Avoiding ecosystem collapse in managed forest ecosystems

David Lindenmayer[1]*, Christian Messier[2,3], and Chloe Sato[1]

Many forest ecosystems are thought to be at risk of ecological collapse, which is broadly defined as an abrupt, long-lasting, and widespread change in ecosystem state and dynamics that has major negative impacts on biodiversity and key ecosystem services. However, there is currently a limited ability to accurately predict the risk of collapse for a given forest ecosystem. Moreover, how ecosystem collapse manifests itself will be ecosystem specific, as will be the associated mitigation strategies. In light of these challenges, we present a checklist of 11 practical principles to help managers reduce the risk of ecosystem collapse. These principles include developing a robust definition of collapse that is appropriate for a given ecosystem, managing for multiple ecosystem stressors under increasing uncertainty, adopting conservative approaches to management that account for potential losses of timber resources and limit the risk of overharvesting, and conducting long-term monitoring to gather data on key ecosystem attributes sensitive to ecological change.

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The concept of collapse has been discussed widely in many fields, including economics, anthropology, and ecology (Diamond 2005; Mann 2006; Barnosky *et al.* 2012). In ecology, ecosystem collapse can be broadly defined as an abrupt and undesirable change in ecosystem state (MacDougall *et al.* 2013). The concept of ecosystem collapse is linked to a range of other concepts in the theoretical literature (Figure 1), including those associated with thresholds (Wissel 1984), resilience (Walker and Salt 2012), tipping points (Rockström *et al.* 2009; Barnosky *et al.* 2012; Dixson *et al.* 2014), regime shifts (Scheffer *et al.* 2001; Biggs *et al.* 2009), and changes in ecosystem functioning via state-and-transition models (Pulsford *et al.* 2016). For the purposes of this paper, we argue that for a forest ecosystem to be considered collapsed, at least three key conditions must be met: collapse must be (1) irreversible (Yelenik and D'Antonio 2013) or time- and energy-consuming to reverse (Frank *et al.* 2011), (2) widespread, and (3) undesirable in terms of impaired ecosystem services or major losses of biodiversity (MacDougall *et al.* 2013). There is increasing discussion about the risk of ecosystem collapse, particularly as a consequence of the extent of environmental change and the rapidity with which humans are modifying the environment and thereby adding further ecosystem stressors (eg acid rain, increase in nitrogen deposition, landscape change, and habitat fragmentation; Valiente-Banuet and Verdu 2013; Steffen *et al.* 2015). Many forests worldwide are thought to be susceptible to ecosystem collapse (Reyer *et al.* 2015) (Figure 2). For example, logging, fire, and post-fire salvage logging have triggered a rapid change from rainforest to exotic grassland in parts of tropical Southeast Asia (eg van Nieuwstadt *et al.* 2001). Elsewhere in the tropics, changes in climate are predicted to substantially increase the susceptibility of tropical rainforests to rapid collapse during the remainder of the 21st century (Cox *et al.* 2004; Phillips *et al.* 2009). Logging, coupled with recurrent wildfire, is threatening the collapse of closed (densely stocked stands of) boreal forest to a shrub-dominated ecosystem in northern Canada (Payette and Delwaide 2003). Analyses by Burns *et al.* (2015) indicate that the mountain ash (*Eucalyptus regnans*) forests of Victoria in southeastern Australia are susceptible to collapse as a consequence of widespread clearcutting, recurrent fire, and post-fire salvage logging. A lack of natural water flow is triggering the widespread death of vast tracks of river red gum (*Eucalyptus camaldulensis*) in inland Australia (Figure 2) (Cunningham *et al.*

In a nutshell:

- Forest ecosystem collapse is an abrupt, long-lasting, and widespread change in ecosystem state and dynamics
- We provide a checklist of 11 general principles to guide management in order to reduce risks of ecosystem collapse
- A rigorous definition of ecosystem collapse is essential because how collapse manifests itself and the management actions needed to prevent it occurring will be ecosystem specific
- Avoiding ecosystem collapse demands a conservative approach to forest management, such as setting sustained timber yields that account for disturbance-related stock losses
- Managers should monitor key spatial areas and components and watch for negative and non-additive effects of multiple stressors, especially novel stressors

