nature ecology & evolution

PERSPECTIVE

https://doi.org/10.1038/s41559-018-0490-x

The exceptional value of intact forest ecosystems

James E. M. Watson[1,2,15]*, Tom Evans[2,15], Oscar Venter[3], Brooke Williams[1,2], Ayesha Tulloch[1,2], Claire Stewart[1], Ian Thompson[4], Justina C. Ray[5], Kris Murray[6], Alvaro Salazar[1], Clive McAlpine[1], Peter Potapov[7], Joe Walston[2], John G Robinson[2], Michael Painter[2], David Wilkie[2], Christopher Filardi[8], William F. Laurance[9], Richard A. Houghton[10], Sean Maxwell[1], Hedley Grantham[1,2], Cristián Samper[2], Stephanie Wang[2], Lars Laestadius[11], Rebecca K. Runting[1], Gustavo A. Silva-Chávez[12], Jamison Ervin[13] and David Lindenmayer[14]

As the terrestrial human footprint continues to expand, the amount of native forest that is free from significant damaging human activities is in precipitous decline. There is emerging evidence that the remaining intact forest supports an exceptional confluence of globally significant environmental values relative to degraded forests, including imperilled biodiversity, carbon sequestration and storage, water provision, indigenous culture and the maintenance of human health. Here we argue that maintaining and, where possible, restoring the integrity of dwindling intact forests is an urgent priority for current global efforts to halt the ongoing biodiversity crisis, slow rapid climate change and achieve sustainability goals. Retaining the integrity of intact forest ecosystems should be a central component of proactive global and national environmental strategies, alongside current efforts aimed at halting deforestation and promoting reforestation.

Although Earth has lost at least 35% of its pre-agricultural forest cover over the past three centuries[1], forests are still widely distributed, covering a total of 40 million km^2 (~25%) of Earth's terrestrial surface[2]. Of the remaining forests, as much as 82% is now degraded to some extent as a result of direct human actions such as industrial logging, urbanization, agriculture and infrastructure[3,4]. This figure is probably an underestimate of the true level of anthropogenic impact as it does not incorporate other, more cryptic forms of degradation, such as over-hunting[5]. As the human footprint continues to expand[4], remaining forest free of significant anthropogenic degradation is in rapid decline (Fig. 1).

Over the past decade, there has been increasing international concern around the loss of forest and the impact this has on climate change, the loss of biodiversity and the provision of ecosystem services[1]. The 2015 Paris Agreement, together with earlier agreements under the United Nations Framework Convention on Climate Change (UNFCCC), acknowledges the importance of forests for limiting a future temperature increase to well below 2 °C above pre-industrial levels[6]. The United Nations' Sustainable Development Goals (adopted in 2016) have the ambitious aim of fully halting deforestation by 2020[7]. However, while these targets are clearly warranted, they fall short of specifically prioritizing the crucial qualities of a forest that contribute most to achieving each convention's specific goals[1]. For example, indicators tracking progress towards the 2015 New York Declaration on Forests — among the most significant global forest conservation targets to date — focus on forest extent and make almost no acknowledgement of forest condition[8].

In this Perspective, we argue that to achieve the goals of global international environmental accords it is insufficient to treat all forests as equal regardless of their condition. Instead, forest that is free of significant anthropogenic degradation (which we term 'intact forest') should be identified and accorded special consideration in policymaking, planning and implementation. Anthropogenic degradation here includes all human actions that are known to cause physical changes in a forest that lead to declines in ecological function[9,10]. Well-studied examples include forest fragmentation, stand-level damage due to logging, over-harvesting of particular species (such as over-hunting) and changes in fire or flooding regimes.

We first summarize published evidence that intact forests support an exceptional confluence of globally significant environmental values relative to forests that have experienced those damaging human actions. We show that intact forests are indispensable not only for addressing rapid anthropogenic climate change, but also for confronting the planet's biodiversity crisis, providing critical ecosystem services and supporting the maintenance of human health. We then show that the relative value of intact forests is likely to become magnified as already-degraded forests experience further intensified pressures (including anthropogenic climate change). While it is beyond the scope of this paper to set thresholds for acceptable forest fragment size and configuration, logging intensity or any other measure of damage, we provide evidence that human activity that exceeds the natural range of variation in a forested system reduces key ecological functions, and the greater the level of alteration, the greater the reduction in function. Here we outline the significant,

[1]School of Earth and Environmental Sciences, The University of Queensland, St. Lucia, Brisbane, Queensland, Australia. [2]Wildlife Conservation Society, Global Conservation Program, Bronx, New York, NY, USA. [3]Natural Resources & Environmental Studies Institute, University of Northern British Columbia, Prince George, British Columbia, Canada. [4]Canadian Forest Service, Sault Ste, Marie, Ontario, Canada. [5]Wildlife Conservation Society Canada, Toronto, Ontario, Canada. [6]The Grantham Institute - Climate Change and the Environment and Department of Infectious Disease Epidemiology, Imperial College London, London, UK. [7]University of Maryland, College Park, MD, USA. [8]Division of Ornithology, American Museum of Natural History, New York, NY, USA. [9]Centre for Tropical Environmental and Sustainability Science (TESS) and College of Science and Engineering, James Cook University, Cairns, Queensland, Australia. [10]Woods Hole Research Center, Falmouth, MA, USA. [11]Swedish University of Agricultural Sciences, Umeå, Sweden. [12]Forest Trends Association, Washington DC, USA. [13]Global Programme on Nature for Development, United Nations Development Programme, New York, NY, USA. [14]Fenner School of Environment and Society, The Australian National University, Canberra, Australian Capital Territory, Australia. [15]These authors contributed equally: James E. M. Watson and Tom Evans. *e-mail: jwatson@wcs.org

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.

