



New Policies for Old Trees: Averting a Global Crisis in a Keystone Ecological Structure

David B. Lindenmayer¹, William F. Laurance², Jerry F. Franklin³, Gene E. Likens^{4,5,6}, Sam C. Banks¹, Wade Blanchard¹, Philip Gibbons¹, Karen Ikin¹, David Blair¹, Lachlan McBurney¹, Adrian D. Manning¹, & John A.R. Stein¹

¹ Fenner School of Environment and Society, The Australian National University, Canberra, ACT 0200, Australia

² Centre for Tropical Environmental and Sustainability Science (TESS), and School of Marine and Tropical Biology, James Cook University, Cairns, Queensland 4878, Australia

³ School of Environmental and Forest Science, University of Washington, Seattle, WA 98195, USA

⁴ Cary Institute of Ecosystem Studies, Millbrook, NY 12545, USA;

⁵ Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs-Mansfield, CT 06269, USA

⁶ Department of Limnology, EBC-Uppsala University, 753 12 Uppsala, Sweden

Keywords

Biodiversity loss; disrupted ecosystem processes; large old trees; threatening processes; tree mortality; tree recruitment.

Correspondence

David Lindenmayer, Fenner School of Environment and Society, The Australian National University, Canberra, ACT 0200, Australia.

Tel: +61 2 61250654; fax: +61 2 61250746.

E-mail: david.lindenmayer@anu.edu.au

Received

15 November 2012

Accepted

4 February 2013

Editor

Phillip Levin

doi: 10.1111/conl.12013

Abstract

Large old trees are critical organisms and ecological structures in forests, woodlands, savannas, and agricultural and urban environments. They play many essential ecological roles ranging from the storage of large amounts of carbon to the provision of key habitats for wildlife. Some of these roles cannot be replaced by other structures. Large old trees are disproportionately vulnerable to loss in many ecosystems worldwide as a result of accelerated rates of mortality, impaired recruitment, or both. Drivers of loss, such as the combined impacts of fire and browsing by domestic or native herbivores, chemical spray drift in agricultural environments, and postdisturbance salvage logging, are often unique to large old trees but also represent ecosystem-specific threats. Here, we argue that new policies and practices are urgently needed to conserve existing large old trees and restore ecologically effective and viable populations of such trees by managing trees and forests on much longer time scales than is currently practiced, and by protecting places where they are most likely to develop. Without these steps, large old trees will vanish from many ecosystems, and associated biota and ecosystem functions will be severely diminished or lost.

Introduction

Animal ecologists have long been aware that populations of large and long-lived species can be particularly vulnerable to decline and hence are often among those taxa considered to be extinction prone (Fritz *et al.* 2009). Examples include whales, island populations of some species of tortoises, and large apex predators. We contend that these concerns also apply to populations of large, old trees, which demonstrably are undergoing major declines in a wide range of ecosystems worldwide (Figures 1 and 2).

Examples of widespread tree mortality in forests have been well documented (van Mantgem *et al.* 2009; Allen

et al. 2010), but it is less well known that large old trees are disproportionately vulnerable to loss from many ecosystems (Lindenmayer *et al.* 2012b). Large old trees are often those deliberately targeted for cutting or removal during logging (Linder & Östlund 1998), firewood collection (Driscoll *et al.* 2000), the intensification of agriculture (Maron & Fitzsimons 2007), and in urban areas where human safety is a concern (Carpaneto *et al.* 2010). In some ecosystems, large old trees can be susceptible to disease, insect attack and dieback (Palik *et al.* 2011; Simard *et al.* 2012).

Rapid declines in large old trees will have major negative impacts on a suite of ecosystem processes and the persistence of species dependent on them. We argue that

