rendering prediction of community level biomass change imprecise.

The contrasting results of Peres *et al.*'s simulations from the Amazon and Harrison *et al.*'s [2] from Borneo (mentioned earlier) are also interesting to consider. The discrepancies could arise simply from methodological differences. But there is also the fascinating possibility of variance in ecosystem function between the continents. Forest canopies in equatorial Asia are dominated by dipterocarp trees with strictly abiotic seed dispersal, whereas Neotropical and African rainforest canopies have mainly animal dispersed species. So hunting, by hindering regeneration of animal dispersed trees, could have less influence on carbon storage in Asia than elsewhere.

What do Peres *et al.*'s findings suggest in terms of policy solutions, given our still-incomplete understanding of plant–animal interactions in tropical forests? Interestingly, complete bans on hunting may not work because the costs of effective enforcement [7] are high relative to the price of the carbon saved. What may be much more cost-effective would be for REDD-type projects to collaborate with local communities in ensuring that subsistence hunting is done sustainably. Most hunting in tropical forests is unsustainable and vast areas have been denuded of large vertebrates; but when rural communities take the initiative, they can ensure that subsistence offtake rates do not deplete mammal populations [8]. (Hunting for markets and international trade is much more difficult to regulate and often leads to Tragedies of the Commons.) Collaborations between local communities, with their prodigious traditional ecological knowledge, and biologists trained in modern wildlife management techniques could be particularly useful.

Hunting sustainability is not an issue addressed by many conservation organizations (with some notable exceptions, e.g., [9]), presumably because most do not want to be seen as pitted against the livelihoods of local people. But this is a short-sighted view. Ensuring that hunting remains (or becomes) sustainable is the ultimate win–win outcome for human livelihood, biodiversity conservation, and – as Peres *et al.* have now shown – climate change mitigation. We need to ensure that wildlife abundance remains high enough for the animals themselves to persist, for subsistence hunters to feed their families, and for high-carbon storing trees to regenerate.

One of the main hurdles to achieving this goal is that plant demography can respond nonlinearly to the density of animal mutualists [10], although we have very little understanding of the generality of this pattern. It might be that even hunting strategies that do not cause mammal extirpations still maintain the animals at densities that are too low for them to provide effective seed dispersal. Therefore, among the most important research priorities in tropical ecology today is to ascertain how to simultaneously optimize offtake rates for human subsistence, game animal persistence, and seed dispersal services. Well-designed field studies that feed data into Bayesian decision network analyses will help us help the monkeys keep excess carbon out of the atmosphere.

[1]Departments of Zoology and Botany, University of British Columbia, Vancouver, Canada

*Correspondence: jedediah.brodie@gmail.com (J.F. Brodie).

http://dx.doi.org/10.1016/j.tree.2016.03.019

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Forum

The Unique Challenges of Conserving Large Old Trees

David B. Lindenmayer[1,*] and William F. Laurance[2,*]

Large old trees play numerous critical ecological roles. They are susceptible to a plethora of interacting threats, in part because the attributes that confer a competitive advantage in intact ecosystems make them maladapted to rapidly changing, human-modified environments. Conserving large old trees will require surmounting a number of unresolved challenges.

Unique Challenges of Studying and Conserving Large Old Trees

Large old trees are among the largest and longest-living organisms on earth. They occupy a revered position in the human psyche, appearing often in iconography, art, books, films, and other cultural expressions [1]. Large old trees also play key ecological and ecosystem roles, having major influences on hydrological regimes, nutrient cycles, disturbance regimes, and the distribution and abundance of populations of their own and other species [2]. Evolutionary and physiological advantages of being large and old include outcompeting other trees for light, water and nutrients, as well as high and prolonged levels of reproductive output. While large old trees have been the subject of many scientific studies, we argue that significant challenges thwart progress in researching and conserving them. These include the lack of an agreed definition, problems in understanding and predicting their distribution and abundance, and the wide span of spatial and temporal scales involved in conserving their populations.

