Research Network, https://www.ltern.org.au/knb/metacat/ltern2.149/html; bird point count data are available at Long Term Ecological Research Network, https://www.ltern.org.au/knb/metacat/ltern7.50/html; and the data for stag and fire severity observations are available at Long Term Ecological Research Network, https://www.ltern.org.au/knb/metacat/ltern2.1055/html.

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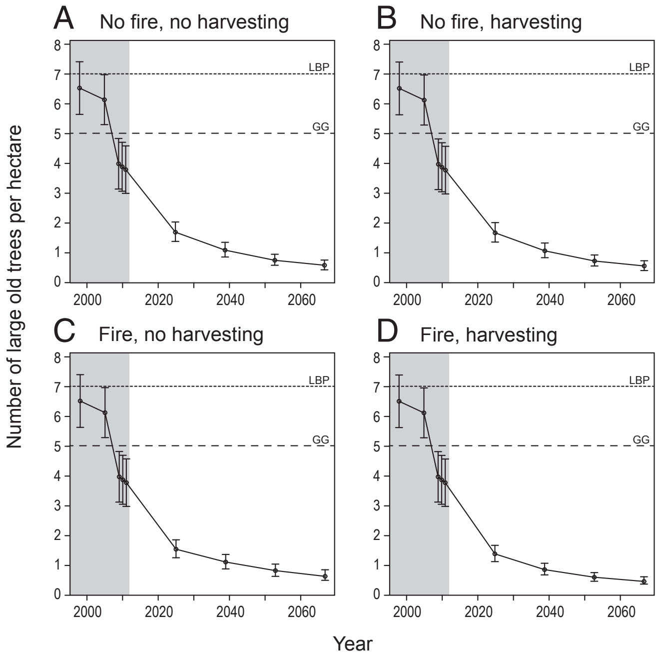

Fig. 1. Temporal changes in the existing abundance and projected future abundance of large, old-cavity trees in the Mountain Ash ecosystem in response to fire and logging. We present four scenarios: (*A*) no fire and no harvesting; (*B*) no fire with harvesting; (*C*) with fire and no harvesting, and (*D*) with fire and harvesting. The shaded area corresponds to the 14-y period of field-based sampling during which rates of collapse of large, old-cavity trees were measured at 156 long-term sites (*SI Methods*). We provide 95% confidence intervals associated with these empirical measurements. The unshaded area shows projections of future abundance of large, old-cavity trees based on Markov chain simulations to 2067, when existing ~80-y-old trees will first begin to develop cavities (*SI Methods*). We present 95% prediction intervals with these projections, which are based on the lower and upper 2.5 percentiles of 10,000 Markov chain simulations. There are strong statistical relationships between the abundance of cavity trees and the occurrence of species such as the critically endangered Leadbeater's Possum (Fig. S3) and the vulnerable Greater Glider (14). The horizontal lines on each diagram show the approximate number of cavity trees per hectare required to achieve a 0.4 probability of the occurrence of these species [seven trees per hectare for Leadbeater's Possum (LBP) and five trees per hectare for the Greater Glider (GG) (14)].

We contextualize this case of collapse with the complexity of interacting drivers in the Mountain Ash ecosystem and provide commentary on insights into ecosystem collapse that arise where there are multiple (and potentially interacting) natural and human-driven stressors. In particular, we discuss the concept of "hidden collapse" and the broad classes of state variables that could be used to provide early warnings of ecosystem collapse in terrestrial socioecological ecosystems.

Results

Declines in Populations of Large, Old-Cavity Trees. Repeated field measurements of 1,129 cavity trees at 156 long-term field sites across the Mountain Ash ecosystem (*SI Methods*) revealed that populations of such trees almost halved between 1997 and 2011 (Fig. 1). By 2067, populations are projected to be less than 10% of what they were in 1997 (Fig. 1). Projections based on four scenarios reflecting different combinations of logging and fire (*SI Methods*), including a scenario in which no fire and no logging occur in the system, all showed the same broad pattern of marked decline in large, old-cavity tree abundance (Fig. 1). Notably, the rate and extent of decline shown in Fig. 1 is likely to be a significant underestimate of the actual levels of decline, because some key feedback processes could not be modeled, including the cumulative spatial and temporal effects of additional logging and fire in the landscape that elevates the collapse of large, old-cavity trees in adjacent undisturbed areas (19, 20). In addition, the impacts of climate change, such as those associated with droughts that significantly increase rates of mortality of large, living trees with cavities (21) also were not modeled in our study.