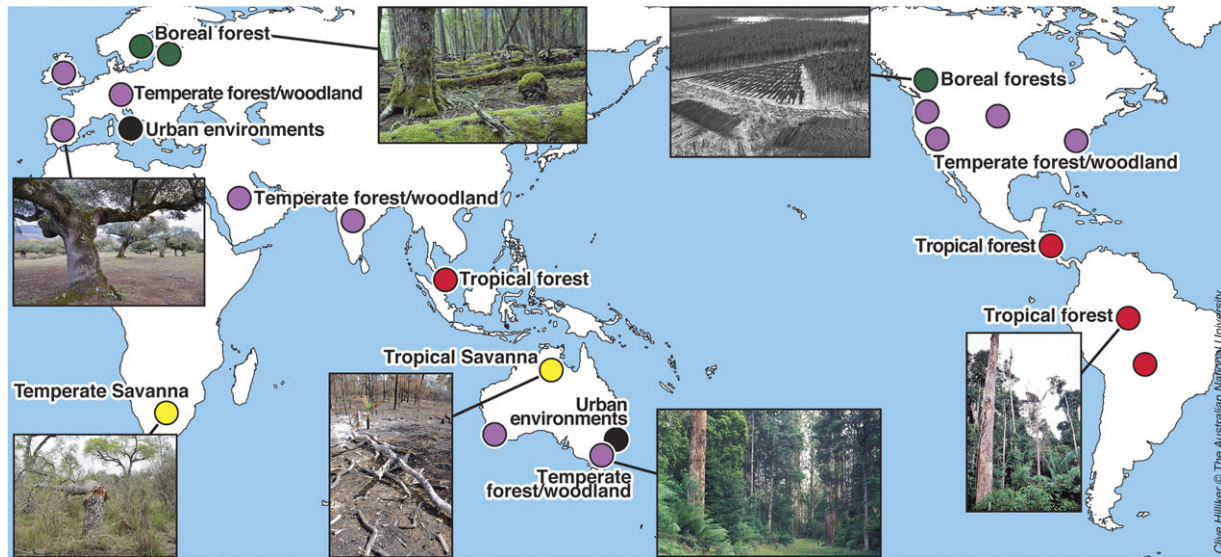


Figure 1 A sampling of locations where the loss of large old trees has been identified as a major ecological problem (Photos clockwise from top left: D. Lindenmayer, K. Hodges, W. Laurance, D. Lindenmayer (x2), FABI www.fabinet.up.ac.za, and www.extremadura-spain.com).

new policies must better protect existing large old trees and promote their recruitment. These new policies must span unprecedented temporal scales (centuries) and be implemented over large spatial scales (landscapes and regions). New policies must lead to fundamental changes in management, including cessation or modification of large old tree harvest, planning to foster future large old tree recruitment, reduction in vegetation clearing, restored natural fire regimes, reduction in grazing pressures, and altered urban planning.

Prior to our policy discussion, we provide a simple definition of large old trees, summarize the ecological roles they play, and outline examples of ecosystems characterized by a rapid loss of large old trees. Although our primary focus is on large old trees, we acknowledge that in some ecosystems, old trees may not be particularly tall or large in diameter, but nevertheless have a range of important ecological roles and be at risk of decline (Silva *et al.* 2010).

Defining large old trees

The definition of both large and old in the context of large old trees is specific to a given ecosystem, tree species, and set of environmental conditions (e.g., site productivity). The combination of large size and prolonged age are critical factors influencing such processes as rates of internal wood decay and habitat suitability for biota. These conditions lead to large old trees having distinctive characteristics reflecting the long-term developmental pro-

cesses they have experienced, such as large cavities, extensive branching patterns, and vertically and horizontally complex canopy structures (Franklin *et al.* 2002). For example, it can be a long time before large cavities develop: more than a century in Douglas-fir forests in North America (*Pseudotsuga menziesii*) (Franklin *et al.* 2002), 120–220+ years in many Australian *Eucalyptus*-dominated forests (Gibbons & Lindenmayer 2002), and >200 years in European Pedunculate Oak forests (*Quercus robur*) (Ranius *et al.* 2009).

Researchers in some ecosystems have rigorous approaches for characterizing large old trees from other trees in the same environment. For example, Van Pelt (2008) developed a dichotomous key for identification of large old trees of several species in the forests of eastern Washington, USA. This was based on distinctive morphological features such as large diameter, dead tops, loss of lower limbs, and deeply fissured bark.

The ecological importance of large old trees

Large old trees play many critical ecological roles (Table S1). They are also an important component of cultural identity for many groups of people (Dafni 2006). Many ecological roles that large old trees play cannot be replaced with other structures. For example, the nesting opportunities for some fauna provided by large old trees cannot be replaced in some ecosystems by artificial structures like nest boxes (Lindenmayer *et al.* 2009).