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[1] *Fenner School of Environment and Society, The Australian National University, Canberra, Australia* *(david.lindenmayer@anu.edu.au); [2] *Institut des Sciences de la Forêt Tempéré (ISFORT), Université du Québec en Outaouais (UQO), Ripon, Canada;* [3] *Center for Forest Research, Université du Québec à Montréal, Montréal, Canada*

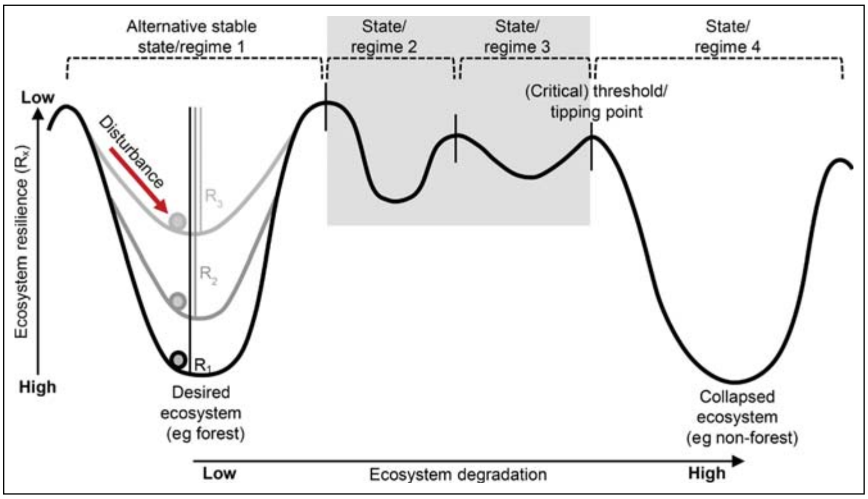

Figure 1. *Conceptual model showing links between ecosystem collapse and a range of other, broadly related concepts. The depth of a basin indicates the resilience of a particular ecosystem state, with the desired and collapsed ecosystem states displaying highest resilience. The ball in the basin represents the current state of the ecosystem. The red arrow represents disturbance to the ecosystem. Disturbance may be cumulative, slowly eroding ecosystem resilience (ie from R_1 to R_2 to R_3), or may be sudden and intense, shifting the system directly from the desired state to an undesired state (ie State 2, State 3, or Collapsed State). The gray shading indicates that multiple, somewhat desirable, alternative stable states or regimes may not always be present for an ecosystem – an ecosystem may shift directly from the desired state to the collapsed state when perturbed.*

2009). The great pine forests of northern North America are thought to be vulnerable to collapse as a result of the recent spread of the mountain pine beetle (*Dendroctonus ponderosae*) epidemic, which has crossed the Rocky Mountains in Canada and has ravaged the lodgepole pine (*Pinus contorta*) forests of British Columbia (Safranyik *et al.* 2009). This epidemic is now threatening all pine species elsewhere in Canada (Cullingham *et al.* 2011); since large tracts of almost monospecific jack pine (*Pinus banksiana*) occur throughout boreal forests, the impact of this novel pest could be considerable (Roy *et al.* 2014), creating large open tracts of boreal forest dominated by shrubs. This new threat is believed to have been the direct result of more than 60 years of forestry practices that have favored lodgepole pine and recent climate warming that has reduced the mortality of pine beetles in winter (Raffa *et al.* 2008).

Despite the extensive literature on ecological collapse, it is clearly very difficult to accurately predict whether and when collapse might occur. Some largely theoretical work (eg Carpenter and Brock 2011) suggests that increasing variability in, and impaired recovery of, certain ecological attributes are a useful early indicator of subsequent ecosystem collapse (Dai *et al.* 2013). However, this kind of work is challenging to apply in practical management because of the extent of detailed background research and prolonged monitoring required. Moreover, some ecosystems that have collapsed have not exhibited these early warning signals (Schreiber and Rudolf 2008; Hastings and Wysham 2010). Indeed, as noted by Boettiger and Hastings (2013), "no one has yet managed to use the theory on early warning signals to predict a natural catastrophe"; they further suggest that "generic early warning signals of tipping points are unlikely to exist".

