Newly discovered landscape traps produce regime shifts in wet forests

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We describe the "landscape trap" concept, whereby entire landscapes are shifted into, and then maintained (trapped) in, a highly compromised structural and functional state as the result of multiple temporal and spatial feedbacks between human and natural disturbance regimes. The landscape trap concept builds on ideas like stable alternative states and other relevant concepts, but it substantively expands the conceptual thinking in a number of unique ways. In this paper, we (*i*) review the literature to develop the concept of landscape traps, including their general features; (*ii*) provide a case study as an example of a landscape trap from the mountain ash (*Eucalyptus regnans*) forests of southeastern Australia; (*iii*) suggest how landscape traps can be detected before they are irrevocably established; and (*iv*) present evidence of the generality of landscape traps in different ecosystems worldwide.

altered ecosystem processes | old growth

In many environments worldwide, key drivers of ecosystem change interact and reinforce one another to trigger cascades of ecosystem modification that are difficult or impossible to reverse (1–3). These cascades are often referred to as regime shifts (4–6). Examples of significant regime shifts include overfishing and trophic cascades in marine predator–prey systems (7) and human disturbance-driven losses of detritivore populations and subsequent changes in the decomposition of organic matter (8). Regime shifts are almost always identified in retrospect, making it difficult to know how to avoid them in advance and problematic to reverse their effects. Therefore, understanding of the mechanistic processes by which regime shifts occur may provide opportunities to change resource management and avoid irreversible and undesirable ecological changes.

In this paper, we describe the "landscape trap" concept, of which the outcome is a regime shift triggered by a series of feedback processes resulting from interacting natural and anthropogenic disturbances. We define a landscape trap as that wherein entire landscapes are shifted into a state in which major functional and ecological attributes are compromised. These shifts in a landscape lead to feedback processes that either maintain an ecosystem in a compromised state or push it into a further regime shift in which an entirely new type of vegetation cover develops. Landscape traps are large-scale ecological phenomena that arise through a combination of altered spatial characteristics of a landscape coupled with synergistic interactions among multiple human and natural disturbances. Thus, changes in the frequency and spatial contagion of large-scale disturbances are the key interacting factors driving entire landscapes into an undesirable and potentially irreversible state (i.e., landscape trap). We demonstrate the concept with examples involving spatial and temporal feedback between logging and fire in forest ecosystems and also provide examples of landscape traps in other environments.

Like other kinds of ecological traps, the landscape trap concept shares characteristics like shifts between alternative stable states and multiple feedback processes (9). However, a focus at a landscape scale and on temporal and spatial changes in disturbances sets the landscape trap concept apart from other kinds of ecological traps and regime shifts, such as population traps and extinction vortices in small populations of animals (10) and elevated rates of animal species loss below threshold levels of native vegetation cover (11).

To the best of our collective knowledge, the landscape trap concept has not been previously reported, yet we argue that landscape traps may be more prevalent in ecosystems around the world than currently recognized. Common ingredients contributing to landscape traps are (*i*) overharvesting of natural resources in a landscape; (*ii*) climate change effects on species' life histories and/or the frequency and severity of ecological disturbances; (*iii*) major changes in the spatial characteristics of landscapes; (*iv*) feedback loops between the changed environmental conditions and other major stressors; and (*v*) severely impaired ecological functions of a landscape in an altered state, such as, for example, reduced populations of species and habitat suitability, reduced carbon storage, and reduced water and timber production. The interaction of these factors is shown in a conceptual model in Fig. 1.

We suggest that landscape traps exist in many ecosystems. For example, logged tropical rainforests in parts of Asia have become more fire-prone (12). Postfire salvage logging in some of these rainforests, in turn, changes the vegetation composition toward more fire-prone grassland taxa. Additional fire further degrades fire-sensitive remnant rainforest, eventually leading to a regime shift to exotic fire-promoting grasslands, limiting opportunities for the vegetation to revert to tropical rainforest (13). Such kinds of interrelationships between logging and altered fire regimes are widespread in tropical rainforests in many other parts of the world, including South America and Africa (14), as are relationships between logging and exotic fire-prone grasses (15).