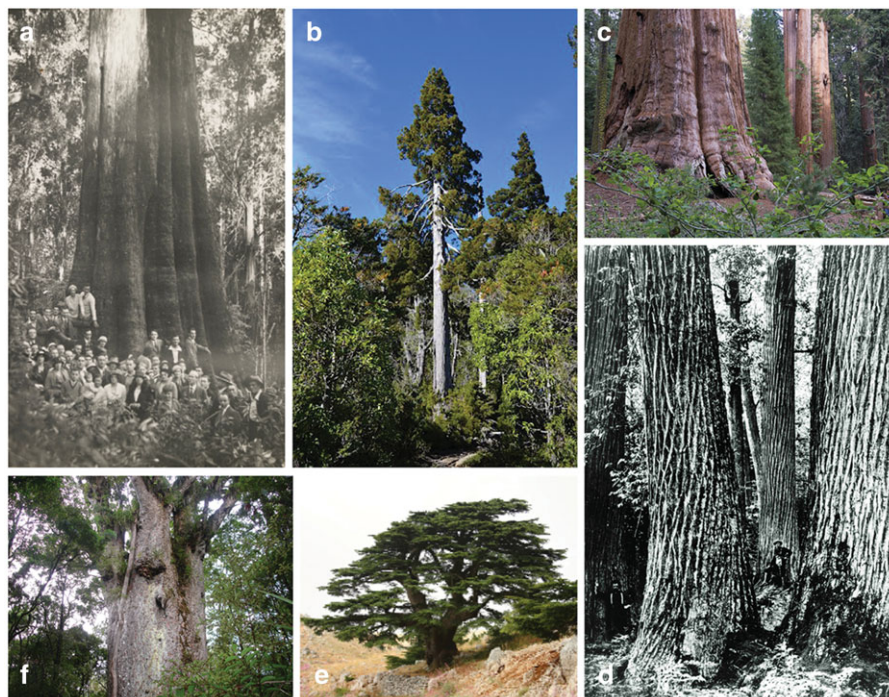


Figure 2 Photo montage of large old tree species that have either been lost entirely or are in danger of becoming so around the world. A: Australian old growth Mountain Ash (The Furmston Tree). B: South American Alerce. C: Californian Giant Sequoia (The General Sherman). D: Old growth American Chestnut. E: Lebanese Cedar. F: New Zealand Kauri (The Father of the Forest). (Photos: A: State Library of Victoria. B: Fib69, Creative Commons. C: Upsilon Andromedae, Creative Commons. D: The Forest History Society, North Carolina. E: Shutterstock. F: D. Nelson, Creative Commons).

Large old trees are not simply enlarged versions of young trees and large young trees cannot duplicate all the functional roles that large old trees can play. For example, in some Scandinavian forests, large young trees lack the deeply fissured rough bark needed by bryophytes (Thor *et al.* 2010). The irreplaceable roles of large old trees make them a “keystone structure”—a disproportionately important provider of resources crucial for other species (Manning *et al.* 2006).

The keystone roles of large old trees mean that declines in populations of these trees can have major negative ecological impacts such as substantially reducing levels of carbon storage (Laurance *et al.* 1997). It also can lead to significant declines in species closely associated with large old trees (Orwig 2002). For instance, the rapid decline in populations of large old Mountain Ash (*Eucalyptus regnans*) trees in mainland southeastern Australia could cause the global extinction of the nationally endangered Leadbeater’s Possum (*Gymnobelideus leadbeateri*) (Lindenmayer *et al.* 2012a). Removal of large old trees within the city of Rome put at risk populations of saproxylic insects of conservation concern (Carpaneto *et al.* 2010).

A global decline in populations of large old trees

Examples of the rapid decline in populations of large old trees

In Table S2 we summarize many examples of the rapid loss of large old trees from all vegetated continents and from a wide range of natural and human-modified environments (Figure 1). For instance, there is an almost complete absence of living trees over 50 cm in diameter in Swedish mid-boreal forest, despite these forests supporting 38–77 such trees per hectare a century earlier (Linder *et al.* 1998). In logged Douglas-fir (*Pseudotsuga menziesii*) forests of western North America, the density of large dead trees (>63.5 cm diameter) is <1% of that in unlogged stands (Wilhere 2003). Projections of the future abundance of large old trees across the Australian mainland Mountain Ash forest estate show a severe population decline from an average of 5.1 large old trees per ha in 1998 to an average of ~0.6 per ha in 50 years’ time (Lindenmayer *et al.* 2012a). Projections from ongoing studies in fragmented Brazilian rainforest (Laurance *et al.* 2000) suggest that ~53% of the large old trees (≥ 60 cm

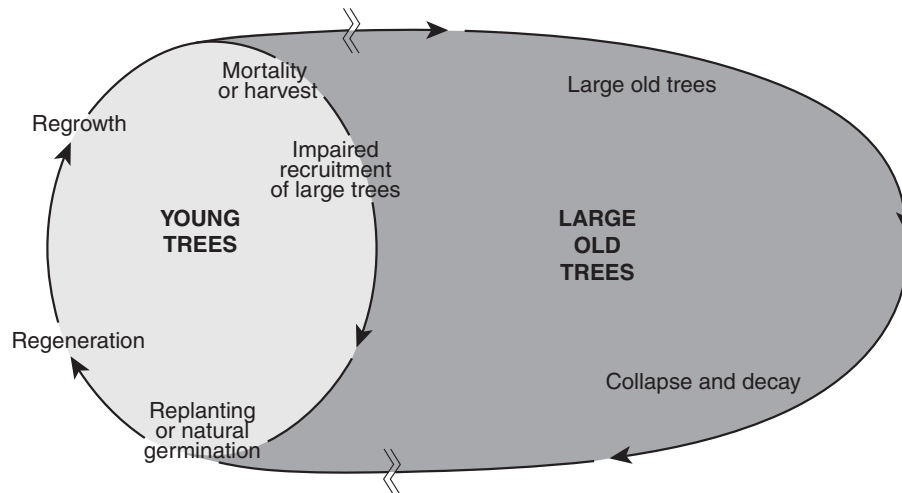


Figure 3 Simple conceptual model of drivers of recruitment failure and accelerated loss of large old trees. The breakpoints in the diagram highlight disruptions to key processes required to maintain existing large old trees and ensure tree recruitment.

diameter) initially present have died in the past three decades.

Major losses of large old trees are occurring in non-forested environments such as agricultural areas, savannas, and urban landscapes. For example, within 50–100 years in Australian agricultural landscapes subject to intensive grazing by domestic livestock, tens of millions of large old trees will be lost and not replaced through recruitment. This will leave ~42.5% of more than one million ha of grazing land supporting <0.5 large old trees per ha (Fischer *et al.* 2010) compared with benchmark densities (i.e., those prior to European settlement) of ~30–40 per ha for this area (Gibbons *et al.* 2010a). Similar problems have been identified in intensively grazed landscapes in North America, Latin America, and southern Europe (Gibbons *et al.* 2008).