If ecological collapses are more likely to occur, but difficult to accurately predict, a key question becomes: are there any practical general principles to guide resource management practitioners to reduce the risk of ecosystem collapse? We argue that resource managers should implement actions to reduce those risks and we provide a list of 11 possible principles. Our focus is on managed forest ecosystems, which we define as those natural forests and tree plantations that are used extensively (and often intensively) for the production of wood products (including sawn timber and pulp) and/or the provision of other key ecosystem services such as control of water quality and quantity, recreation, or landscape aesthetics. We recognize that ecological collapse will likely manifest itself differently in different ecosystems (Boettiger and Hastings 2013) and specific insights from a given ecosystem will therefore be difficult to translate to another ecosystem. Hence, unique strategies to prevent collapse will probably be needed in different ecosystems. There is therefore an urgent need to have general principles and approaches that can be applied to any forest ecosystem, so as to attempt to limit the risks of ecosystem collapse in light of the rapidly changing biological, political, social, and climatic conditions that are its likelihood. We present our checklist (see below) as a logical sequence of action items, but we are cognizant of the potential interactions between many of these items, as indicated in the conceptual framework presented in Figure 3.

What could managers do to limit the risks of forest ecosystem collapse?

1. Carefully define ecosystem collapse

Ecosystem collapse is ecosystem specific (Keith *et al.* 2013), so ecosystem-specific management actions will be required. It is therefore essential to define what constitutes collapse for a given ecosystem, possibly relative to some benchmark or reference conditions, to the spatial scale of the collapse (small affected areas might be considered part of landscape heterogeneity rather than collapse), and to well-defined goods and services that we expect from that ecosystem. One example comes from an ecosystem assessment of mountain ash in Victoria, southeastern Australia, where ecosystem collapse was defined in terms of historically low levels of old-growth cover (~1% of the total forest estate) and historically low levels of key structural features such as large old trees (<1% of baseline population levels) (Burns *et al.* 2015). In some other regions, ecosystem collapse could be defined as the permanent loss of a key tree species, due to the introduction of exotic pests (including insects) that negatively affects biodiversity and key human activities. There are many cases of widespread losses of tree species attributable to pests, with negative associated effects for both biodiversity and human activities (Roy *et al.* 2014).

2. Identify potential pathways to collapse

Managers should identify possible pathways to collapse so as to hedge against the risk of this occurring. Identifying such pathways can be based on the current understanding of ecosystems or as an extension of available conceptual models and/or state-and-transition models (eg those provided by Perry and Enright [2002] and Costanza *et al.* [2015]). Models of ecosystem collapse should incorporate long-term scenarios that specifically acknowledge possible future disturbances and stressors that could trigger major, undesirable changes (Bowman *et al.* 2013; Messier *et al.* 2015). For instance, possible future increases in fire severity and/or frequency in forest ecosystems supporting few or no fire-adapted tree species should alert managers to the likelihood of ecosystem collapse (Payette and Delwaide 2003). As an example, simulation studies by Westerling *et al.* (2011) suggest that elevated fire frequency over the next century resulting from climate change may promote the transformation of conifer forests to more open vegetation in the Greater Yellowstone Ecosystem in Wyoming. Under such conditions, the planting of fire-resistant or -resilient tree species may be necessary as a mitigation strategy (eg Aubin *et al.* 2016; Sánchez-Pinillosa *et al.* 2016).