Temperate forests are not immune to such traps. In moist temperate forests of western North America, logging-related alterations in stand structure increase the risk for both occurrence and severity of subsequent wildfires through changes in fuel types and conditions (16, 17). High-severity wildfires kill young trees planted following previous logging operations. This necessitates reforestation efforts, but these young stands are susceptible to being killed in subsequent recurring high-severity fires (16). Similar kinds of relationships between logging regimes and altered fire regimes have been reported in a range of forest types elsewhere around the world (reviewed in 18).

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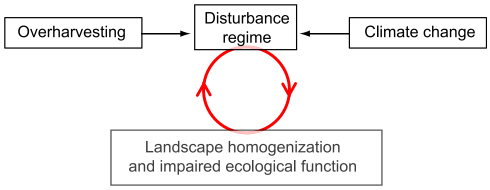

Fig. 1. Conceptual model of a landscape trap. The trap results from the reinforcing feedback loop shown in red.

Results and Discussion

Specific Example of a Landscape Trap: Mountain Ash Forests of Victoria, Southeastern Australia. The specific example of a landscape trap that we present comes from the mountain ash (*Eucalyptus regnans*) forests of southeastern Australia in the central highlands of Victoria. The likely regime shift is from landscapes dominated by old-growth forests that are 200–450 y of age to those dominated by young fire-prone forests that do not survive to become old growth. Evidence comes from new spatial information following massive wildfires in 2009, perhaps the most economically destructive in Australian history (19), coupled with understanding that has emerged from 28 y of extensive field information and associated data analyses in mountain ash forests (20).

The central highlands of Victoria support ∼121,000 ha of mountain ash forest. These are spectacular forests with old-growth trees reaching 90 m or more in height (14). Mountain ash forests persist only within a particular fire regime (*sensu* 21). Before European settlement over 150 y ago, the fire regime was infrequent severe wildfire that occurred in late summer (22). Young seedlings germinate from seed released from the crowns of burned mature trees to produce a new even-aged stand (20). Wildfires may be stand-replacing, because the young trees regenerating after fire belong to a single age cohort (23). When the interval between stand-replacing disturbances is less than 20–30 y (which is the period required for trees to reach sexual maturity and begin producing seed) (24), stands of mountain ash forest will be replaced by other species, particularly wattle (*Acacia* spp.) (20).

In the past century, a new disturbance regime (logging) has been added to the previous natural fire regime. Large areas of mountain ash have been subject to timber and pulpwood harvesting (Fig. 2). In the past 40 y, the traditional method of logging has been clear-cutting, in which all merchantable trees within a 15- to 40-ha area are cut in a single operation (25). Following clear-cutting, logging debris is burned to create a bed of ashes in which the regeneration of a new eucalypt stand takes place, often by artificial reseeding. The vast majority of mountain ash landscapes have become dominated by large areas of regrowth forest with small areas of old forest embedded within them. Old-growth mountain ash forest (*sensu* 20) typically covers less than 3% of the majority of the 3,000- to 6,000-ha wood production forest blocks in the central highlands; however, in some cases, it is less than 1% (20). Indeed, following more than a century of logging and wildfires in 1926, 1932, 1939, 1983, and, most recently, 2009, ∼1.1% of the entire mountain ash forest estate is now in an old-growth stage. This landscape is in stark contrast to mountain ash landscapes 100–150 y ago, which historical accounts (e.g., 26), coupled with stand reconstruction work relating to tree age and stem diameters of large dead (snag) trees remaining within young stands (27), suggest were dominated by large areas of old growth, possibly as high as 60–80% total cover in the central highlands of Victoria (20) (Fig. 2).

Development of a Landscape Fire-Trap in Mountain Ash Forests. The interacting effects of wildfire, logging, and the combination of wildfire and logging (i.e., salvage logging) (*sensu* 28) are creating a previously unrecognized landscape trap in which the disturbance dynamics of "trapped" mountain ash forest landscapes are markedly different from those before European settlement (Figs. S1 and S2). The core process underlying this landscape trap is a positive feedback loop between fire frequency/severity and a reduction in forest age at the stand and landscape levels, leading to an increased risk for dense young regenerating stands repeatedly reburning before they reach a more mature state (Fig. 3). The landscape trap will potentially create irreversible changes in disturbance dynamics, forest cover, landscape pattern, and vegetation structure, and thereby lead to a major regime shift or alternative state. We explain below the evidence for the positive feedback process that underpins this landscape trap (Fig. S2) and discuss why it is historically unprecedented and why it is beginning to dominate the contemporary landscape.