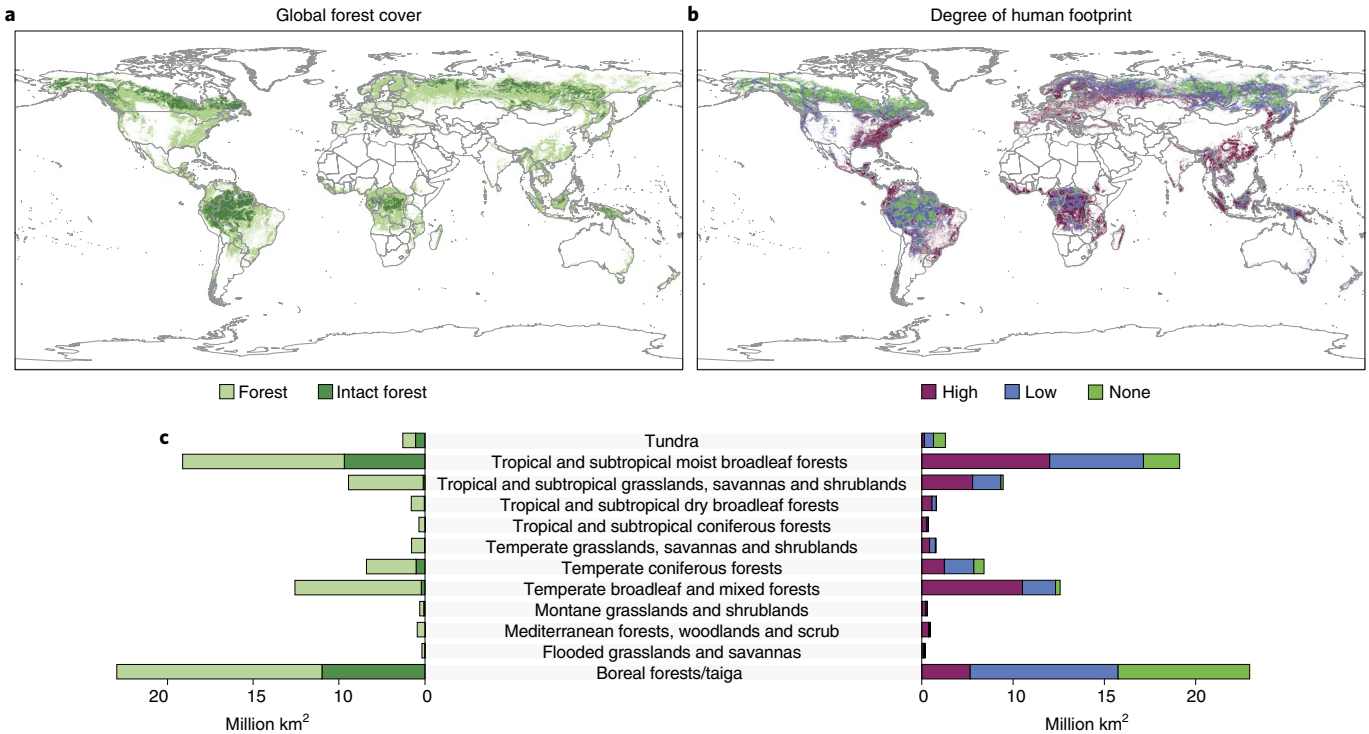


Fig. 1 | The global extent of intact forest. a–c, There are many ways to map intact forest: the first example is mapped as defined by Intact Forest Landscape methodology[3] (**a**), the second example by the global Human Footprint methodology[138] (**b**) and, for both measures, by biome (**c**). The definition of overall forest estate was based on ref. [136], with forests defined as >75% tree coverage.

and probably intensifying, threats to intact forests and argue that action is required to halt and reverse their loss. Such action requires explicit consideration on global, national and sub-national scales, and we conclude by identifying specific policy mechanisms where intact forests should be addressed.

Our call for an increased emphasis on intact forests does not imply that other forms of forest are unimportant. Given the scale of the environmental challenges facing humanity, there is also an undoubted need to cease deforestation and degradation at forest frontiers[11], and to promote large-scale reforestation[12]. We believe that coherent environmental policy should give due weight to intact forests, clearance frontiers and restoration opportunities, because all three have crucial and complementary roles to play. The primary reasons why we focus on intact forests are twofold. First, they are overlooked in international policy. Second, intact forest protection can typically secure very high environmental values with often relatively low implementation and opportunity costs[13], which serves to reinforce the need for their direct inclusion in global environmental accords.

Evidence for the exceptional values of intact forest ecosystems

There has been rapid growth in our understanding of the link between anthropogenic pressures on forest and impacts on ecosystem service values across a range of forest types (Box 1). Anthropogenic pressures, especially at industrial intensities and large spatial scales, have been shown to alter forest characteristics, including physical structure, species composition, diversity, abundance and functional organization compared with their natural state, and as a result, to reduce a wide range of environmental values[14–17]. These pressures also interact with natural disturbance regimes such as fire and pests to perturb forests beyond their capacity to regenerate[18]. The following sections show how the loss of forest intactness leads to declines or changes in these key environmental values: global and regional scale climate regulation; local climate and watershed regulation; biodiversity conservation; indigenous cultures; and human health.

Climate mitigation. Climate change is causing pervasive and potentially irreversible impacts on ecosystems and people[19]. Of the anthropogenic contribution to atmospheric CO_2 since 1870, 26% is due to emissions from deforestation and forest degradation[20]. It is now accepted that actions that avoid emissions from the land sector, especially forests, and maximize removals of greenhouse gases are critical if the goals of the UNFCCC Paris Agreement are to be achieved[12,21].

Degradation typically causes fewer emissions per hectare than deforestation, but is much more widespread[3,4,9]. In the tropics, where most net forest emissions occur, degradation may account for 10–40% of total emissions of aboveground carbon[22]. Industrial-scale logging (that is, large-scale market-orientated logging using heavy machinery, with offtakes that exceed natural rates of tree mortality) directly reduces carbon stocks through a combination of tree removal, collateral damage to non-target trees, decomposition of logging waste and wood fibre products[23], and the depletion of soil and peatland carbon stocks[24,25]. Industrial logging creates forested systems dominated by regenerating stands of younger, smaller trees, and although some regrowth does occur during each logging cycle, the cyclical peaks in biomass typically do not return to pre-logging levels, and the time-averaged carbon stocks can be expected to decline progressively over subsequent cutting cycles in many cases[26]. Reported carbon losses through industrial logging vary widely across forest types and due to the different types of logging undertaken (Fig. 2).

As forest patches are fragmented by agriculture and infrastructure, the area exposed to edge effects increases disproportionately; already 70% of the world's forests lie within 1 km of a forest edge and this proportion is rising[27]. Globally, locations up to 500 m from a forest edge average 25% less biomass carbon than locations

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.

Box 1 | Evidence of the exceptional values intact forest ecosystems have when compared with degraded ecosystems

Climate change mitigation

More above- and belowground carbon stored. Intact forests store more carbon than logged, degraded or planted forests in ecologically comparable locations. Industrial logging and conversion of forest to cropland causes heavy erosion and contributes to the loss of belowground carbon[21,22,144] (see Fig. 2 and Supplementary Table 1).

More faunal complexity, which helps carbon storage and sequestration. Defaunation can significantly erode the long-term carbon storage potential of forests by depriving key, high-carbon tree species of seed-dispersal agents, and through other ecological disruptions such as reduced vegetation diversity and composition or increased herbivory by non-hunted species (see Box 2)[29,31].

Major carbon sequestration. Intact forests continue to function as major net carbon sinks, actively sequestering carbon into soils and living biomass[12,34,37].

Regulating local and regional weather regimes

Effects on weather. Local and regional weather patterns are partly a function of the amount of intact forest cover and its condition[40,42,167].

Generation of rain and reduced risk of drought. When intact forests are cleared or degraded, there is a reduction in cloud cover and rainfall. Degradation and loss of intact forest can increase the number of dry and hot days, decrease daily rainfall intensity and wet day rainfall, and increase drought duration during El Niño years[41,168,169].

Ensuring hydrological services are maintained

Effects on water runoff availability. Intact forests have a positive effect on the redistribution of runoff, stabilize water table levels and retain soil moisture by altering soil permeability. These processes interact with physiography to regulate the flow distribution of energy and materials across the land surface and help stabilize slopes, prevent water and wind erosion, and regulate the transport of nutrients and sediments[48,50].

Buffer human settlements against negative effects of extreme climatic events. Non-degraded forests diminish the impact of heavy rain events by decreasing runoff and reducing the negative consequences of climate extremes[50,170].