3. Conserve biodiversity

Conserving biodiversity is a key part of reducing the risks of forest ecosystem collapse (Valiente-Banuet and Verdu 2013), given that biodiversity plays critical roles in ecosystem function, dynamics, and stability (eg Reich *et al.* 2012). Conversely, biodiversity loss is a major driver of ecosystem change (Hooper *et al.* 2012) and increases the vulnerability of ecosystems to collapse (MacDougall *et al.* 2013), particularly when biodiversity loss is accompanied by persistent, and often interacting,

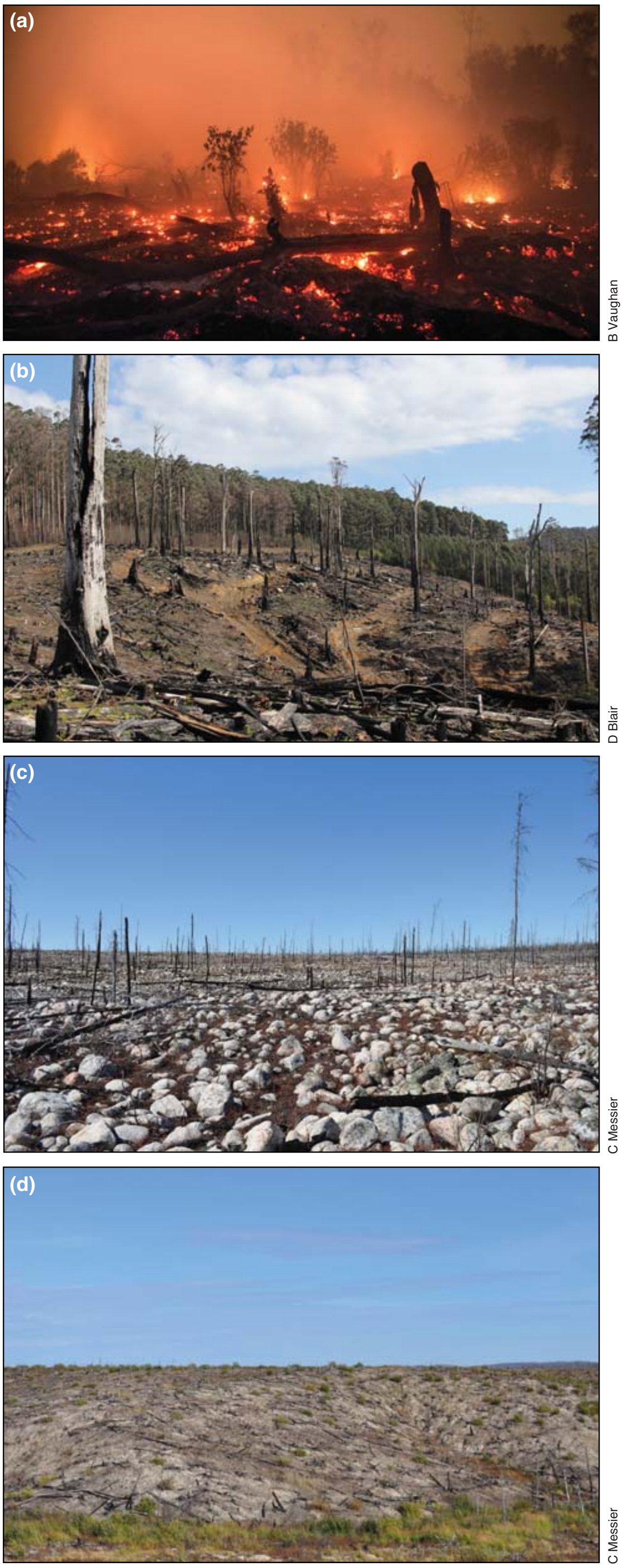

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Figure 2. *Examples of managed forest ecosystems that have been heavily disturbed and are considered vulnerable to collapse: (a) tropical rainforests in Southeast Asia; (b) mountain ash forests in southeastern Australia; (c) pine forests in western Canada; (d) closed black spruce forests in northern Quebec, Canada.*