In Australian tropical savannas, repeated fire resulted in the death of ~75% of large old trees and killed numerous intermediate-sized trees that might otherwise have replaced older stems (Williams *et al.* 1999). Widespread large tree loss also has characterized African savannas, largely through the effects of elephant browsing, fire, and other factors (Shannon *et al.* 2011). In Rome, Italy, more than one-third of large old Holm Oaks (*Quercus ilex*) are planned for removal because of human safety concerns (Carpaneto *et al.* 2010).

Drivers of decline in populations of large old trees

The drivers of declines in populations of large old trees are intentional removal, elevated rates of mortality, insuffi-

cient recruitment, and interacting combinations of these factors (Figure 3). Large old trees are intentionally removed for land clearing (Maron & Fitzsimons 2007) and human safety or infrastructure development (Carpaneto *et al.* 2010). In wood production forests, large old trees are selectively sought for harvesting (Gibbons *et al.* 2010b) although in others there are now prohibitions on removal of larger trees (Franklin & Johnson 2012).

Large old trees are particularly prone to elevated mortality through a range of factors including:

- Wildfire (Lindenmayer *et al.* 2012a) and prescribed burning (Linder *et al.* 1998).
- Drought (Nepstad *et al.* 2007).
- Altered grazing and browsing regimes (Fischer *et al.* 2010; Paltto *et al.* 2011).
- Competition with invasive plants (Bhagwat *et al.* 2012).
- Climatic extremes (Allen *et al.* 2010).
- Air pollution including herbicide drift (Marrs *et al.* 1993).
- Disease or insect attack (van Mantgem *et al.* 2009; Simard *et al.* 2012).
- Habitat fragmentation and associated edge effects (Laurance *et al.* 2000).

Recruitment of large old trees can be diminished due to high-intensity grazing or browsing from domestic or native herbivores (Fischer *et al.* 2010; Shannon *et al.* 2011) or competition with other plants (Phillips *et al.* 2002) including exotic species (Ramaswami & Sukumar 2011). Recruitment of large old trees also can be substantially curtailed by high-severity wildfires which remove

cohorts of young and intermediate aged trees (Williams *et al.* 1999) as well as by prescribed burning which can induce high levels of mortality in young stems (Linder *et al.* 1998). In other cases, a complete absence of fire can impair recruitment such as in Californian Giant Sequoia (*Sequoiadendron giganteum*) forests (Harvey *et al.* 1980).

Drivers of large old tree loss can interact (Figure 3). Examples include: (1) the combined impacts of fire and browsing by herbivores (Shannon *et al.* 2011), (2) the interaction of fire and fire-prone exotic plants (Setterfield *et al.* 2005), (3) the interaction between fire, beetle attack, and tree age (Santoro *et al.* 2001), and (4) salvage logging whereby a natural disturbance (e.g., fire, insect attack) is followed by cutting of remaining trees (Lindenmayer *et al.* 2008).

In some ecosystems, such as those subject to intensive industrial forestry, there is little or no intent to provide a continuous supply of large old trees, which results in the effective extinction of these keystone structures. In others, drivers of large old tree loss can create a “temporary extinction,” that is, a prolonged period between the loss of existing large old trees and the recruitment of new ones (Gibbons *et al.* 2010b). The length of a temporary extinction may vary (e.g., 50 to 300 + years), depending on a tree species’ life history (e.g., growth rate, decay rate, and reproductive strategy) and the nature of the drivers of the problem (and whether the problem is addressed).

Temporary extinction has the potential to drive species strongly dependent on large old trees to permanent local or even global extinction. In other cases, existing large old trees may be doomed to eventual extinction because the animals that dispersed their seeds have disappeared—as has been documented in tropical forests (Janzen 1986).

Policy and conservation management implications

The drivers of the loss of large old trees often manifest as ecosystem-specific threats (Table S2). Examples include: (1) the burning of slash left after logging (Gibbons *et al.* 2010b), (2) chemical spray drift in agricultural and urban environments (Landsberg & Wylie 1991), and (3) agricultural land abandonment in parts of Scandinavia in which large old trees become susceptible to being shaded by surrounding young regrowth stems and lose their distinctive microhabitat attributes and associated biota (Paltto *et al.* 2011). A key policy and management directive must be to develop strategies to limit such ecosystem-specific threats. Such new policies will need to span unprecedented temporal scales (centuries) and very large spatial scales (landscapes and regions). These new policies also

must go beyond past traditional approaches, such as those focusing on the need to conserve old-growth forest. This is because the issue of conserving large old trees extends beyond forest ecosystems and, in agricultural and urban environments, entails maintaining small stands of scattered trees or even individual stems (Manning *et al.* 2006; Carpentio *et al.* 2010).