Defining Large Old Trees

An initial conundrum is simply defining large old trees, as the features that characterize them vary greatly among species and ecosystems (Figure 1). Beyond extreme age, height, and girth, large old trees have key attributes not characteristic of young trees, large or small. These can include extensive buttressing, numerous cavities, expansive and vertically heterogeneous crowns, and large lateral branches. Such traits vary both among and within species, with the latter being influenced by local site conditions as well as a tree's disturbance history, growth form, and other factors including its genotype. Using age-specific criteria to define old trees is hindered by the great difficulty of acquiring reliable age data for entire tree populations or multiple species. We therefore suggest that large old trees be defined operationally, on a species- and ecosystem-specific basis, based on their relative size. This involves (i) establishing the typical minimum diameter of reproductively mature (flowering and fruiting) individuals, and (ii) defining 'large' trees as being above a certain percentile (e.g., the top 5% by diameter) of all reproductive trees. A weakness of this approach is that the largest individuals of a tree species are not always the oldest, but otherwise it should be tractable to define large and generally older trees for any particular species and ecosystem type.

Challenges in Quantifying Tree Distributions

The distribution of large old trees is often the result of interacting natural and human influences that act over multiple spatial and temporal scales. Understanding these factors is highly relevant for management, such as identifying refugia for large old trees. However, such efforts face at least three interrelated complications. First, different factors influence trees at different stages of their life cycle [3], with the growth stage of 'large old trees' likely occupying a small subset of the overall environmental envelope for a given species. Further, some long-lived tree species may have germinated under markedly different environmental conditions from those that now prevail at a given location, with current conditions possibly being unsuitable for new cohorts of the species. Second, because of past and current land uses, large old trees have often been removed from much of their former distribution [4]. This can create a biased picture of the actual environmental tolerances of a species. Finally, tree distributions can be strongly affected by rare or episodic events such as intense fires or floods, the timing of which can be difficult to predict.

Understanding Threats

Large old trees are susceptible to a plethora of threats, including deforestation, logging, agriculture, drought, fire, windstorms, invasive species, the development of human infrastructure, and climate change. A major challenge is to understand how such varied

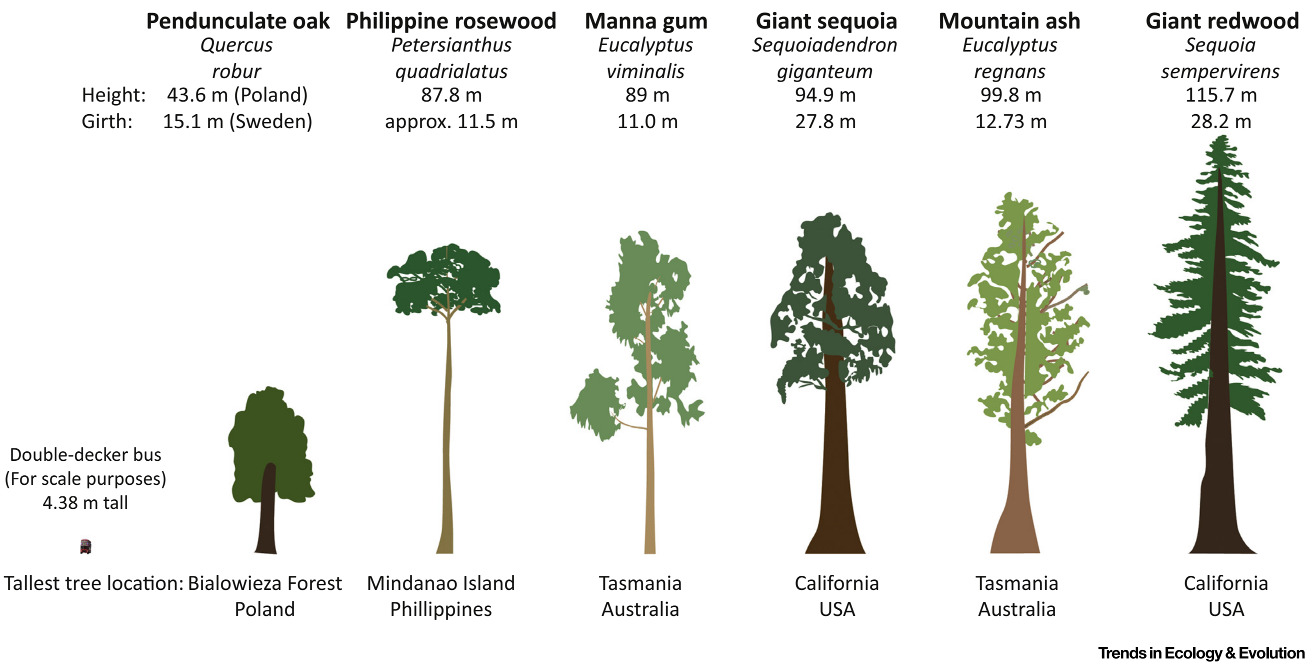

Figure 1. The Height, Girth, and Locations of Some of the World's Largest Tree Species.

threats affect different tree life stages and potentially interact in additive, synergistic, or opposing ways.