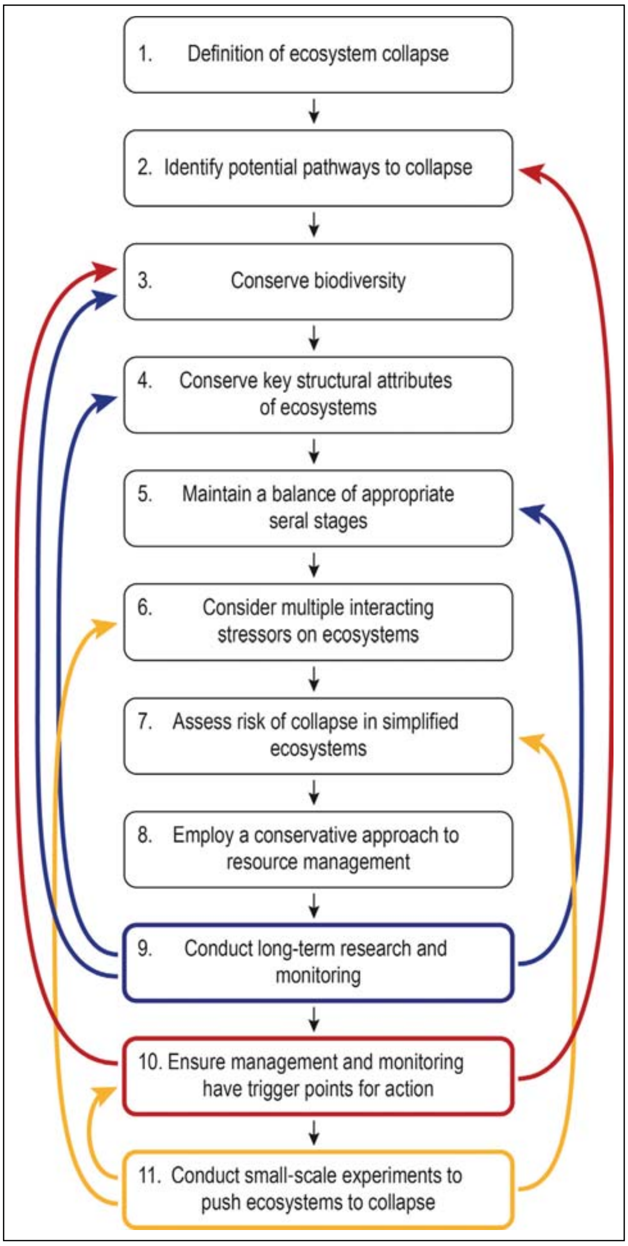

Figure 3. *Conceptual framework showing links between the 11 general principles to guide management, research, and monitoring in managed forests to reduce the risk of ecosystem collapse. The numbers in the figure correspond to the sequence of general principles described in the text. The color of the arrows matches the color of the box from which they originate. The principles are presented in numerical sequence, but several are interrelated and data generated from implementing them can be informative for other principles. As one of several examples, small-scale experiments to push ecosystems to collapse (Principle #11) can also provide insights into the impacts of multiple interacting stressors as well as informing trigger points for management action (Principle #10), and consider multiple interacting stressors on ecosystems (Principle #6).*

human disturbances (Valiente-Banuet and Verdu 2013). Moreover, in conserving biodiversity, we preserve the information legacy of ecosystems and their coevolution with human society – information that is critical to understanding and slowing the rate of ecosystem collapse.

4. Conserve key structural attributes of forest ecosystems

Management and/or monitoring (see below) should focus on some of the key attributes of ecosystems that play keystone roles but are very sensitive to change, are hard to replace, or take a long time to recruit. Examples include large old trees (Lindenmayer and Laurance 2016), fire refuges (Mackey *et al.* 2012), and vernal pools (Calhoun and deMaynadier 2008).

5. Maintain a balance of seral stages in managed forests

A key part of management must be to maintain important life-cycle components of dominant plants that would otherwise make forest ecosystems vulnerable to collapse. For example, the regeneration niche is a critical part of the life cycle of all forest tree species and therefore to the maintenance of forest ecosystems. However, the regeneration niche of many forest trees can be sensitive to recurrent human and natural disturbances as well as to the impacts of exotic taxa that can greatly impair regeneration (Bhagwat *et al.* 2012; Smith *et al.* 2016). In the southwestern US, ponderosa pine (*Pinus ponderosa*) forests can be vulnerable to regeneration failure after high-severity fires (Friederici 2003). Likewise, in many eastern North American forests, overbrowsing by deer (*Odocoileus virginianus*) can interact with disturbance regimes to severely modify forest structure and composition (Nuttle *et al.* 2013).