Positive feedback loop between reduced forest stand age and fire. Young stands of mountain ash forest are created by natural regeneration following wildfire. Detailed on-site measurements following the 2009 wildfires have revealed that young forest burns at higher severity than mature forest. We suggest this is for four key reasons:

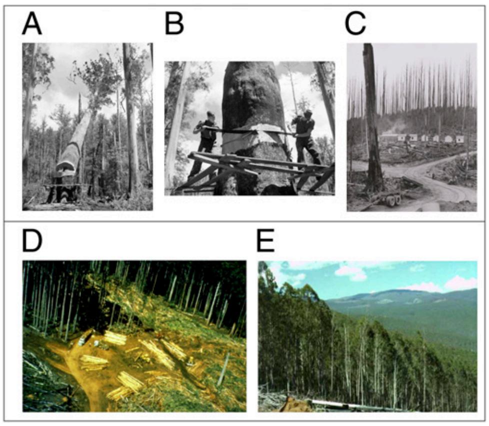

Fig. 2. Photo montage showing historical logging in extensive stands of old-growth forest (*A*–*C*) and extensive clear-cut areas of forest cut in the past 10 y (*D* and *E*) in the mountain ash forest in the central highlands of Victoria. (Photos courtesy of National Archives of Australia, State Library of Victoria and D.B.L.)

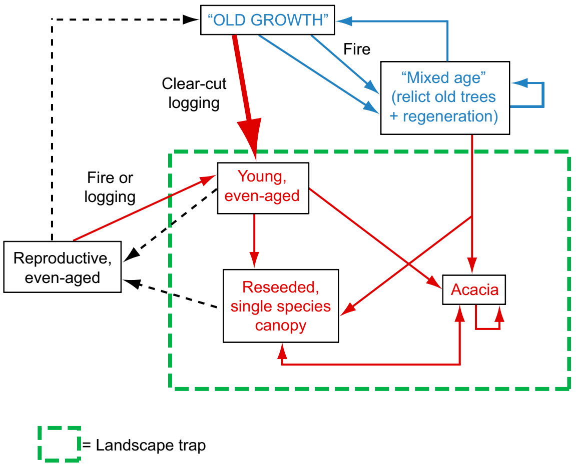

Fig. 3. Development of a landscape trap in the mountain ash forests of the central highlands of Victoria.

i) Young regenerating stands of mountain ash trees are characterized by densely spaced regrowth saplings. There can be several million eucalypt seedlings per hectare soon after a fire or logging. Through processes of rapid natural self-thinning, this declines to ∼400 stems per hectare at 40 y and 40–80 stems per hectare in mature forest after 150–200 y (29). The marked reduction in the number of stems per unit area over time is primarily attributable to competition-derived death and collapse of small suppressed pole and sapling trees, which add greatly to the density of the vegetation in young regrowing forests but do not generally occur in mature and old-growth mountain ash forests (30). Densely spaced stands of regrowth saplings, coupled with the subsequent natural processes of rapid self-thinning that characterize the early stages of stand regeneration in mountain ash forests, create significantly more fine and medium fuels than in old forests (31).

ii) The closely spaced crowns in densely stocked young stands are readily susceptible to carrying a crown fire. This is in contrast to old-growth stands, which are characterized by large relatively well-spaced trees with open crowns and small lateral subcrowns (24).

iii) Trees in young stands are shorter than those in old-growth stands. The flame height needed to scorch or consume the canopy in young stands is therefore significantly lower than in old-growth stands (22).

iv) Young forests support significantly smaller diameter logs on the ground than old-growth stands (32). Such smaller diameter logs support significantly less dense and luxuriant moss mats than larger diameter fallen trees. Moss mats hold large amounts of water (1,100% of dry weight) (33); they play a significant role in moisture retention within logs, and thereby may reduce the risk for burning.