Preventing the deliberate removal of large old trees

A critical step in large old tree management is to stop felling them where they persist and begin restoring populations where they have been depleted. This is appropriate both in natural environments and in human-dominated environments such as urban landscapes. Improved regulation is critical for tackling this issue. Importantly, in some industrial forest estates such as those in Scandinavia and western North America, large old trees are no longer targeted for deliberate removal because of logging bans (Franklin & Johnson 2012), or because they are too large for harvesting equipment and processing infrastructure. However, large old trees are often extremely rare in such landscapes and policies to ensure their protection as well as promote the recruitment of new cohorts of large old trees remain relevant (see below).

Within wood-production forests, new retention-harvesting approaches (Gustafsson *et al.* 2012) are needed to conserve existing large old living and dead trees. In multiple-use landscapes where there are demands to harvest commodities such as timber and cereal crops, extraction or production should focus on areas where large old trees have the lowest probability of developing.

New policies are needed to limit deliberate removal of large old trees in agricultural areas, such as where central-pivot irrigation systems are used or where pastures with scattered trees are converted into treeless cropland (Maron & Fitzsimons 2007). In other agricultural ecosystems, such as those in parts of northern Europe, large old trees have developed on farmland over many hundreds of years as a result of human activities like recurrent pruning, mowing, and livestock grazing. These trees, and the key ecological roles they play, are now threatened by land abandonment and the subsequent development of secondary regrowth forest. Although forest regeneration is broadly desirable, there might be special circumstances in which dense regrowth may threaten large old trees and there may be a need to maintain open areas around them (Widerberg *et al.* 2012).

Large old trees can have cultural as well as ecological values in urban environments (e.g., see Thaiutsa *et al.* 2008), and activities like strategic pruning or cabling

rather than outright removal may be needed to protect them while ensuring human safety.

In some natural ecosystems, enhanced protection may require a return to past disturbance regimes such as patchy, low-intensity fires rather than infrequent but high-intensity fires which can devastate large old trees (Murphy & Russell-Smith 2010). In other cases, it may be necessary to implement mechanical treatments to reduce fuels prior to the restoration of historical fire regimes—as for example in the Ponderosa Pine (*Pinus ponderosa*) forests of western North America (Franklin & Johnson 2012).

An important policy development in many environments will be the creation of a register of large old trees that aims to promote their protection. Such registries have already been established in some jurisdictions such as the Australian States of Victoria and Tasmania (e.g., http://www.gianttrees.com.au/index.php?option=com_content&view=article&id=49&Itemid=83), the United Kingdom (<http://www.treeregister.org/>), and North America (e.g., <http://bigtrees.forestry.ubc.ca/>). This is a welcome development. However, the locations of some trees may need to be kept secret to reduce the risks of vandalism, but this may preclude other kinds of formal protection. Second, the criterion for listing can sometimes be so demanding that very few trees meet the qualification requirements and hence the approach fails to meet the need to maintain viable populations of large old trees. For example, during ~30 years of work in the Mountain Ash forests of Victoria, more than 1,550 large old trees have been measured on a repeated basis (Lindenmayer *et al.* 2012a). However, only four of these trees have dimensions (>4m in diameter or 85m in height) that would result in them being eligible for listing (see [http://www.vicforests.com.au/assets/protecting%20victoria's%20giants%20\(march%20'11\).pdf](http://www.vicforests.com.au/assets/protecting%20victoria's%20giants%20(march%20'11).pdf)). Finally, few registries of large old trees make provision for the recruitment of new trees to replace existing ones as they die and collapse. Hence, they do not foster the development of appropriate age cohorts of trees and thus a viable age class structure (see below).

Promoting tree recruitment

While limiting rates of removal and mortality can be critical for limiting losses of large old trees, there is also a need to protect and manage the tree recruitment and maturation process in some ecosystems. Examples include environments subject to recurrent high-intensity grazing by domestic livestock that impairs the effective recruitment of new young trees (Fischer *et al.* 2009) or those ecosystems where the recruitment of native trees is thwarted

by intense competition with invasive exotic plants (Ramaswami & Sukumar 2011).

New policies to promote the recruitment of large old trees should include: (1) fostering low-intensity rotational grazing regimes for domestic livestock and reducing fertilizer and herbicide use in agricultural landscapes (Fischer *et al.* 2009); (2) applying silvicultural practices within wood-production forests such as variable retention harvest systems (Gustafsson *et al.* 2012) and ecological thinning regimes (Carey *et al.* 1999); and (3) controlling invasive plants (Ramaswami & Sukumar 2011).

Protecting refugia for large old trees

Large old trees are more likely to be recruited and to persist in particular parts of landscapes like deep sheltered valleys (Mackey *et al.* 2002). Entire landscapes may need to be managed to maintain refugia for large old trees. For instance, refugia might be excluded from commodity production activities like timber extraction and the cultivation of crops. The management of landscapes to maintain refugia also should control other kinds of human disturbances so they do not interact with natural disturbances and create “landscape traps” (Lindenmayer *et al.* 2011), in which entire landscapes are shifted into highly compromised, irreversible states as the result of temporal and spatial feedbacks between human and natural disturbance regimes. In Mountain Ash forests, for example, industrial logging interacts with wildfires, leading to spatial contagion of repeated high-severity fires. This situation has created homogenized, young regenerating stands that have an increased risk of reburning before they can mature, promoting the loss and recruitment failure of large old trees over entire landscapes (Lindenmayer *et al.* 2011). Landscape traps are developing in disturbed, increasingly fire-prone tropical rainforests (Cochrane & Laurance 2008), temperate forests (Thompson *et al.* 2007), and tropical savannas (Williams *et al.* 1999), making these ecosystems vulnerable to the widespread decline of large old trees.