Conserving biodiversity

Consistently higher numbers of forest-dependent species. More forest-dependent species are found in intact ecosystems than degraded ones. In some regions, the loss of large tracts of forest has meant wide-ranging forest-dependent species have either retreated to the last remaining intact forest systems or gone extinct[14,68,171].

More effectively sustain important large-scale ecological processes. Key functions supported by intact forests include natural disturbance regimes that sustain habitat resources, constitute selective forces to which species are adapted, or otherwise influence community composition[17,172,173].

Intact forests have higher functional diversity. Degrading activities such as selective logging lead to trait shifts in communities that can affect ecosystem functioning, in addition to taxonomic diversity[5,33,173] (see also Box 2).

Higher intra-species genetic diversity. The larger populations of forest-dependent species that inhabit intact forests provide greater options for local adaptation and phenotypic plasticity, which will facilitate species' potential for evolutionary and plastic responses to the rapidly changing environmental conditions[69,126,128].

Higher ability for species to undertake dispersal or retreat to refugia. The connectivity provided by large, contiguous areas spanning environmental gradients, such as latitude, altitude, rainfall or temperature, maximize the potential for key processes such as gene flow and genetic adaptation to play out, while also allowing species to track shifting climates[131,152].

Refuge for forest species from increased fire frequencies in degraded landscapes under changing climates. Intact forests act as fire refuges in landscapes where non-intact forests burn too frequently to support persistence of plant and animal communities dependent on long time intervals between burning[100,124].

Increased likelihood of providing key pollination and dispersal processes. Direct logging and secondary effects of degradation such as loss of vertebrate seed dispersers or pollinators leads to reduced ecosystem functions, such as seed dispersal and pollination services, for example, reduced fruit set due to reduced pollinations in fragmented forests[31,174].

Indigenous cultures

Increased basis for the material and spiritual aspects of traditional indigenous cultures to function. Long-established cultural norms intricately linked to the ecology of intact areas and vulnerable to damaging change[80,91,92].

Human health benefits

Reduced health impacts of wildfires. Fires attributed to forest degradation activities such as burning for land clearing result in premature deaths due to generation of haze. Lower burning rates in intact forests mean that health effects of wildfires are lower than in degraded landscapes with larger, more frequent fires[99].

Reduced infectious disease risks. The emergence of novel diseases from forests and the increase of endemic disease impacts in forested landscapes are thought to be related to encroachment and degradation arising from increasing human presence in these habitats[96,97,175].

remote from forest edges, and even locations up to 5 km from an edge can have >10% less biomass carbon[28]. These edge effects are mediated by a wide range of ecological changes, including increased windthrow and evaporation, and increased access for people, fire and invasive species[27]. Another form of degradation is loss of fauna through over-hunting, which can significantly disturb vegetation composition and the long-term carbon storage potential of tropical forests by depriving key, high-carbon tree species of their seed dispersal agents, and through other ecological disruptions[29,30] (see Box 2). Such effects can extend over vast areas (for example, at least 36% of the Amazon[31]) because over-hunting is pervasive where human access is facilitated by new infrastructure, and can also occur even in very remote areas[32,33].

Degradation reduces the capacity of forests to function as major net carbon sinks, actively sequestering carbon into soils and living biomass[34,35]. The global residual terrestrial sink, much of which is considered to take place in intact forests, removes an extraordinary 25% (2.4 Pg C yr^{-1}) of anthropogenic emissions from all sources, and hence greatly slows the pace of climate change[36,37]. This aspect of global carbon dynamics is often under-emphasized in climate policy because it is seen as part of the background of natural fluxes. However, the large-scale degradation of intact forests would result in a major anthropogenic reduction in this critical ecosystem service[38]. The intact forest sink is distinct from the sink resulting from reforestation and forest recovery following cessation of degradation. Both are large and both are likely to be indispensable in efforts to meet global climate targets[36,39].

Regulating local climate regimes and providing watershed services. There is increasing evidence that forests are a key factor in the regulation of local and regional climate regimes through the exchange of radiation, moisture and wind energy between the

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.

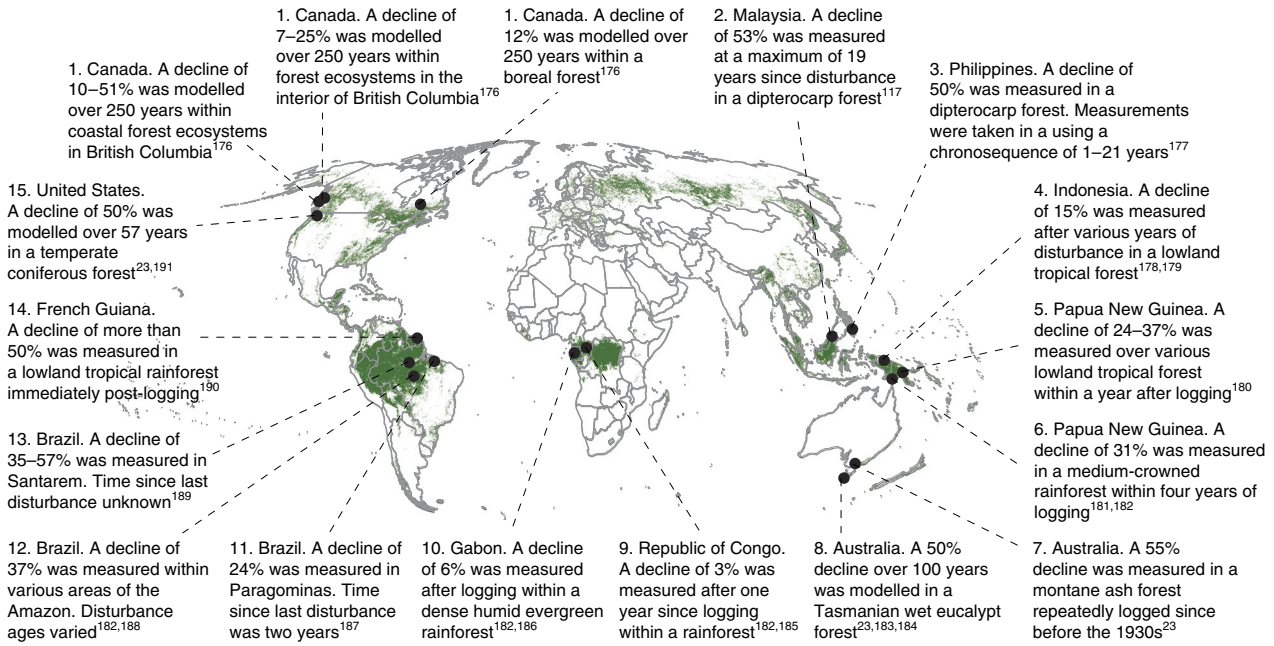


Fig. 2 | Forest degradation and carbon loss. Examples of published case studies that have examined the effects of forest degradation on carbon loss[23,117,176–191]. Supplementary Table 1 provides in-depth summaries of each of the 15 case studies.

land and atmosphere. Local and regional weather patterns are therefore a function of not just the amount of forest cover but also its state and condition[40].

