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Global Decline in Large Old Trees

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cal regions of the world, but is rare in large areas of central and western Africa where many individuals lack Duffy-antigen receptor expression on red blood cells. Thus, this "Duffy-negative" phenotype appears to have evolved as an innate resistance mechanism to *P. vivax* infection.

McMorran *et al*. extend previous work that demonstrated an important role for platelets in resistance to malaria (*8*) by identifying platelet factor 4 (PF4) as a key molecule in platelet-mediated killing of *P. falciparum*. PF4 is released from α granules in activated platelets to promote blood coagulation (*9*). It binds the Duffy-antigen receptor, along with several other chemokines (*10*). McMorran *et al.* found that a functional Duffy-antigen receptor is required for the antiparasitic activity of PF4.

The implications of lacking this antiparasitic mechanism for Duffy-negative individuals living in *P. falciparum* malaria endemic regions are not yet clear. One might predict that these individuals will be more prone to episodes of severe malaria. Indeed, mortality among African children with malaria-induced coma is higher than in children with the same condition from Papua New Guinea, where Duffy-negative individuals are less common (*11*). However, further evidence is required to support this proposition. Alternatively, compensatory antiparasitic mechanisms may have evolved in Duffy-negative individuals to help control parasite growth and/or reduce pathology following infection. The identification of other such mechanisms will offer further insights into innate immune responses to infection, and potentially identify vulnerable aspects of parasite biology.

Platelets decrease in number (thrombocytopenia) during acute malaria. McMorran *et al*. suggest that this is not to the host's advantage, limiting this innate form of resistance. However, other data show that platelets can contribute to cerebral malaria, a major cause of mortality. Platelets at normal physiological concentrations cause clumping of parasitized red blood cells from African children, a phenomenon associated with cerebral malaria (*12*). Thrombocytopenia may therefore reduce pathology by protecting the host against cerebral malaria, which may explain in part why there has been less pressure to maintain platelet-associated parasite killing mechanisms in Africans. The Duffy-negative phenotype to prevent *P. vivax* invasion of red blood cells seems to have been under stronger selective pressure than the maintenance of a PF4-dependent antiparasitic mechanism in central and western Africa. However, given the potentially different origins and timelines of *P. falciparum* and *P. vivax* adaptations to humans (*13*, *14*), another possibility is that the Duffy-negative phenotype has simply been under selective pressure in this part of Africa for longer. In addition, nonmalaria pressures may also have influenced this selection over time.

Cells of the innate immune system—macrophages, natural killer cells, dendritic cells, and γδ T cells—play an important role in defending against parasites, often providing a first line of defense and augmenting acquired (adaptive) immunity. By understanding how innate mechanisms of protection against malaria have been under strong selective pressure during evolution, we may better understand how to protect people from malaria. For example, how PF4 kills *P. falciparum* is not yet clear, but when this knowledge is available, vulnerable features of parasites will be identified that could be targeted with appropriate drugs. Understanding new antiparasitic mechanisms selected by evolution will enable us not only to complement existing cellular and molecular approaches to identifying drug targets to kill parasites, but also to select safer targets that have less effect on the host.

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ECOLOGY

Global Decline in Large Old Trees

The loss of large old trees in many ecosystems around the world poses a threat to ecosystem integrity.

David B. Lindenmayer,[1] William F. Laurance,[2] Jerry F. Franklin[3]

Large old trees are among the biggest organisms on Earth. They are keystone structures in forests, woodlands, savannas, agricultural landscapes, and urban areas, playing unique ecological roles not provided by younger, smaller trees. However, populations of large old trees are rapidly declining in many parts of the world, with serious implications for ecosystem integrity and biodiversity.

The definition of "large and old" trees depends on the ecosystem, tree species, and environmental conditions under consideration. Both the size and the age of a tree affect characteristics such as the large internal cavities, complex branching patterns, and idiosyncratic canopy architectures that distinguish large old trees from younger and smaller trees (*1*).

Large old trees (see the figure, panels A to C) play critical ecological roles. They provide nesting or sheltering cavities for up to 30% of all vertebrate species in some ecosystems (*2*). Large old trees also store large quantities of carbon, create distinct microenvironments characterized by high levels of soil nutrients and plant species richness, play crucial roles in local hydrological regimes, and provide abundant food for numerous animals in the form of fruits, flowers, foliage, and nectar. In agricultural landscapes, large old trees can be focal points for vegetation restoration, facilitate ecosystem connectivity by attracting mobile seed dispersers and pollinators, and act as stepping stones for many animals.

Younger and smaller trees cannot provide most of the distinctive ecological roles played by large old trees (*3*). For instance, large old trees in Mountain Ash (*Eucalyptus regnans*) forests of mainland Australia provide irreplaceable shelter and nesting sites for more