Effectively, conserving large old trees requires a spectrum of management actions from preserving large intact stands of old-growth forest to maintaining single trees within highly modified urban environments. General strategies cannot be applied uncritically, as managing threats to large old trees will require ecosystem-specific actions. For instance, micro-fencing can promote plant regeneration and faunal use around large old trees in Australian agricultural landscapes, yet would reduce habitat suitability for species-rich invertebrate assemblages associated with open areas near large trees in Nordic agro-ecosystems [5].

The competitive advantages of features such as extreme height, which are adaptive in intact habitats, make large old trees particularly susceptible to certain threats. Large trees become thicker and less flexible as they grow, making them particularly vulnerable to wind damage in fragmented landscapes [6]. Extreme adult longevity may mean that the environmental and regeneration niches that older individuals experienced in the past may differ from those at present. This could create inherent lag effects that are destabilizing for population persistence, especially when climatic conditions are changing rapidly.

Other potential effects of climate change on large old trees are highly uncertain. Some authors have suggested that rising CO_2 levels, which may fertilize trees and thereby increase their growth rates, may create the environmental prerequisites for the development of more large old trees [7]. Others, however, have argued that climate change could negatively affect large trees by increasing droughts or storm intensity [8] or favoring the proliferation of vines, which are important structural parasites of trees and may be advantaged by storms, drying conditions, and rising CO_2 [9]. Indeed, across many ecosystems, competitive interactions with other plants have pushed trees to maximize their growth rates, increasing their water demands for photosynthesis and forcing them to live 'near the edge' in terms of their vulnerability to droughts [10]. This raises a conundrum: if trees are already near the physiological limits of their drought tolerance, how can large old trees persist in a world that has long been beset by droughts? As CO_2 levels continue to rise, the water-use efficiency of plants is expected to increase (because they do not need to leave their stomata open as long to take in CO_2 for photosynthesis, and thereby transpire less water), but whether this will simply be offset by accelerated plant growth is unknown. Because of such complexities, the impacts of climatic change and changing atmospheric chemistry on large old trees remain highly uncertain [11].

Beyond tackling individual and multiple threats, the conservation of large old trees will demand innovative approaches to management over unprecedented timeframes. For example, traditional broad-scale actions such as conserving old-growth forests will rarely apply in desert, savanna, agricultural, and urban environments where many large old trees occur as individual stems or small clusters of trees. Small-scale or even individual tree-level conservation will be needed. At landscape scales, a priority will be protecting the locales where large old trees are most likely to develop and persist. One obvious example is mesic refugia, given the narrow hydraulic margins that large old trees apparently need to survive [10].

The pace and diversity of contemporary environmental changes is likely to pose unique challenges and vexing decisions for conserving long-lived species such as large old trees. For instance, assisted colonization to new, previously unoccupied locations may be required for large old trees. This, in turn, could create novel ecosystems [12] in which large old trees become part of new species assemblages. The notion of devising management and monitoring strategies for species that can live for many centuries or millennia is an enormous challenge (for instance, the longest environmental monitoring program globally, running for ~170 years at Rothamsted Research, West Common, Harpenden AL5 2JQ, UK, is brief in comparison). Yet such thinking is essential to protect existing trees and ensure successful recruitment of new cohorts. Clearly, safeguarding large old trees will demand new kinds of perspectives and action for conservation managers.

Acknowledgments

We thank Tabitha Boyer and Claire Shepherd for suggestions and assistance.

[1]Fenner School of Environment and Society, The Australian National University, Canberra, Australian Capital Territory 2601, Australia

[2]Centre for Tropical Environmental and Sustainability Science (TESS) and College of Marine and Environmental Sciences, James Cook University, Cairns, Queensland 4878, Australia

*Correspondence: David.Lindenmayer@anu.edu.au (D.B. Lindenmayer) and Bill.Laurance@jcu.edu.au (W.F. Laurance).

http://dx.doi.org/10.1016/j.tree.2016.03.003

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