6. Consider potentially negative and non-additive effects of multiple stressors

The risks of ecosystem collapse may be magnified in ecosystems that are subject to the interaction of multiple threatening processes, including novel sets of drivers that could lead to novel spatial patterns such as the extent of old-growth forest. Our concern about combinations of drivers stems from research that suggests that co-occurring disturbances can interact to produce different outcomes than those based on summing individual effects (Didham *et al.* 2007; Foster *et al.* 2016). As an example, altered (and intensive) herbivore grazing regimes interact with fire regimes in Australian coastal forests and have considerably greater negative effects on vegetation than either of these in isolation (Foster *et al.* 2015). Foster *et al.* (2016) provided a valuable experimental framework for studies to help distinguish the potential impacts of multiple interacting stressors, including how to underpin such studies with relevant ecological theory (Figure 4). Notably, many investigations have demonstrated that the demise of individual species stems from multiple interacting factors (eg Woinarski *et al.* 2015), and we hypothesize that the risks of ecosystem collapse will also be a function of multiple drivers.

7. Be aware of the potential risks facing highly simplified ecosystems

Niche theory and other theories suggest that structurally simplified ecosystems will, in general, support fewer species. In turn, simplified ecosystems may be vulnerable to collapse, particularly in the face of multiple ongoing human disturbances (MacDougall *et al.* 2013) or unexpected invasions of pests or pathogens (Herms and McCullough 2014). Forestry practices typically simplify nature to facilitate and maximize the harvesting of the few desirable tree species (Puttmann *et al.* 2009). These practices have had a negative impact on the overall biodiversity found in these simplified forests, which have in some cases totally or partially collapsed. Many monospecific tree plantations established in Japan after World War II are now on the verge of collapse, because they are too expensive to harvest and replant and there has been little or no natural tree regeneration in the understory (Nagaike *et al.* 2006) (Figure 2). Planning for managed forest ecosystems, even simplified ones that are able to self-regenerate and organize if left unmanaged, is an important precautionary approach (Lindenmayer *et al.* 2015a).

8. Adopt a conservative approach to natural resource management

Many stocks of natural resources are characterized by chronic overharvesting, which may precipitate ecosystem collapse (Frank *et al.* 2011; Burns *et al.* 2015). It is therefore important to adopt a conservative approach to ecosystem resource use and management. For instance, most forest management agencies calculate sustained yields of timber and pulpwood without accounting for inevitable losses that will occur as a result of natural disturbances such as wildfires (eg Burgman *et al.* 1994). This convention "locks in" expected harvesting levels and impedes efforts to sustain other forest values like biodiversity conservation. In the wet forests of southeastern Australia, simulation modeling suggests that 45% of the forest estate will be damaged by wildfire over a nominal rotation time of 80 years and hence should not be included as available timber stock for logging (M McCarthy, pers comm). However, the agency responsible for forest management makes no provision for any stock losses through fire (or any other natural disturbances), the consequence being that levels of sustained yield are set too high and overcutting is inevitable. There are useful examples of conservative stock harvesting from other industries that may provide insights for forest management. These include the kangaroo harvesting industry in Australia, where annual quotas are set well below theoretical maximum sustained yield levels to account for uncertainty, natural variability, and a range of other factors (Lindenmayer and Burgman 2005). Conservative resource management should be underpinned by well-known concepts such as the precautionary principle and a safe operating space approach (Rockström *et al.* 2009).