Declines in Arboreal Marsupial and Bird Biodiversity. Based on repeated surveys at our permanent field sites since 1997 (*SI Methods*), we have documented declines of 50–65% in site occupancy for arboreal marsupial species dependent on large, old-cavity trees. Examples include Leadbeater's Possum (*Gymnobelideus leadbeateri*) (Fig. 2*A*) and the Greater Glider (*Petauroides volans*) (Fig. 2*B*). Since 2004, there have been significant declines in almost all species of tree cavity-associated bird species; examples include the Striated Pardalote (*Pardalotus striatus*), White-throated Treecreeper (*Cormobates leucophaea*), Laughing Kookaburra (*Dacelo novaeguineae*), and Crimson Rosella (*Platycercus elegans*) (Fig. 2 *C*–*F*). There also have been declines in other species associated with resources provided by large, old trees.

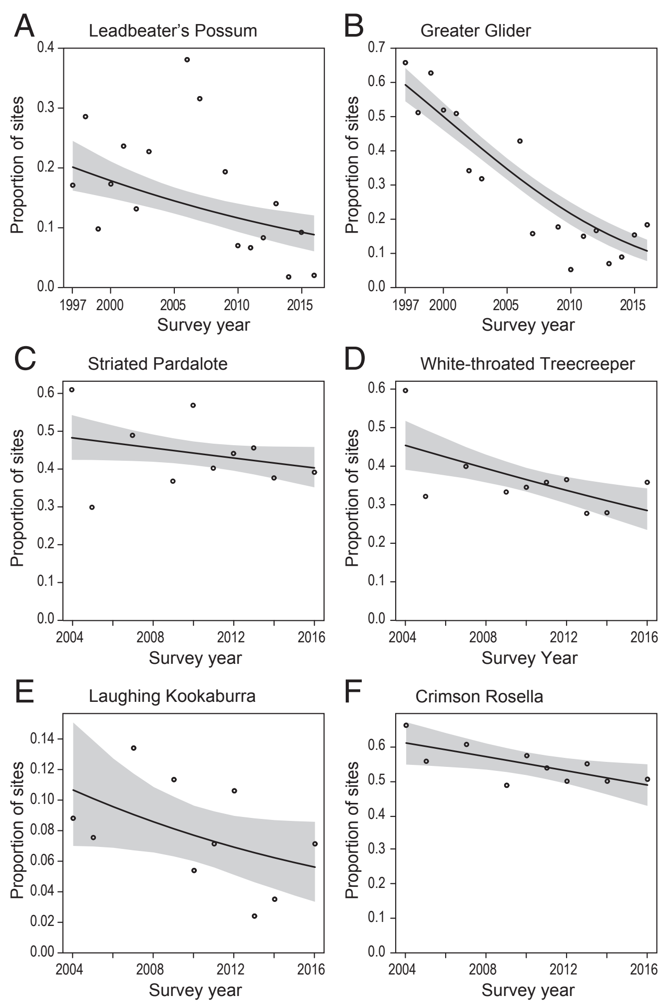

Fig. 2. Temporal changes in the presence/absence of examplar tree cavity-dependent species on sites in the Mountain Ash ecosystem based on a Bayesian multilevel logistic regression model of long-term monitoring data (*SI Methods*). The solid line represents the posterior mean, and the shaded region indicates the 95% credible interval (see Table S1 for model coefficients). Species shown are (*A*) Leadbeater's Possum; (*B*) Greater Glider; (*C*) Striated Pardalote; (*D*) White-throated Treecreeper; (*E*) Laughing Kookaburra; and (*F*) Crimson Rosella.

These include the Crested Shrike-tit (*Falcunculus frontatus*), which is associated with hanging bark (extensive clumps of which develop on large, old trees), the Red Wattlebird (*Anthochaera carunculata*) and Brown-headed Honeyeater (*Melithreptus brevirostris*), which are associated with flowering and large canopies of big trees, and the Pink Robin (*Petroica rodinogaster*), which is often associated with rainforest that develops as an understory component of old-growth stands of Mountain Ash (Fig. S2). We report model estimates and 95% credible intervals for model parameters for arboreal marsupials and birds in Table S1.