Intact tropical forests are critical for rain generation because air that passes over these forests produces at least twice as much rain as air that passes over degraded or non-forest areas[41]. When intact forests are degraded, there is a resulting reduction in convective cloud cover and rainfall[42]. The influence of intact forests on precipitation, temperature and surface hydrology is particularly relevant in reducing the risks of drought imposed by climate extremes[42]. In Australia, the degradation and loss of intact forest can increase the number of dry and hot days, decrease daily rainfall intensity, and increase drought duration during El Niño years[43]. The last pattern also has been shown in Amazonia, where deforestation and forest degradation produce warmer and drier conditions that favour more frequent and intense droughts than in the past[44]. Importantly, the local climate benefits of tropical and sub-tropical forests occur primarily during the dry season and in regions with low rainfall, and during heat waves where the temperature is buffered by the cooling effects of evapotranspiration[45].

Intact forests also have a direct influence on water availability through the redistribution of runoff, water table levels and soil moisture by altering soil permeability[46]. These processes interact with physiography to regulate the flow distribution of energy and materials across the land surface and help stabilize slopes, prevent water and wind erosion, and regulate the transport of nutrients and sediments[46]. Several studies have shown that when forests are degraded, the soil infiltration rates and water infiltration capacity are decreased because of changes in soil structure and aggregation by organic matter and plant litter production[47]. For example, intact mountain ash (*Eucalyptus regnans*) forested ecosystems of southern Australia have been shown to produce >12 Ml ha^{-1} yr^{-1} more water than equivalent forested ecosystems that have been degraded through logging[48]. In many cases, intact forests also buffer the negative effects of heavy rainfall events by reducing peak discharge and regulating runoff, and by diminishing the negative consequences of climate extremes[49,50].

Conservation of biodiversity. The global biodiversity crisis is heavily driven by anthropogenic threats to forests[51], as forested ecosystems support the majority of global terrestrial biodiversity[52]. Biodiversity has intrinsic value and there is also increasing evidence that diverse, intact species assemblages underpin ecosystem functions such as tree productivity, nutrient cycling, seed dispersal, pollination, water uptake and pest resistance that are critical for human well-being[53].

Intact forests have particular value for the conservation of biodiversity[54]. Beyond outright forest clearance (which is the greatest threat facing biodiversity[51]), forest degradation from logging is the most pervasive threat facing species inhabiting intact forests[3]. Many species are sensitive to logging, and studies across many taxonomic groups have shown impacts increasing with the intensity of logging and with the number of times a forest has been logged[17,55]. Fragmentation of intact forest blocks (and associated edge effects) is also a severe threat to forest-dependent species, especially those requiring large areas to maintain viable populations (for example, wide-ranging predators and tree species that occur naturally at very low densities)[27,56]. In temperate, boreal and tropical forest regions, the loss of large contiguous tracts of forest has meant wide-ranging forest-dependent species have either retreated to the last remaining intact forest systems or are extinct[57–60]. Furthermore, there is evidence that — even for some forest species that may persist for a time in degraded fragments — intact forests are necessary to ensure their persistence over the long term[18,61,62].

Defaunation resulting from commercial and subsistence hunting is a critical threat for large-bodied forest vertebrates, especially in the tropics[5,63]. Many large carnivores and ungulates that play important roles as ecosystem engineers (for example, Sumatran serow (*Capricornis sumatraensis*), gaur (*Bos gaurus*) and forest elephant (*Loxodonta cyclotis*)) are now found only as remnant populations in the remaining intact tropical forests[33,64]. The synergistic interaction of stand damage, fragmentation and hunting is an increasingly significant challenge for biodiversity conservation[65,66] as it is well known that forest fragmentation increases access for hunters[67], and logging damage has more severe impacts when combined with fragmentation[17]. Forest biodiversity is best conserved by minimizing the

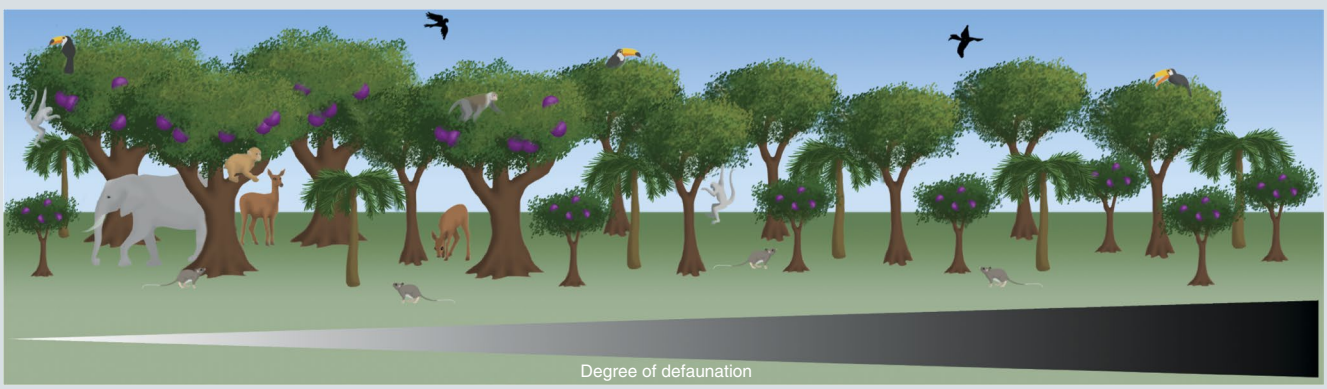
© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.

Box 2 | The effect of defaunation on carbon storage and sequestration in intact forests

Even where forests have not been cleared, many are not functioning as they once were[166]. Species such as the Asian and South American tapirs (*Tapirus* spp.), forest elephant (*L. cyclotis*) and the great apes have disappeared across much of their ranges. Habitat degradation and fragmentation are major causes of this defaunation, as many large-bodied species depend on great expanses of high-quality forest to sustain viable populations[5,192]. Increased human accessibility to forests is another, with unsustainable hunting now affecting greater areas of tropical forest than the combined extent of deforestation, selective logging and wildfires[193]. Wildlife species are not equally affected by hunting, with stronger impacts of hunting pressure on larger-bodied primates and ungulates compared with smaller-bodied vertebrates such as birds and rodents[31,75,194].

Defaunation significantly erodes key ecosystem services and functions through direct and indirect cascading effects on species diversity and trophic webs[195–197]. There is evidence for negative effects on pollination, seed dispersal, pest control, nutrient cycling, decomposition, water quality and soil erosion[192,198]. Studies across the African and Atlantic tropical forests indicate that the disappearance of large frugivores and subsequent loss of seed dispersal reduces recruitment and natural regeneration of large-seeded hardwood plant species, which are key contributors to carbon storage[199–201]. By simulating the local extinction of trees that depend on large frugivores in 31 Atlantic forest communities, one study[29] found that defaunation has the potential to significantly erode carbon storage even when only a small proportion of large-seeded trees are extirpated. This is because of strong functional relationships between seed diameter, wood density and tree height, which are traits related to carbon storage[202]. Similar results have been shown for the Amazon[31] and other parts of the tropics[203].

There is also likely to be another link between defaunation and lowered carbon storage in tropical forests; lower herbivory rates in defaunated forests allow fast-growing herbivore-sensitive plants to outcompete slower-growing animal-dispersed trees that have better defence mechanisms against hunted frugivores[31,204,205]. In defaunated forests, carbon storage is potentially reduced when these fast-growing carbon-poor plants replace an equal basal area of carbon-rich animal-dispersed trees[206] — a process that may be irreversible once the seed stock is lost.