Long-term policy implementation

Policies must be implemented long before problems result from the loss of large old trees. This is because, unlike many other organisms with a shorter life history, once old trees are gone, it can take centuries to restore them. Delayed action, such as a failure to address problems leading to even slightly elevated accelerated rates of mortality among large old trees, can significantly promote rates of loss (Ball *et al.* 1999) and prolong temporal extinction. This further underscores the importance of the strategies

outlined above about the need to protect existing large old trees.

Long-term policies to retain and restore large old tree populations run counter to much existing resource management where action is forthcoming only once a “crisis” has developed—when it is too late to avoid “temporary extinction” of the large old tree growth stage. Demographic modeling, for instance, can highlight the importance of long-term policies by illustrating the long-term impacts of factors that lead to even modest but nevertheless chronic increases in the mortality of large old trees (Laurance *et al.* 2000).

Going beyond traditional endangered species in conservation management

Policies aimed at sustaining large old trees must accommodate differences from the traditional conservation approaches that aim to prevent the extinction of endangered species. In some cases, rather than a given tree species going extinct, its large old tree life stage may go extinct temporarily or permanently. Hence, there is “functional extinction” where the key ecological roles of large old trees are lost even though the particular tree species remains extant. As an example, large overstorey American Chestnut (*Castanea dentata*) trees have been decimated by Chestnut Blight (*Cryphonectaria parasitica*). The tree species has not gone extinct but several invertebrate species closely associated with the American Chestnut have (Orwig 2002). Thus, new policies and practices must be formulated and implemented to conserve a tree population age structure through proactive management decades or even centuries in advance. One option may be to list particular tree species under Appendix II of CITES based on their key functional ecological roles in a given ecosystem. This may create a policy pathway for protecting large old trees if the trade in timber or other commodities can be demonstrated to cause irreversible harm.

Conclusions

Large old trees are critical organisms and key structural attributes in forests, agricultural areas, and urban environments worldwide. However, they are vulnerable to intentional or incidental destruction and are at risk of rapid temporary or even permanent extinction. Existing policies are failing. New policies and management actions are required to conserve existing large old trees, provide for their recruitment, and maintain an age structure for tree populations that ensures a perpetual supply of large old trees thereby sustaining the critical functional properties that such trees provide. Without urgent action this iconic growth stage and the biota and ecological func-

tions associated with it are in danger of being seriously depleted or even lost in many ecosystems.

Acknowledgments

This work is supported by the Australian Research Council, the Australian Government’s National Environmental Research Program, and Victorian Government agencies including the Department of Sustainability and Environment and Parks Victoria. J. Bauhus, P. Burton, L. Gustafsson, M. Hunter, A. Löhmus, J. Lutz, C. Messier, R. Noss, D. Orwig, B. Palik, G. Pastur Martínez, provided background information that enriched the content of this article. C. Shepherd and C. Hilliker assisted in the array of complexities associated with manuscript preparation. We thank the Editors, Dominick DellaSala, Kristoffer Hylander and a third anonymous referee for constructive comments which significantly improved an early version of the manuscript.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher’s web site:

Table S1: Some of the key ecological roles of large old trees.

Table S2: Examples of forests and other vegetation types where the decline in large old trees has been identified as a significant ecological problem.

References

- Allen, C.D., Macalady, A.K., Chenchouni, H. *et al.* (2010). A global review of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecol. Manage.*, **259**, 660–664.
- Ball, I.R., Lindenmayer, D.B. & Possingham, H.P. (1999). A tree hollow dynamics simulation model. *Forest Ecol. Manage.*, **123**, 179–194.
- Bhagwat, S.A., Breman, E., Thekaekara, T., Thornton, T.F. & Willis, K.J. (2012). A battle lost? Report on two centuries of invasion and management of *Lantana camara* L. in Australia, India and South Africa. *PLOS One*, **7**, e32407.
- Carey, A.B., Lippke, B.R. & Sessions, J. (1999). Intentional systems management: managing forests for biodiversity. *J. Sustain. Forest.*, **9**, 83–125.
- Carpaneto, G.M., Mazziotta, A., Coletti, G., Luiselli, L. & Audisio, P. (2010). Conflict between insect conservation and public safety: the case study of a saproxylic beetle (*Osmoderma eremita*) in urban parks. *J. Insect Conserv.*, **14**, 555–565.