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Figure 4. *The fencing system and associated burning employed in a replicated experiment in coastal southeastern Australia. The experiment is designed to quantify the interacting effects of fire and altered grazing regimes by native herbivores and provides rapid feedback to park managers about best practice vegetation management (Foster* et al. *2015).*

9. Conduct long-term ecosystem research and monitoring

By maximizing the chances of detecting a problem before it manifests itself, long-term research and monitoring is essential for reducing the risks of forest ecosystem collapse (Contamin and Ellison 2009; Lindenmayer and Likens 2010). For example, resource managers in the northeastern US were alerted to the potential problems of acid rain by long-term monitoring efforts and triggered appropriate actions before changes in aquatic and forest ecosystem conditions approached possible irreversibility (Holmes and Likens 2016). Long-term research and monitoring may also contribute to better prediction of future problems in a given ecosystem (Boettiger and Hastings 2013) but must be well designed and implemented to detect ecosystem change. This includes gathering data on ecosystem attributes sensitive to change, which we suggest can be best identified through developing conceptual models of the key drivers of a given ecosystem (Holmes and Likens 2016).

Monitoring programs also need to be nimble and adaptive (Adaptive Monitoring; Lindenmayer and Likens 2009) – capable of changing in response to emerging issues and problems while at the same time maintaining the integrity of long-term datasets. Although the responses of ecosystems to management interventions should ideally be quantified through long-term research and monitoring, occasionally this is omitted. For instance, important opportunities for studying the effects of outbreaks of mountain pine beetle in British Columbia were lost because the vast majority of beetle-damaged areas were salvage logged, thereby diminishing the capacity to learn about ecosystem recovery.

10. Ensure that ecosystem management has well-defined trigger points for action

Trigger points or "management thresholds" (Hunter *et al.* 2009) that, when approached, instigate a change in management and associated policy setting are essential to avoid potentially irreversible deterioration in ecosystems. For example, rates of cutting and rotation times might be altered directly after a wildfire if the extent of burned forest in a landscape exceeds a given level (eg 30% of a landscape or region) to avoid overcutting the remaining unburned forest. In plantation-dominated regions where fire-adapted tree species are absent, altered fire regime attributes (such as increased fire frequency) may trigger new plantation establishment strategies based on tree species better adapted to wildfire. These management thresholds are different from ecological thresholds (Hunter *et al.* 2009). Such redundancy is important to enhance management certainty and decrease the risk of management mistakes based on poorly performing indicators (Lindenmayer *et al.* 2015b). Moreover, the consequences of breaching management thresholds need to be clearly communicated to stakeholders (eg policy makers) to avoid perverse policy outcomes (eg retraction of conservation investments; Mumby *et al.* 2011).

11. Conduct small-scale experiments and other studies to quantify the risks of ecosystem collapse

Conservative management approaches should be complemented by small-scale experimental actions that "push" a given ecosystem beyond the bounds of natural variability to improve our understanding of probable future impacts of known or novel disturbances (Belovsky *et al.* 2004).

Conclusions

Many authors are warning about the risks of ecosystem collapse in both the popular and scientific literatures (Diamond 2005; Mann 2006; Biggs *et al.* 2009). At the same time, predicting ecosystem collapse is clearly an inexact (and still largely theoretical) science (eg Hastings and Wysham 2010; Carpenter and Brock 2011). Even if its current but limited predictive capabilities are improved over time, the science may still be restricted to forecasting collapse only for particular well-studied ecosystems (Boettiger and Hastings 2013). To tackle this problem, we have presented a checklist of 11 principles (listed above) that managers should consider in order to limit the risks of ecosystem collapse.

Finally, we argue that collapse should not be an endpoint for management. Although collapsed ecosystems are undesired states, they are not necessarily without value. Ecosystem collapse can result in large losses of biodiversity (MacDougall *et al.* 2013) but the collapsed system is likely to retain some biodiversity value that may continue to offer important ecosystem services and/or an opportunity to restore the system to a near pre-collapse state. However, the limited availability of collapsed ecosystem conceptualizations or definitions indicates that the value of collapsed ecosystems – in their own right, as opposed to being the degraded version of their former selves – is rarely quantified. Indeed, as discussed above, opportunities to rigorously study and understand the ecology and conservation value of collapsed systems are not always taken (eg pine beetle dieback in British Columbia). This limits our general understanding of such collapsed systems and our ability to effectively manage the new system to maximize ecological or conservation values. We suggest that researchers may contribute to the scientific understanding of ecosystem collapse by ensuring that in those cases where ecosystem collapse has taken place, the reasons for its occurrence are better documented.

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