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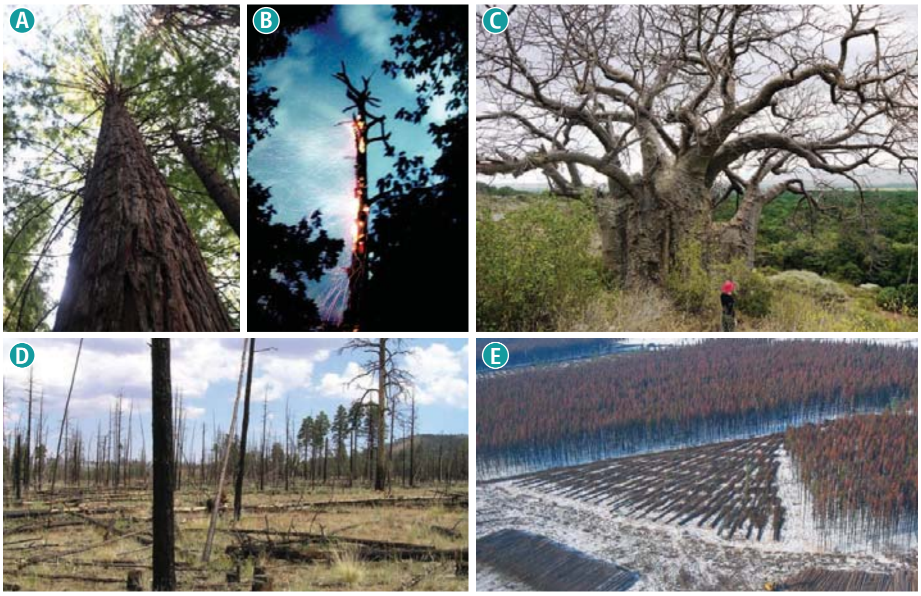
than 40 species of cavity-using vertebrates (*4*). For many dependent species, the keystone roles of large old trees continue for decades or even centuries after tree death, when they become standing dead trees or large logs (*1*).

The loss of large old trees is a recognized concern in many ecosystems worldwide. For example, populations of large old trees are plummeting in intensively grazed landscapes in California, Costa Rica, and Spain, where such trees are predicted to disappear within 90 to 180 years (*5*). In southeastern Australia, millions of hectares of grazing lands are projected to support less than 1.3% of the historical densities of large old trees within 50 to 100 years (*6*).

Large old trees are declining in forests at all latitudes. Larger trees (>45 cm in diameter) throughout southern Sweden have declined from historical densities of ~19 per hectare to 1 per hectare (*7*). In California's Yosemite National Park, the density of the largest trees (see the figure, panel A) declined by 24% between the 1930s and 1990s (*8*). Large old *E. regnans* trees—Earth's tallest flowering plants (see the figure, panel B)—are predicted to decline from 5.1 in 1997 to 0.6 trees per hectare by 2070 (*4*). Fragmented Brazilian rainforests are likely to lose half of their original large trees (≥60 cm diameter) in the first three decades after isolation (*9*).

Large old trees are exceptionally vulnerable to intentional removal, elevated mortality, reduced recruitment, or combinations of these drivers (see the figure, panel C). They are removed during logging, land clearing, agricultural intensification, fire management, and for human safety. Droughts, repeated wildfires, competition with invasive plants, edge effects, air pollution, disease, and insect attack (*10*) can all increase tree mortality. The likelihood of new trees growing into large old trees can be diminished by overgrazing or browsing by native herbivores (*11*) and domestic livestock (*6*), by competition with exotic plants, and by altered fire regimes.



Global decline. (**A**) Over 95% of California's majestic coastal redwoods have been lost to logging and forest clearing (*8*). (**B**) Large old Mountain Ash (*E. regnans*) trees in mainland southern Australia are critical habitats for many elements of the biota but are also readily killed and often consumed by wildfires (*4*). (**C**) Baobab trees, like this giant in Tanzania, are under threat from land clearing, droughts, fungal pathogens, and overharvesting of their bark for mat-weaving (*3*). (**D**) Efforts to conserve large old Ponderosa Pine (*Pinus ponderosa*) trees include reducing the risk of stand-replacing fire by removing small trees and applying low-severity prescribed fire. (**E**) During post-insect attack salvage logging operations in British Columbia, Canada, all large trees are removed.

Drivers of large old tree loss often interact to create ecosystem-specific threats (*12*). In agricultural landscapes, chronic livestock overgrazing, excessive nutrients from fertilizers, and deliberate removal for firewood and land clearing combine to severely reduce large old trees (*6*). Populations of large old pines in the dry forests of western North America declined dramatically in the last century because of selective logging, uncharacteristically severe wildfires, and other causes, although efforts are now made to reduce the density of the stands so that high-severity fires do not occur and large trees are saved (see the figure, panel D). Salvage logging is equally damaging, whereby natural disturbances, such as fire or insect attack, are followed by removal of all remaining live and dead trees (see the figure, panel E). In certain tropical savannas and temperate forests, interactions among drivers occur over vast areas and result in entire landscapes supporting few large old trees (*13*). Modeling suggests that even modest increases in adult mortality can seriously erode populations of long-lived organisms such as large old trees (*14*).

Although large old trees are declining across much of the planet, not all ecosystems are losing such trees. Elevated plant-growth rates in tropical forests, possibly in response to rising concentrations of atmospheric carbon dioxide, might result in larger numbers of large old trees, at least where such forests escape other human disturbances.

Large old trees are more likely to persist in particular parts of landscapes such as disturbance refugia. Research is needed to determine the locations and causes of such refugia and to devise strategies to protect them (*15*). For example, timber or other commodity extraction (e.g., cropping) in managed landscapes might be concentrated where large old trees are least likely to persist or develop. Maintenance of appropriate population age structures can help to ensure the perpetual supply of large old trees. This requires policies and management practices that intentionally grow such trees and reduce their mortality rates (*5*).

Just as large-bodied animals such as elephants, tigers, and cetaceans have declined drastically in many parts of the world, a growing body of evidence suggests that large old trees could be equally imperiled. Targeted research is needed to better understand their key threats and devise strategies to counter them. Without such initiatives, these iconic organisms and the many species dependent on them could be lost or greatly diminished.

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