Discussion

A diverse range of forested ecosystems globally are thought to be at high risk of collapse, including those in boreal, tropical, and temperate ecosystems (e.g., refs. 3 and 22–24). Our study of the collapse of the Mountain Ash ecosystem is unusual among these examples in describing a forest during, rather than after, the process of collapse. Based on all relevant criteria of ecosystem change, the Mountain Ash ecosystem is collapsing; we have shown it is suffering rapid changes in key components of ecosystem structure, such as populations of large, old trees (Fig. 1). Given that ~98.8% of the Mountain Ash ecosystem is dominated by forest stands that are 80 y or younger (*SI Methods*) and that trees do not begin developing cavities until they 120 y old (25) but those used by cavity-dependent fauna are often >190 y old (12), it will be at least 2065 (and as late as 2130) before new cohorts of cavity trees will be recruited to this ecosystem. Moreover, rates of collapse of existing cavity trees are fastest and resulting populations are lowest in the regrowth and young forests that dominate ~98.8% of the Mountain Ash ecosystem (26). As such, it is unsurprising that our results also reveal extensive losses of biodiversity in Mountain Ash forests, especially those species associated with large, old trees (Fig. 2 and Fig. S3). In addition, previous research in the Mountain Ash ecosystem has shown that the loss of large, old-cavity trees is also impairing key ecosystem processes such as germination (27) and is eroding the carbon storage and water production potential of the ecosystem (13). These changes are widespread and pervade the entire ecosystem. We do note, however, that our projected extent of cavity decline in the Mountain Ash ecosystem is likely to be a substantial underestimate, in part because some important feedback processes could not be adequately simulated, indicating a limitation of our Markov chain approach. For example, rates of tree collapse in undisturbed areas increase when adjacent areas are logged (19) and are dramatically elevated with additional further logged cutblocks in the surrounding landscape [up to 2 km away (20)]. Hence, there are feedbacks between the spatial and temporal patterns of disturbance and accelerated rates of tree fall that we have not modeled. In addition, climate change effects, such as those associated with droughts and high temperatures, lead to significantly increased rates of mortality among large, old-cavity trees in the Mountain Ash ecosystem (21), but these were not included in our Markov chain projections because they are likely to be high-impact, episodic events which are hard to parameterize in the approach we adopted for this study. There are a range of other important interactive effects affecting large, old-cavity trees and ecosystem collapse per se in the Mountain Ash ecosystem (Fig. 3), but these also have not been included in our analyses and projections presented in Fig. 1.

The Concept of Hidden Collapse. The most challenging aspect in managing the declining condition of Mountain Ash forests is that the collapse of the ecosystem has remained largely hidden. Hidden collapse, such as we have discovered, occurs where an ecosystem superficially appears to be relatively intact. However, a prolonged period of decline coupled with long lag times required to recover dominant ecosystem components mean that ecosystem collapse is almost inevitable. This is because key ecosystem components continue to decline for long periods even after drivers of collapse are removed (Fig. 1).

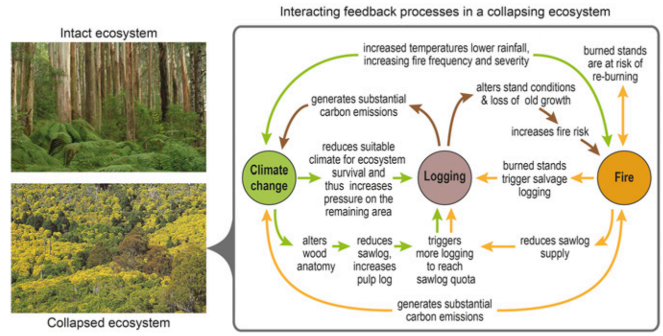

Fig. 3. (*Left*) Representative photographs of an intact (*Upper*) and collapsed (*Lower*) ecosystem; *Upper* image of intact ecosystem courtesy of David Blair (photographer). (*Right*) Interacting drivers of decline and potential collapse in the Mountain Ash ecosystem. The different colored arrows indicate whether an interacting driver is initially driven by fire (orange), logging (brown), or climate change (green).