- Cochrane, M.A. & Laurance, W.F. (2008). Synergisms among fire, land use, and climate change in the Amazon. *Ambio*, **37**, 522-527.
- Dafni, A. (2006). On the typology and the worship status of sacred trees with a special reference to the Middle East. *J. Ethnobiol. Ethnomed.*, **2**, 26.
- Driscoll, D., Milkovits, G. & Freudenberger, D. (2000). Impact and use of firewood in Australia. *CSIRO Sustainable Ecosystems Report*. CSIRO, Canberra.
- Fischer, J., Stott, J., Zerger, A., Warren, G., Sherren, K. & Forrester, R.I. (2009). Reversing a tree regeneration crisis in an endangered ecoregion. *Proc. Natl. Acad. Sci. USA*, **106**, 10386-10391.
- Fischer, J., Zerger, A., Gibbons, P., Stott, J. & Law, B.S. (2010). Tree decline and the future of Australian farmland biodiversity. *Proc. Natl. Acad. Sci. USA*, **107**, 19597-19602.
- Franklin, J.F. & Johnson, K.N. (2012). A restoration framework for federal forests in the Pacific Northwest. *J. Forest.*, **110**, 429-439.
- Franklin, J.F., Spies, T.A., van Pelt, R. *et al.* (2002). Disturbances and the structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecol. Manage.*, **155**, 399-423.
- Fritz, S.A., Bininda-Emonds, O.R.P. & Purvis, A. (2009). Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.*, **12**, 538-549.
- Gibbons, P. & Lindenmayer, D.B. (2002). *Tree hollows and wildlife conservation in Australia*. CSIRO Publishing, Melbourne.
- Gibbons, P., Lindenmayer, D.B., Fischer, J. *et al.* (2008). The future of scattered trees in agricultural landscapes. *Conserv. Biol.*, **22**, 1309-1319.
- Gibbons, P., Briggs, S.V., Murphy, D.Y., Lindenmayer, D.B., McElhinny, C. & Brookhouse, M. (2010a). Benchmark stem densities for forests and woodlands in south-eastern Australia under conditions of relatively little modification by humans since European settlement. *Forest Ecol. Manage.*, **260**, 2125-2133.
- Gibbons, P., McElhinny, C. & Lindenmayer, D.B. (2010b). What strategies are effective for perpetuating structures provided by old trees in harvested forests? A case study on trees with hollows in south-eastern Australia. *Forest Ecol. Manage.*, **260**, 975-982.
- Gustafsson, L., Baker, S., Bauhus, J. *et al.* (2012). Retention forestry to maintain multifunctional forests: a world perspective. *BioScience*, **62**, 633-645.
- Harvey, H.T., Shellhammer, H.S. & Stecker, R.E. (1980). Giant Sequoia Ecology. Page 182 in N.P.S. US Department Of The Interior editor. *Scientific Monograph Series 12*. Washington, D.C.
- Janzen, D.H. (1986). The future of tropical biology. *Ann. Rev. Ecol. Syst.*, **17**, 305-324.
- Landsberg, J. & Wylie, R. (1991). A review of rural dieback in Australia. Pages 3-11 in T. Offor, R.J. Watson, editors. *Growback '91*. Growback Publications, Melbourne.
- Laurance, W.F., Laurance, S.G., Ferreira, L.V., Rankin-de Merona, J., Gascon, C. & Lovejoy, T.E. (1997). Biomass collapse in Amazonian forest fragments. *Science*, **278**, 1117-1118.
- Laurance, W.F., Delamonica, P., Laurance, S.G., Vasconcelos, H.L. & Lovejoy, T.E. (2000). Rainforest fragmentation kills big trees. *Nature*, **404**, 836.
- Lindenmayer, D.B., Burton, P.J. & Franklin, J.F. (2008). *Salvage logging and its ecological consequences*. Island Press, Washington, DC.
- Lindenmayer, D.B., Welsh, A., Donnelly, C.F. *et al.* (2009). Are nest boxes a viable alternative source of cavities for hollow-dependent animals? Long-term monitoring of nest box occupancy, pest use and attrition. *Biol. Conserv.*, **142**, 33-42.
- Lindenmayer, D.B., Hobbs, R.J., Likens, G.E., Krebs, C. & Banks, S.C. (2011). Newly discovered landscape traps produce regime shifts in wet forests. *Proc. Natl. Acad. Sci. USA*, **108**, 15887-15891.
- Lindenmayer, D.B., Blanchard, W., McBurney, L. *et al.* (2012a). Interacting factors driving a major loss of large trees with cavities in an iconic forest ecosystem. *PLoS ONE*, **7**, e41864.
- Lindenmayer, D.B., Laurance, W.F. & Franklin, J.F. (2012b). Global decline in large old trees. *Science*, **338**, 1305-1306.
- Linder, P., Jonsson, P. & Niklasson, M. (1998). Tree mortality after prescribed burning in an Old-growth Scots Pine forest in northern Sweden. *Silva Fennica*, **32**, 339-349.
- Linder, P. & Östlund, L. (1998). Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. *Biol. Conserv.*, **85**, 9-19.
- Mackey, B., Lindenmayer, D.B., Gill, A.M., McCarthy, M.A. & Lindsay, J.A. (2002). *Wildlife, fire and future climate: a forest ecosystem analysis*. CSIRO Publishing, Melbourne.
- Manning, A.D., Fischer, J. & Lindenmayer, D.B. (2006). Scattered trees are keystone structures – implications for conservation. *Biol. Conserv.*, **132**, 311-321.
- Maron, M. & Fitzsimons, J.A. (2007). Agricultural intensification and loss of matrix habitat over 23 years in the West Wimmera, south-eastern Australia. *Biol. Conserv.*, **135**, 587-593.
- Marrs, R.H., Frost, A.J., Plant, R.A. & Lunnis, S. (1993). Determination of buffer zones to protect seedlings of non-target plants from the effects of glyphosate spray drift. *Agr. Ecosyst. Environ.*, **45**, 283-293.
- Murphy, D.P. & Russell-Smith, J. (2010). Fire severity in a northern Australian savanna landscape: the importance of time since previous fire. *Int. J. Wildland Fire*, **19**, 46-51.
- Nepstad, D.C., Tohver, I.M., Ray, D., Moutinho, P. & Cardinot, G. (2007). Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology*, **88**, 2259-2269.