Why has this positive feedback loop not occurred historically? Before European settlement, frequent, widespread, high-severity wildfires in mountain ash forests would have been suppressed by a combination of extended periods of wet climatic conditions and the absence of the intensive human disturbances resulting from clear-cut logging. This favored a negative feedback loop between forest age and fire, enabling young forest to mature into a less fire-prone state that was not conducive to widespread high-severity wildfire (Fig. S1).

Why is this positive feedback loop now beginning to develop? Two major changes have occurred relatively recently to favor the positive feedback loop: reduced forest age in mountain ash forests and increased fire frequency (Fig. 3 and Figs. S1 and S2). First, there has been a 25% reduction in rainfall in southeastern Australia over the past few decades (34). Second, logging has converted more than 90% of formerly old forest to young regenerating stands. Young forest resulting from clear-cut logging has two added elements of fire proneness: (*i*) fine fuels created by logging operations are added to those from the collapse of small-diameter stems and shedding of branches during natural self-thinning and self-pruning processes in densely stocked regenerating stands, and (*ii*) the spatial pattern of stand age classes in mountain ash landscapes has been altered, with an increased prevalence of young densely stocked forest and a significantly reduced area of (mesic) old-growth forest. This, in turn, has increased the fire contagion in the landscape.

Codes of logging practice and the practical logistics of harvesting operations mean that clear-cutting is applied to flatter and more accessible parts of mountain ash landscapes. However, these places are also where old-growth stands were formerly most likely to occur. Evidence for this comes from work in closed-water catchments of the central highlands of Victoria, where there were no confounding effects of past and present human disturbances that would have otherwise obscured key spatial patterns of forest age classes (22). Before the 2009 wildfires, old growth mountain ash occupied a subset of the overall environmental domain of mountain ash per se, typically within a narrow band of mesic sites rather than ridges or steep slopes. This environmental domain was not only favorable for tree growth but interacted with spatial differences in natural disturbance regimes (35). Mesic sites support taller trees. They are also places where both the fire frequency and the intensity of past wildfires were attenuated (22). Former areas of old-growth forest on flat terrain have now been converted to young regenerating stands and are spatially connected to young burned or logged forest on midslopes and ridges. Importantly, the more widespread that young logged and regenerated forest becomes, the greater is the risk for increasing spatial contagion in the spread of wildfire through landscapes (31), because moist remnant areas that would have slowed or halted the spread of fire (and formerly supported old forest) have been converted to young forest. Spatial contagion in recurrent high-severity fire may therefore reinforce a pattern of increasing homogeneity in the cover of young forest in a landscape (Fig. S2). This pattern occurs because some areas of fire refugia (e.g., flat plateau, deep south-facing valley floors) that were traditionally characterized by a long absence of fire (particularly high-severity fire) and supported stands of multiaged forest or old-growth forest (35) become more susceptible to being burned by high-severity conflagrations that spread from adjacent more flammable logged and young regenerating areas (Figs. S1 and S2). Notably, although natural disturbance regimes often increase heterogeneity in many landscapes (36), the opposite frequently occurs in areas subject to landscape trap phenomena, in which the combination of human and natural disturbance regimes can lead to increased landscape homogeneity.

Research in moist forests around the world suggests that other factors associated with logging may increase susceptibility of young regenerating forests to being burned or reburning at high severity. For example, the large quantities of logging slash created by harvesting operations can sustain fires for longer than fuels in unlogged forest (12). Similarly, lightning strike ignition is more likely to occur in harvested stands because of increased fine fuels resulting from logging slash, and this effect may remain for 10–30 y following logging (37). Finally, the removal of trees by logging creates microclimatic conditions that lead to increased drying of understory vegetation and the forest floor, and a correspondingly elevated fire risk (38).

Once a mountain ash forest landscape is dominated by widespread areas of young fire-prone forest, the elevated risk for high-severity spatially contagious fire decreases the probability that the landscape can return to its former mature state, particularly under the drier and warmer conditions associated with climate change. Hence, the dynamics of trapped mountain ash forest landscapes are different from those in the past (>100 y ago) (Fig. 3 and Figs. S1 and S2). The current set of interacting disturbance regimes of fire, logging, and postfire (salvage) logging did not exist before European settlement. Importantly, there is a major asymmetry in the period during which mountain ash forest ecosystems have coevolved with natural disturbances (>20 million y) compared with the 20–100 y during which the interacting human and natural disturbance regimes have produced a landscape trap.