Schematic representation of the transition (from left to right) of a non-hunted, faunally intact tropical forest to an overhunted, defaunated forest. Shown is the degree to which large arboreal or terrestrial forest frugivores such as elephants and apes decline in abundance and, with these declines, the associated replacement of large-fruited high-biomass trees by smaller-fruited and wind-dispersed trees that have lower biomass and carbon storage. Credit: Blake Alexander Simmons.

encroachment of productive activities that promote forest loss and fragmentation because the initial intrusion leads to rapid degradation of intact forests, via not only the direct effects of habitat loss, but also the coinciding effects of wildfires, overhunting, selective logging and biological invasions, alongside other stressors[65,68]. For example, a recent global analysis of nearly 20,000 vertebrate species showed that even minimal initial deforestation within an intact landscape had severe consequences for vertebrate biodiversity in a given region, emphasizing the special value of intact forests in minimizing extinction risk[68]. Moreover, those forest ecosystems that are more affected by humans support less genetic diversity than those systems that are still intact, which has potentially significant ramifications for evolutionary change[69].

Indigenous peoples. At least 250 million people[70] live in forests, and for many of them, their cultural identities are deeply rooted in the plant and animal species found there[71]. Archaeological and ethnographical evidence indicate that forests have been inhabited by people for millennia: in Latin America, records go back 13,000 years[72]; in Asia, some 40,000 years[73]; and in Central Africa, more than 250,000 years[74]. Forest-dwelling indigenous peoples have tended to do so at very low population densities distributed in dispersed settlements[75]. Today, tropical forest societies that depend almost exclusively on the direct use of natural resources to meet their basic needs seldom exceed population densities of 1–2 people km^{-2} (ref. [76]), and tend to change location from time to time to ensure that their taking of food and other products will not permanently deplete an area of key resources. Through their selection and management of useful plants and animals, these communities have significant and long-lasting impacts on the structure and composition of the forests in which they live[77,78].

Industrial-scale degradation of intact forest erodes the material basis for the livelihoods of indigenous forest peoples, depleting wildlife and other resources[79]. It also renders traditional resource management strategies ineffective, and undermines the value of traditional knowledge and authority[80]. Fragmentation and degradation of the forest makes a traditional life style no longer tenable, pushing indigenous peoples off their land[81], and driving people to adopt

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.

production systems that are incompatible with the maintenance of intact forests[82–85]. As traditional forest peoples become increasingly sedentary and connected to urban markets, gender roles, diets and cultural values also change[86–88]. These changes in the life styles of indigenous and traditional peoples create greater dependence on urban markets for provisioning, which can lead to effects that erode their cultural identities[89]. Indeed, for many indigenous forest peoples their cultural sense of self is inextricably linked to intact forests[80].

Forcible alienation from their territories has even more severe impacts, with the forest homes of many indigenous and traditional peoples being taken from them, often by force, by more powerful state, corporate and private actors, whose interests often involve forest conversion for cattle pasture, agricultural fields, oil-palm plantations[90] and mining concessions[91–93]. This can have serious impacts on the health of these peoples as they are often exposed to new disease vectors and hostile settlers and ranchers. As many indigenous and traditional peoples are motivated to conserve their forests (because they are the foundation of their economic and cultural well-being), there is now mounting evidence (which we discuss below) that strengthening the land tenure of indigenous peoples is a powerful way to protect intact forests[94,95].

Human health. Forested ecosystems are major sources of many medicinal compounds that supply millions of people with medicines worldwide[96,97]. Degradation and outright forest loss compromise the supply of these benefits as medically relevant species decline or are lost[98]. Degradation can also cause substantial negative health impacts. For example, during the 2015 human-caused forest fires in Indonesia, the haze generated after 261,000 ha of degraded forest and peatland was burned caused more than 100,000 premature deaths across Indonesia, Malaysia and Singapore[99]. Fragmented forests experience more numerous and intense edge-related wildfires in comparison with intact forests[100], which severely exacerbates the extent of health impacts of both intentional and unintentional burning.

Forest degradation may also lead to infectious disease impacts. Against a backdrop of declining overall burden of infectious diseases on a global scale[101], an increasing rate of novel disease emergence and an increase in the incidence of some endemic diseases in forested landscapes have been, at least in part, attributed to increasing human presence in, and degradation of, these habitats[102,103]. For example, deforestation and resultant environmental changes are considered key drivers of zoonotic malaria in Malaysian Borneo[104]. Although wildlife and arthropod vector species within forests are natural sources of potential human infections[105], increasing human presence and anthropogenic land-use changes often promote opportunities for disease transmission, as human-reservoir/vector contact rates increase or as impacts on host or vector distributions or community composition perturb natural disease dynamics[106]. Numerous infectious diseases associated with forests, including Ebola virus[103], dengue fever[107], Zika virus[108], several hantaviruses[109], yellow fever[110] and malaria[111], are undergoing changes in risk to humans due to deforestation, forest degradation and human encroachment.

The increasing significance of intact forests

The differences in important environmental and social values of intact forests relative to degraded forests are likely to become magnified in the future due to two negative processes in degraded areas: progressive anthropogenic damage and reduced resilience to environmental change.

Vulnerability of degraded forests to further degradation. Once initiated, forest degradation often intensifies over time[112]. This is mediated by: (1) increased levels of human accessibility; (2) successive cycles of logging of often progressively lower value trees[113]; (3) increased hunting pressure[5]; (4) forest clearance and fragmentation due to colonization by farmers and loggers facilitated by new roads[114]; and (5) the entry of new extractive development projects such as mining[55]. For example, in the Brazilian Amazon, 16% of logged areas are cleared for agriculture in the first year following logging, with further losses of more than 5% per year for the next four years[115]. This cycle is exacerbated if conversion becomes more politically acceptable once a forest has been labelled 'degraded'[116]. Once identified as 'lower value' for conservation, degraded forests can mistakenly be considered to have 'no value' by some stakeholders, despite extensive evidence to the contrary[17,117].

Degraded forests also have increased risk of, and susceptibility to, natural disturbances such as fire, as forests are drier along their edges[118]. There is clear evidence that forests that are logged are at high risk of burning at uncharacteristically high severity[119], with an elevated fire proneness lasting for decades[120]. Degraded forests are also at higher risk from invasion by exotic invasive species[18] when compared with non-degraded forests. With fire frequency in many forest areas predicted to increase under climate change scenarios[121–123], intact forests might become refuges from fire in many landscapes where degraded forests burn too frequently to support the persistence of plant and animal communities dependent on old forests. This cascade of damage, referred to as a 'landscape trap'[124], is becoming more common and many forests are now subject to repeated disturbances that lock them in early successional states.