- Orwig, D.A. (2002). Ecosystem to regional impacts of introduced pests and pathogens: historical context, questions and issues. *J. Biogeogr.*, **29**, 1471-1474.
- Palik, B.J., Ostry, M.E., Venette, R.C. & Abdela, E. (2011). *Fraxinus nigra* (black ash) dieback in Minnesota: regional variation and potential contributing factors. *Forest Ecol. Manage.*, **261**, 128-135.
- Palto, H., Nordberg, A., Norden, B. & Snall, T. (2011). Development of secondary woodland in Oak Wood pastures reduces the richness of rare epiphytic lichens. *PLOS One*, **6**(9), e24675.
- Phillips, O.L., Martinez, R.V., Arroyo, L. *et al.* (2002). Increasing dominance of large lianas in Amazonian forests. *Nature*, **418**, 770-774.
- Ramaswami, G. & Sukumar, R. (2011). Woody plant seedling distribution under invasive *Lantana camara* thickets in a dry-forest plot Mudumalai, southern India. *J. Trop. Ecol.*, **27**, 365-373.
- Ranius, T., Niklasson, M. & Berg, N. (2009). Development of tree hollows in pedunculate oak (*Quercus robur*). *Forest Ecol. Manage.*, **257**, 303-310.
- Santoro, A.E., Lombardero, M.L., Ayers, M.P. & Ruel, J.J. (2001). Interactions between fire and bark beetles in an old growth pine forest. *Forest Ecol. Manage.*, **144**, 245-254.
- Setterfield, S.A., Douglas, M.M., Hutley, L.B. & Welch, M.A. (2005). Effects of canopy cover and ground disturbance on establishment of an invasive grass in an Australian savanna. *Biotropica*, **37**, 25-31.
- Shannon, G., Thaker, M., Vanak, A.T., Page, B.R., Grant, R. & Slotow, R. (2011). Relative impacts of elephant and fire on large trees in a savanna ecosystem. *Ecosystems*, **14**, 1372-1381.
- Silva, L.R., Anand, M. & Leithead, M.D. (2010). Recent widespread tree growth decline despite increasing atmospheric CO₂. *PLOS One*, **5**, e11543.
- Simard, M., Powell, E.N., Raffa, K.F. & Turner, M.G. (2012). What explains landscape patterns of tree mortality caused by bark beetle outbreaks in Greater Yellowstone? *Glob. Ecol. Biogeogr.*, **21**, 556-567.
- Thaiutsa, B., Puangchit, L., Kjelgren, R. & Arunpraparut, W. (2008). Urban green space, street tree and heritage large tree assessment in Bangkok, Thailand. *Urban Forest. Urban Greening*, **7**, 219-229.
- Thompson, J.R., Spies, T.A. & Ganio, L.M. (2007). Reburn severity in managed and unmanaged vegetation in a large wildfire. *Proc. Natl. Acad. Sci. USA*, **104**, 10743-10748.
- Thor, G., Johansson, P. & Jonsson, M.T. (2010). Lichen diversity and red-listed lichen species relationships with tree species and diameter in wooded meadows. *Biodivers. Conserv.*, **19**, 2307-2328.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C. *et al.* (2009). Widespread increase of tree mortality rates in western United States. *Science*, **323**, 521-524.
- Van Pelt, R. (2008). *Identifying old trees and forests in eastern Washington*. Page 166. Washington State Department of Natural Resources, Olympia, Washington.
- Widerberg, M.K., Ranius, T. & Drobyshev, I. (2012). Increased openness around retained oaks increases species richness of saproxylic beetles. *Biodivers. Conserv.*, **21**, 3035-3059.
- Wilhere, G. (2003). Simulations of snag dynamics in an industrial Douglas-fir forest. *Forest Ecol. Manage.*, **174**, 521-539.
- Williams, R.J., Cook, G.D., Gill, A.M. & Moore, P.H.R. (1999). Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Aust. J. Ecol.*, **24**, 50-59.