End point: Regime shift? The positive feedback cycle of widespread young regenerating stands and frequent high-severity wildfire means that either extensive areas of trapped young mountain ash forest will be maintained or a further regime shift will occur in which a new type of vegetation cover develops, particularly wattle (*Acacia* spp.) (Fig. 3 and Figs. S1 and S2). Once mountain ash has been eliminated from an extensive area, it recolonizes slowly because the seed released from the crowns of burned mature trees disperses ∼1.5–2.0 crown heights from a source

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tree and successful regeneration (fire) events may occur every 30–400 y. Therefore, the regeneration niche, which is a key part of the life cycle of mountain ash (39), is maladapted to the altered landscape conditions and altered fire regime created by recurrent logging and wildfire. Recurrent high-frequency wildfire may result in repeatedly burned areas that were formerly dominated by mountain ash being colonized by other eucalypt species that do not depend on seedling regeneration but, instead, recover after wildfire via strategies like epicormic resprouting [e.g., shining gum (*Eucalyptus nitens*), messmate (*E. obliqua*)].

Irrespective of whether mountain ash forest landscapes remain trapped as widespread, young, fire-prone stands or undergo a regime shift to extensive areas dominated by *Acacia* spp. and other species, such changes will result in significant impairment of ecological functions like carbon storage, water production (40, 41), and biodiversity conservation. For example, neither young small-diameter mountain ash trees nor *Acacia* spp. support the cavities that are crucial nesting and denning sites for many species of animals. They also lack critical structural features, such as extensive bark streamers, that are key foraging microhabitats for wildlife (42). These changes in vegetation structure are likely to lead to irreversible losses in habitat suitability for $\sim$40 species of vertebrates in mountain ash forests that are dependent on large 120- to 150+-y-old trees with hollows.

Avoiding a Landscape Trap in Mountain Ash Forests of Victoria. Three important strategies are needed to reduce the problems created by the landscape trap in the mountain ash forests of Victoria. First, large (>1,000 ha) areas of currently unburned forest need to be retained, wherein the number of anthropogenic stressors is reduced. The area of green forest was reduced dramatically by the 2009 wildfires; hence, relative biodiversity, carbon storage, and water production values of remaining unburned forest have increased. However, such uncommon areas of unlogged forest are increasingly sought after for timber and pulpwood harvesting because (*i*) they are among the declining number of places suitable for cutting as a consequence of past fires and past (prefire) logging operations, (*ii*) there are legislated guarantees to provide logging contractors with forest to cut for timber and pulpwood (43), and (*iii*) cutting burnt forest (i.e., salvage logging) has major negative environmental impacts and long-term effects on forest recovery and forest biodiversity (28). Targeting limited remaining areas of unburned forest for logging depletes the overall amount of these forests, with long-term economic implications for harvest contractors. Increased logging pressure on green areas has other ecological implications: Remaining areas of green forest are important refugia for biodiversity following wildfires and are critical for underpinning postfire ecological recovery (32). Legislative and other impediments to reducing harvest levels highlight the existence of management and socioeconomic traps within landscape traps, and these need serious and timely review.

A second strategy to avoid the development of a landscape trap in the now highly fire-prone mountain ash landscapes of Victoria is to recalculate the sustained yield to accommodate future losses of timber resulting from the inevitable burning of some parts of forest landscapes. This strategy has the advantage of not overcommitting remaining unlogged green forest in the event of wildfires, thereby resulting in more conservative management of natural resources and more explicit recognition of the uncertainty created by major natural disturbances.