Loss of resilience following forest degradation. In addition to present direct anthropogenic threats, forested ecosystems also have to adapt to large-scale environmental changes, including changes in climate[19], which interact with the myriad of current threats that they already face[125]. Intact forest ecosystems have greater capability to overcome these regional and global stressors than degraded ones, as they have inherent properties that enable them to maximize their adaptive capacity[126]. For example, intact forested ecosystems often house important populations of forest-dependent species and high intraspecific genetic diversity, which both provide options for the local adaptation and phenotypic plasticity[127] that facilitates species' ability to survive changing environmental conditions[128]. Large, connected and functionally intact forest ecosystems also enable species to undertake adaptive responses such as dispersal or retreating to refugia[129], which will be critical as the climate changes and species react[130]. Moreover, the connectivity provided by large, contiguous areas spanning multiple environmental gradients, such as altitude, latitude, rainfall or temperature, will maximize the potential for key processes such as gene flow and genetic adaptation to play out naturally, while also allowing species to track shifting climates in space[131,132]. Intact forests have been shown to be more resilient in response to short-term climatic anomalies (for example, droughts and wildfires during drought) than degraded forests[133].

Intact forest ecosystems sustain large-scale ecological processes, such as natural disturbance regimes, which maintain disturbance-adapted species that influence native community composition[18,127]. For example, the biodiversity of boreal and temperate forests includes evolutionary lineages that are uniquely adapted to survive major seasonal temperature changes and landscape-level disturbances over time, such as large fires and insect infestations[134].

The future of intact forests

The capacity to map human pressures on the environment on global scales is rapidly improving[135] and published results so far show that not only has loss of global forest cover accelerated since the 1990s[8,136,137] but also that there are higher levels of degradation within the shrinking forest estate. The recently updated global Human Footprint[138], a composite index of eight human pressures that is believed to be a good proxy for overall intactness, found that in 2009, 18% of forests had no detectable human pressure, a 35%

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.

decline since 1993 (Fig. 1b). According to a related but distinct metric, Intact Forest Landscapes covered 24% of the world's forests in 2013, a decline of 7.2% since 2000[3]. Recent mapping of roadless forest[139] and hinterland forest[140] shows similar declines using alternative data sources.

These assessments underestimate the total loss of intactness as they do not fully take into account other forms of forest degradation, including invasive species, some forms of logging, over-hunting, and altered fire and flood regimes, nor do they address the impacts of climate change. For example, vast areas of Central Africa that are mapped as 'intact' by both satellite imagery and the Human Footprint have lost their forest elephant (*L. cyclotis*) populations in the past 20 years due to poaching. This causes dramatic long-term ecological changes, given the role of this species as an 'ecosystem engineer' though seed dispersal, trampling and herbivory[33].

These figures suggest that even if existing global targets to halt deforestation are achieved, much of what is saved will be no longer intact. Outright deforestation is currently concentrated in the tropics and sub-tropics[136], but the loss of intactness is a pervasive global forest phenomenon[3]. It seems likely that this rapid decline in forest intactness will accelerate in line with the underlying drivers of change (including human economic demands, which are growing rapidly as a result of rising population and even more quickly rising per-capita consumption[141]). One stark forecast is that 25 million km of new roads will be built globally by 2050[142], threatening many intact areas.

Focal mechanisms for action on intact forests. It is clear that many intact forests are under severe and rising pressure, and there is an urgent need for greater conservation efforts[3]. Below, we offer some potential avenues for enhanced action, while acknowledging that the scale of the challenge is very significant, and will achieve long-term success only if nations turn away from 'business as usual' activities that extract natural resources without appropriately valuing the cost of lost natural capital. An essential first step towards greater success is achieving widespread recognition that rapid loss of forest intactness represents a major threat to sustainable development and human well-being. Policymakers need to understand the challenge that the loss of forest intactness represents for achieving strategic goals outlined in key multilateral environmental agreements, including the Convention of Biological Diversity, the UNFCCC and the UN Sustainable Development Goals[139,143], and this recognition needs to be translated into meaningful changes on the ground.

A fundamental constraint to progress is the fact that international definitions of forests have not differentiated among types of forest and, in most policy settings, they treat all forests, regardless of their condition, as equivalent[1,144]. As such, international policy processes seldom acknowledge the special qualities and benefits that flow from intact ecosystems as compared with those that are degraded. The consequence is that few policy processes (or participating nations) clearly articulate conservation goals for intactness, forest quality or integrity[143]. There is an emerging, critical role for the science community to develop policy-relevant metrics of forest intactness that account for the different forms and levels of forest degradation, and assess how they impact on different globally important social and environmental values. The lack of recognition of the varying qualities and condition among forest types has implications for targeting by international funding programmes such as the Global Environment Facility, Green Climate Fund and Critical Ecosystems Partnership Fund, which are distributing billions of dollars annually to help developing countries achieve the goals of multilateral environmental agreements. All three of these mechanisms could adjust their criteria for funding so as to explicitly recognize the value of investments that protect intact forests.

A number of emerging policy opportunities for the global community to recognize the special values that intact forests preserve, when compared with degraded ones, are within the UNFCCC. Because the scientific community has not worked out a practicable definition for emissions from land use, land use-change and forestry (LULUCF) that would separate direct human-induced effects from indirect human-induced and natural effects, parties to the UNFCCC in reporting on LULUCF in their greenhouse gas inventories may choose to apply the managed land proxy[145]. Under the managed land proxy, land where human practices have been applied is considered 'managed' and included in reporting under the UNFCCC. However, by definition, many intact forest landscapes are located on 'unmanaged lands' and therefore their contribution to meeting mitigation goals is not quantified or understood. Increased attention to unmanaged lands, and to transitions between the managed and unmanaged lands categories, through key venues such as the Intergovernmental Panel on Climate Change Special Reports and the Global Stocktake and Facilitative Dialogue will not just improve understanding of the climate mitigation role of intact forests but also support nations in articulating interventions, targets and funding needs for protecting these forests in formulating and implementing their nationally determined contributions.

Further policy enhancements could be identified in existing frameworks and programmes for financing for tropical intact forest conservation, such as the UNFCCC REDD+ process (reducing emissions from deforestation and forest degradation and the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries), the Green Climate Fund and the Forest Carbon Partnership Facility. To date, these processes have been focused on rewarding countries and jurisdictions with performance-based payments for reducing near-term threats of deforestation and (to a much lesser extent) degradation, based on a historical emissions baseline. Given this goal of achieving near-term climate mitigation results (that is, typically within five to ten years), programme rules often directly limit the eligibility or amount of support for conservation of intact forests that have, by definition, low historical emissions from deforestation and degradation, and that may be under threat over one or more decades. For example, so-called 'high forest, low deforestation' nations have relied on projections that implicitly or explicitly assume higher rates of emissions in the future. A more straightforward approach would focus on existing stocks and reservoirs of forest carbon, which could be elaborated within the '+' in REDD+ (the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries). Such an approach may require new incentives that differ from and are complementary to existing results-based payment approaches; instead, they would reward the long-term maintenance of existing carbon stocks and the other '+' activities, and bypass rules stipulating that this financing must target areas with high historical ('baseline') levels of emissions[146]. Additional climate-related policy approaches are also clearly needed for temperate and boreal intact forests, especially those in developed countries that would not expect to receive finance support under the Paris Agreement and related UNFCCC mechanisms.

There are current efforts underway to generate new 2030 global biodiversity targets, and operationalizing a clear, mandated target on preserving ecosystem intactness is critical to this[143]. The first steps are underway, with the International Union for the Conservation of Nature recently adopting a new key biodiversity area criterion (criterion C) covering those sites that contribute significantly to the global persistence of biodiversity because they are exceptional examples of ecological integrity and naturalness[147]. If the key biodiversity area standard becomes formally recognized within the 2030 strategic plan for biodiversity, this would be a very positive step in proactively conserving intact forests.