At the heart of the concept of hidden collapse are marked differences between the actual trajectory of an ecosystem and political and management perceptions of the same system. In the case of the Mountain Ash ecosystem, extensive historical logging and repeated past wildfires followed by postfire salvage logging have set the ecosystem on a collapse trajectory. However, management and policy actions have not recognized the problem or made provision sufficiently long in advance to ensure the maintenance of adequate populations of large, old trees, adequate areas of old-growth forest, or viable populations of species that have strong dependencies on these ecosystem features. When our research commenced in 1983, considerable modification of the Mountain Ash ecosystem had already occurred, and the ecosystem was likely already on a collapse trajectory. Logging has taken place in the Mountain Ash ecosystem since at least the 1860s (28), intensifying after that time across ~80% of the estate which is broadly designated for timber harvesting (29). This intensification was due to the need to meet fixed timber production quotas for a slowly regenerating and dwindling resource that has been drastically affected by wildfire (30). In this regard, the 1939 wildfires burned more than 70% of the Mountain Ash ecosystem (31), affecting a large proportion of intact old-growth stands and large, old trees. Across the estate, these fire-damaged large, old trees were then subject to a further two decades of postfire salvage logging (32).

Important management-relevant information about the size and age of large, old trees required by cavity-dependent animals did not begin to emerge until 1988 (33), and the long lag time to recover declining populations of large, old-cavity trees began to be recognized only in 1990 (34). By the time the importance of the lag and the extent of degradation of the system were fully realized, it was apparent that immediate action was essential to protect the Mountain Ash ecosystem (and large, old trees specifically). However, provisions to begin to ensure the perpetual supply of trees have still not eventuated (35). Some measures such as the cessation of logging of old-growth stands exceeding 5 ha in size were implemented in the early 1990s (36), but these have been inadequate, and continued degradation of the system has occurred. Moreover, there have been no effective further attempts to implement legislation or policy that appropriately protects trees, stabilizes the ecosystem, or reverses the risk of ecosystem collapse (26).

Direct Drivers of Mountain Ash Ecosystem Collapse. Fast- and slow-acting drivers, such as fire, logging, and climate change, are pushing the Mountain Ash ecosystem toward collapse. These drivers may interact to exacerbate the loss of large, old trees and the communities associated with these structures, which adds further complexity to managing Mountain Ash forests to avert system-wide collapse. Fire and clearcut logging have caused, and continue to cause, extensive and considerable changes to Mountain Ash 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 early-warning indicators derived from large, old tree data may not be sufficiently responsive to allow management to avert collapse or may not accurately reflect the state of the ecosystem (without simultaneously considering recruitment rates). If this is the case, shorter-lived entities strongly coupled with keystone ecosystem structures may be an alternative for assessing collapse risk. Our results show that fauna dependent on large, old trees, such as arboreal marsupials, show patterns of decline remarkably similar to those of large, old trees (Fig. 2 *A* and *B*) and may be suitable state variables for predicting ecosystem collapse. The varying resilience exhibited by these animals to the loss of large, old trees [e.g., the requirement for more than five versus seven trees per hectare for the Greater Glider versus Leadbeater's Possum (ref. 14, figure 1)] suggests that indicators derived from arboreal marsupial data may provide more sensitive and responsive signals of collapse risk than large, old tree data. Increased sensitivity and responsiveness may allow land managers sufficient advance warning to implement actions to avert system-wide collapse.

Coupled socioecological systems such as Mountain Ash forests also offer opportunities to use economic state variables to inform assessments of collapse risk. Economic state variables can be used to reflect the risk of the collapse of industries reliant on a collapsing ecosystem. However, these variables can also reflect the risk of ecosystem collapse if they are strongly coupled with ecosystem attributes of interest (e.g., timber yield and large, old trees). An additional advantage of economic state variables is that they may be collected at a higher temporal resolution than biotic variables, increasing the likelihood that high-intensity data requirements for temporal early-warning analyses (see ref. 53) are met in appropriate timeframes. For example, it may take up to 200 y to collect sufficient data for analysis of biotic variables (assuming these data are collected annually) but 50 y to collect sufficient data for analysis using economic variables (assuming a business model with quarterly reporting). Given that industries based on intensive resource extraction may collapse in well-defined stages (54), a variety of economic state variables can be identified based on these stages of collapse. For example, metrics associated with the difficulty in accessing resources, levels of resource extraction, and the extent of financial subsidies reflect the increasing rarity of the target resource and increasing difficulty and expense in harvesting that resource. These two factors can sometimes herald the collapse of resource-extraction industries (30) and, in turn, the collapse of the ecosystem on which they rely.