Given the extent of recently burned forest in Victoria, a third important strategy to reduce the risks for development of a landscape trap is to try to limit the amount of future fire. Although mountain ash trees are dependent on fire to promote regeneration, fires have been extensive in the past 25–100 y; another fire in the coming 20 y within currently young regenerating stands is likely to lead to a major regime shift (Fig. 3). Reducing the amount of fire in mountain ash forests is a significant challenge. Broad-area prescribed burning is not a viable management option because high levels of moisture in the vegetation and large quantities of biomass make planned fires extremely difficult to control (20). However, prescribed burning as part of a regime of fire can be an appropriate management option in drier forest types that are adjacent to mountain ash forests. Carefully applied strategic burning in such drier environments may help to reduce the extent of spatial contagion in wildfire that occurs in these areas and, in turn, reduce the risk for adjacent stands of mountain ash forest being burned (44).

Examples of Landscape Traps in Ecosystems Other Than Forests. We contend that landscape traps may be prevalent in many ecosystems. For example, climate change and overfishing have facilitated the conversion of subtidal kelp (*Macrocystis pyrifera*) forests in Tasmanian coastal waters to "barrens" habitat resulting from overgrazing by the sea urchin *Centrostephanus rodgersii*. Ocean warming and altered circulation patterns have enabled the poleward spread of this sea urchin (45), and overfishing of predators, such as the southern rock lobster (*Jasus edwardsii*), has enabled *C. rodgersii* to establish high-population density barrens that result in the loss of biodiversity and a reduction in the productivity of fisheries and contribute to the decline of such predators as *J. edwardsii* (46). Aquatic environments where water quality can be radically altered by nutrient inputs from human activities (e.g., 47) also are susceptible to the development of landscape traps.

Grazing on public lands in the western United States has been blamed for reducing biodiversity and, together with exotic weeds, may have led these grassland ecosystems into a landscape trap that produces a plant community from which there is no going back (48). Livestock grazing in western United States may have reduced the abundance of preferred plant species while subjecting the soil to weed invasion, such that large areas are now degraded rangelands in the same manner illustrated in eastern Australia by the "woody weed" problem in semiarid woodlands (49). Introduced grasses, such as cheatgrass (*Bromus tectorum*), can similarly move grassland communities in the intermountain western United States into a regime change that is nearly impossible to reverse (50, 51). A lack of reversible change may be best illustrated by landscape traps in regions heavily impacted by disturbances like mountaintop mining (52).

Concluding Comments

We suggest that strategies and management interventions are needed to reduce the probability of landscape traps developing (Fig. 4). One approach is to recognize that landscape traps can exist and identify the suite of spatial and temporal characteristics that can combine to give rise to them, including (*i*) exploitation of the natural resources in a landscape through unsustainable levels of harvesting; (*ii*) alteration in the spatial characteristics of landscapes, including modifications to the frequency and severity of ecological disturbances; (*iii*) feedbacks between altered environmental conditions and other major anthropogenic stressors;

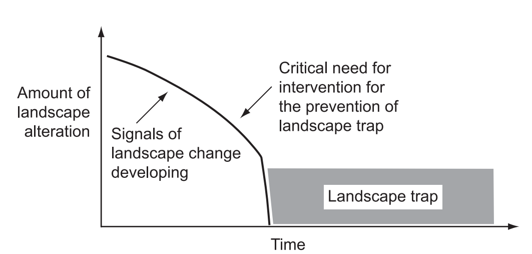

Fig. 4. Conceptual model highlighting signals and interventions required to reverse the development of a landscape trap.

and (*iv*) severely impaired landscape processes and functions. A second approach is to limit the number of anthropogenic stressors in landscapes and reduce the potential for negative interactions among multiple stressors. This may equate to a more conservative approach to the harvesting of natural resources or, in other cases, application of management strategies that reduce feedbacks (e.g., fuel reduction through prescribed burning). Sustained yields of natural resources also may need to be rapidly reassessed following catastrophic events to avoid overcommitting remaining intact areas and further increasing the risk for creating a landscape trap.

We suggest that the need for proactive management to prevent the development of landscape traps is critical, given that (*i*) landscape traps might be at increased risk for development in response to significant "events" like major natural disturbances, which are likely to become more frequent, more severe, or both under rapid climate change in many regions (e.g., 53, 54), and (*ii*) marked asymmetry exists between the rapidity with which landscape traps may develop and the prolonged time scales (hundreds to thousands of years) that characterize natural ecological processes and natural disturbance regimes.

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