Change in policy at the global level should be reflected in the design and implementation of effective national and sub-national policies, and forest management plans that recognize the value of

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.

intact forests to the host nation and specify policies for their protection and restoration. National and sub-national policies can be supported by longer-term planning that is incentivized by climate funding streams (for example, conditional targets in nationally determined contributions, the Green Climate Fund) that recognize the mitigation contribution of intact forest landscapes. These policies will vary based on the specific context of different nations, but there is a clear need to focus on halting degrading activities, including limiting road expansion[142], reducing negative impacts of hunting through legal controls coupled with sustainable resource use strategies[5], preventing large-scale developments such as mining, forestry and agriculture in intact forests[51], and investing in restoration activities. One obvious intervention that nations can prioritize is the creation of large protected areas, including transboundary areas. When well designed, financed and enforced, protected areas have been shown to be effective in slowing the impacts of industrial logging[3], land clearance[148] and over-hunting[33,148].

A range of other designations exists beyond protected areas that can prevent the loss of intactness or promote its restoration. There is evidence that the designation of 'roadless areas' in the USA, for example, has led to an effective expansion in the degree of ecoregional representation under protection and increases in the number of areas big enough to provide refugia for species needing large tracts relatively undisturbed by people[149]. There is a need for mechanisms relating to the private sector that prioritize the protection and restoration of intact forest, including specific investment and performance standards for lenders and investors (for example, the World Bank, International Finance Corporation and regional development banks) and increasing the effectiveness of existing forest and extractive industry certification standards. Recent initiatives to make supply chains deforestation-free need to be strengthened, and to include measures to protect intact forests. While there are some signs of success (for example, the Brazil Soy Moratorium[150]), implementation is lagging well behind pledges and it is too early to demonstrate lasting impacts[151].

One emerging strategy that can be effective in slowing the degradation of intact forests is enabling indigenous communities to establish title and management over their traditional lands. Although comprehensive global analyses are lacking, some regional data reveal the remarkable contribution of stewardship by forest peoples to sustaining high-integrity forest systems, often in the face of substantial pressures to liquidate forest timber or mineral resources. For instance, the creation and management of indigenous territories has reduced (although, as with protected areas, not halted) deforestation across the Amazon Basin[152–154]. It is believed over half of the Amazon Basin's 7 million km^2 are under some form of protection, and nearly 1.8 million km^2 are indigenous lands[155]. In the boreal north of Canada, First Nations peoples have been able to sign formal agreements with the government and the private sector to ensure that national economic development policies and practices respect their rights and commit to conserving their lands and waters. For example, the Final Recommended Peel Regional Land Use Plan, co-developed by the government of Yukon and four First Nation governments, has an explicit goal of "managing development at a pace and scale that maintains ecological integrity", and has placed 81% of the 67,000 km^2 area under protection[156]. These examples are drawn mostly from regions where indigenous peoples live at very low densities and have made cultural choices not to exploit the territories they own for timber or minerals; where population densities are higher, or where communities make different cultural choices, levels of forest degradation associated with subsistence and income-generating activities will also tend to be proportionately higher, as with non-indigenous communities.

Funding for protection and restoration of intact forests could also be used to establish payments for ecosystem services. The approach has many challenges, but there are some encouraging examples where these types of activities are being undertaken. For example, in Brazil, the Amazon Regional Protected Areas programme, partly funded by international performance-based payments under a prototype REDD+ framework, supports the creation and management of protected areas and sustainable natural resource use[157]. This is being accomplished in collaboration with local peoples with the overarching aim to maintain forest carbon stocks and protect large-scale ecological processes[158].

There is also a need for increased efforts to restore the intactness of degraded systems. This should not be seen as a substitute for conserving fully intact systems in their current state, as forest degradation can often only be partially reversed over reasonable timescales[112], and it is generally more cost-effective to conserve at-risk intact forests than to protect or restore fragmented and degraded ones. If the goal of restoration is to achieve sustainably managed production forests, this may serve to alleviate pressure on intact forests, while also providing some biodiversity and ecosystem service benefits[159]. Further intensifying production systems in previously degraded land may allow even more intact forests to be spared. Such a 'land sparing' approach has been shown to achieve biodiversity benefits in agricultural landscapes relative to 'land sharing' (integrating biodiversity and production objectives on the same land)[160], and emerging evidence suggests the same is true in timber production landscapes[161]. In both cases, it is imperative that strong regulation and governance systems are in place to ensure intact forests are actually spared in practice; otherwise, the higher economic returns that come from intensifying production may create incentives for further forest degradation[162]. Nonetheless, in already-degraded systems, partial restoration will clearly bring significant environmental benefits in many cases[112]. Important efforts are being undertaken worldwide, for example through UN-REDD and the Bonn Challenge, ranging from enabling natural regeneration, active replanting of native forests, removal of invasive exotic species[163], fire management[164], reconnecting landscapes through the establishment of corridors[165], and 'rewilding' initiatives to re-establish top predators and large-scale ecosystem processes in regenerating forests[166].

Conclusion

There are still significant tracts of forest that are free from the damaging impacts of large-scale human activities. These intact forests typically provide more environmental and social values than forests that have been degraded by human activities. Despite these values, it is possible to envisage, within the current century, a world with few or no significant remaining intact forests. Humanity may be left with only degraded, damaged forests, in need of costly and sometimes unfeasible restoration, open to a cascade of further threats and lacking the resilience needed to weather the stresses of climate change. The practical tools required to address this challenge are generally well understood and include well-located and managed protected areas, indigenous territories that exemplify sound stewardship, regulatory controls and responsible behaviour by logging, mining, and agricultural companies and consumers, and targeted restoration. Currently these tools are insufficiently applied, and inadequately supported by governance, policy and financial arrangements designed to incentivize conservation. Losing the remaining intact forests would exacerbate climate change effects through huge carbon emissions and the decline of a crucial, under-appreciated carbon sink. It would also result in the extinction of many species, harm communities worldwide by disrupting regional weather and hydrology, and devastate the cultures of many indigenous communities. Increased awareness of the scale and urgency of this problem is a necessary pre-condition for more effective conservation efforts across a wide range of spatial scales.

Received: 14 July 2017; Accepted: 30 January 2018;
Published online: 26 February 2018

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.