The state variables proposed in the preceding paragraphs are of a temporal nature and lend themselves to temporal analysis of ecosystem collapse. However, the identification of collapse signals in temporal data is hindered by the short time series and/or data of low temporal resolution, which often characterize ecological datasets (53). The use of spatial data has been suggested as a solution to temporal data constraints in early-warning analyses (53, 55) and previously has been used to model the collapse of coupled human–environment systems (56). Spatial early-warning indicators such as the spatial extent of stands of old growth, where structural attributes such as large, old trees are often most common (44), including in the Mountain Ash ecosystem (38), can be readily mapped with technology such as satellite imagery. However, remote sensing of many such trees (particularly standing but decayed dead trees) is not currently feasible (57) because they persist below the canopy of overstory regrowth trees. Consequently, coarser remotely sensed data (e.g., forest extent) may be substituted for finer, ecologically appropriate data (e.g., cover of large, old trees), in turn overestimating large, old tree cover and potentially leading to underestimates of collapse risk. That said, remotely sensed products are rapidly evolving, and new technologies such as Light Detection and Ranging (LIDAR) offer potential to resolve this problem (58).

The Need for New Kinds of Multifaceted and Very Long-Term Monitoring. A lack of long-term monitoring data to forecast ecosystem collapse has been identified as a key shortcoming that limits not only the understanding of ecosystems (59) but also the identification of strategies to manage natural capital that are critical to both ecosystem and industry function (60). Moreover, given that what constitutes ecosystem collapse is ecosystem specific, a sound conceptual understanding of an ecosystem is needed to identify robust state variables that can be used to predict collapse, emphasizing the importance of long-term monitoring of ecological, social, and economic variables.

In the Mountain Ash ecosystem, detailed long-term monitoring data are available, and there is a good conceptual understanding of the drivers contributing to ecosystem collapse (Fig. 3). Indeed, we have been able to quantify the ongoing decline in the Mountain Ash ecosystem only because of long-term monitoring (conducted on an almost continuous basis since 1983) that has encompassed critical attributes of ecosystem function, key ecological processes, a range of elements of biodiversity, and changes in economic assets and ecosystem goods and services (13). This monitoring has allowed us to identify potentially useful state variables for assessments of collapse risk, but even after 34 y of monitoring we are still unable to determine the point at which the Mountain Ash system began to collapse. However, such information is critical to determining time points for action to avert collapse. Available information suggests that monitoring should have begun at least 80 y ago, if not earlier, to determine these time points (at least for iconic, long-lived features of the Mountain Ash ecosystem such as large, old trees).

We suggest that detailed empirical data gathered through long-term ecological monitoring will be fundamental to expanding the currently very limited number of detailed descriptions of ecosystem collapse. In turn, long-term monitoring data will improve understanding of why collapse occurs and how to better predict its likelihood. This kind of work will become increasingly important in the future because of the increasing prevalence of both natural and human disturbances (and their interaction) in forest ecosystems (61) that increase risks of ecosystem collapse in such environments.

Concluding Comments

We present a rare example of an ecosystem currently undergoing collapse (rather than one in which collapse has already occurred). From our empirical analyses, we identify potential state variables that can be used to provide early warnings of collapse for terrestrial socioecological systems, including attributes fundamental to ecosystem function and spatial and socioecological metrics strongly coupled with key ecosystem attributes of interest. We find that drivers leading to ecosystem collapse manifest over much longer time scales than often previously recognized. Even with the knowledge we have gathered about the Mountain Ash ecosystem, it continues to degrade and be managed unsustainably. More monitoring data may help predict timeframes for eventual, irreversible collapse but will not avert collapse in the Mountain Ash ecosystem. Political decisions may do so, particularly if they are implemented soon. However, the protracted timescales over which drivers act on ecosystems foster the superficial perception that an ecosystem is intact, thereby stalling effective action that would avert collapse. This process of hidden collapse (where perceptions of ecosystem condition are at odds with reality) indicate that intervention to avert collapse will likely be required decades before many resource managers become cognizant of the need for change. Greater agility enabling faster policy responses also will be needed, although this is often the antithesis of current policy for resource extraction in many forest ecosystems.

Methods

The study area, field-sampling methods, and statistical analysis are described in *SI Methods*.

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