References

1. Mackey, B. et al. Policy options for the world's primary forests in multilateral environmental agreements. *Conserv. Lett.* **8**, 139–147 (2015).
2. MacDicken, K. et al. *Global Forest Resources Assessment 2015: How are the World's Forests Changing?* 2nd edn (FAO, Rome, 2016).
3. Potapov, P. et al. The last frontiers of wilderness: tracking loss of intact forest landscapes from 2000 to 2013. *Sci. Adv.* **3**, e1600821 (2017).
4. Venter, O. et al. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat. Commun.* **7**, 12558 (2016).
5. Redford, K. H. The empty forest. *Bioscience* **42**, 412–422 (1992).
6. *Adoption of the Paris Agreement: Proposal by the President* Draft Decision -/CP.21 (UNFCCC, Geneva, 2015).
7. *Progress Towards the Sustainable Development Goals: Report of the Secretary-General* (UN Economic and Social Council, 2016).
8. *Progress on the New York Declaration on Forests Achieving Collective Forest Goals: Updates on Goals 1-10* (Climate Focus, 2016).
9. Thompson, I. D. et al. An operational framework for defining and monitoring forest degradation. *Ecol. Soc.* **18**, 20 (2013).
10. Ghazoul, J. & Chazdon, R. Degradation and recovery in changing forest landscapes: a multiscale conceptual framework. *Annu. Rev. Environ. Resour.* **42**, 161–188 (2017).
11. Zarin, D. J. et al. Can carbon emissions from tropical deforestation drop by 50% in 5 years?. *Glob. Change Biol.* **22**, 1336–1347 (2016).
12. Houghton, R. A., Byers, B. & Nassikas, A. A. A role for tropical forests in stabilizing atmospheric CO_2. *Nat. Clim. Change* **5**, 1022–1023 (2015).
13. Balmford, A., Gaston, K. J., Blyth, S., James, A. & Kapos, V. Global variation in terrestrial conservation costs, conservation benefits, and unmet conservation needs. *Proc. Natl Acad. Sci. USA* **100**, 1046–1050 (2003).
14. Gibson, L. et al. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* **478**, 378–381 (2011).
15. Lewis, S. L., Edwards, D. P. & Galbraith, D. Increasing human dominance of tropical forests. *Science* **349**, 827–832 (2015).
16. De Leo, G. & Levin, S. The multifaceted aspects of ecosystem integrity. *Conserv. Ecol.* **1**, 3 (1997).
17. Edwards, D. P., Tobias, J. A., Sheil, D., Meijaard, E. & Laurance, W. F. Maintaining ecosystem function and services in logged tropical forests. *Trends Ecol. Evol.* **29**, 511–520 (2014).
18. Lindenmayer, D., Thorn, S. & Banks, S. Please do not disturb ecosystems further. *Nat. Ecol. Evol.* **1**, 0031 (2017).
19. Scheffers, B. R. et al. The broad footprint of climate change from genes to biomes to people. *Science* **354**, aaf7671 (2016).
20. Le Quéré, C. et al. Global carbon budget 2016. *Earth Syst. Sci. Data* **8**, 605–649 (2016).
21. Sanderson, B. M., O'Neill, B. C. & Tebaldi, C. What would it take to achieve the Paris temperature targets? *Geophys. Res. Lett.* **43**, 7133–7142 (2016).
22. Houghton, R. A. Carbon emissions and the drivers of deforestation and forest degradation in the tropics. *Curr. Opin. Environ. Sustain.* **4**, 597–603 (2012).
23. Keith, H. et al. Managing temperate forests for carbon storage: impacts of logging versus forest protection on carbon stocks. *Ecosphere* **5**, 1–34 (2014).
24. Page, S. E., Rieley, J. O. & Banks, C. J. Global and regional importance of the tropical peatland carbon pool. *Glob. Change Biol.* **17**, 798–818 (2011).
25. Turetsky, M. R. et al. Global vulnerability of peatlands to fire and carbon loss. *Nat. Geosci.* **8**, 11–14 (2015).
26. Zimmerman, B. L. & Kormos, C. F. Prospects for sustainable logging in tropical forests. *Bioscience* **62**, 479–487 (2012).
27. Haddad, N. M. et al. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **1**, e1500052 (2015).
28. Chaplin-Kramer, R. et al. Degradation in carbon stocks near tropical forest edges. *Nat. Commun.* **6**, 10158 (2015).
29. Bello, C. et al. Defaunation affects carbon storage in tropical forests. *Sci. Adv.* **1**, e1501105 (2015).
30. Sobral, M. et al. Mammal diversity influences the carbon cycle through trophic interactions in the Amazon. *Nat. Ecol. Evol.* **1**, 1670–1676 (2017).
31. Peres, C. A., Emilio, T., Schietti, J., Desmoulière, S. J. M. & Levi, T. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proc. Natl Acad. Sci. USA* **113**, 892–897 (2016).
32. Robinson, J. G. & Bennett, E. L (eds) *Hunting for Sustainability in Tropical Forests* (Columbia Univ. Press, New York, 2000).
33. Maisels, F. et al. Devastating decline of forest elephants in Central Africa. *PLoS ONE* **8**, e59469 (2013).
34. Lewis, S. L. et al. Increasing carbon storage in intact African tropical forests. *Nature* **457**, 1003–1006 (2009).
35. Luyssaert, S. et al. Old-growth forests as global carbon sinks. *Nature* **455**, 213–215 (2008).
36. Houghton, R. A. The emissions of carbon from deforestation and degradation in the tropics: past trends and future potential. *Carbon Manag.* **4**, 539–546 (2013).
37. Pan, Y. et al. A large and persistent carbon sink in the world's forests. *Science* **333**, 988–993 (2011).
38. Griscom, B. W. et al. Natural climate solutions. *Proc. Natl Acad. Sci. USA* **114**, 11645–11650 (2017).
39. Bongers, F., Chazdon, R., Poorter, L. & Peña-Claros, M. The potential of secondary forests. *Science* **348**, 642–643 (2015).
40. Pielke, R. A., Mahmood, R. & McAlpine, C. Land's complex role in climate change. *Phys. Today* **69**, 40–46 (2016).
41. Sheil, D. & Murdiyarso, D. How forests attract rain: an examination of a new hypothesis. *Bioscience* **59**, 341–347 (2009).
42. Bonan, G. B. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* **320**, 1444–1449 (2008).
43. Deo, R. C. et al. Impact of historical land cover change on daily indices of climate extremes including droughts in eastern Australia. *Geophys. Res. Lett.* **36**, L08705 (2009).
44. Medvigy, D., Walko, R. L., Otte, M. J. & Avissar, R. Simulated changes in northwest US climate in response to Amazon deforestation. *J. Clim.* **26**, 9115–9136 (2013).
45. Ahlström, A. et al. The dominant role of semi-arid ecosystems in the trend and variability of the land CO_2 sink. *Science* **348**, 895–899 (2015).
46. D'Odorico, P. et al. Ecohydrology of terrestrial ecosystems. *Bioscience* **60**, 898–907 (2010).
47. Ludwig, D., Brock, W. & Carpenter, S. Uncertainty in discount models and environmental accounting. *Ecol. Soc.* **10**, 13 (2005).
48. Vertessy, R. A., Watson, F. G. R. & Sharon, K. O. Factors determining relations between stand age and catchment water balance in mountain ash forests. *For. Ecol. Manag.* **143**, 13–26 (2001).
49. Alila, Y., Kuras, P. K., Schnorbus, M. & Hudson, R. Forests and floods: a new paradigm sheds light on age-old controversies. *Water Resour. Res.* **45**, W08416 (2009).
50. Brookhuis, B. J. & Hein, L. G. The value of the flood control service of tropical forests: a case study for Trinidad. *For. Policy Econ.* **62**, 118–124 (2016).
51. Maxwell, S. L., Fuller, R. A., Brooks, T. M. & Watson, J. E. M. Biodiversity: the ravages of guns, nets and bulldozers. *Nature* **536**, 143–145 (2016).
52. Pimm, S. L. et al. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**, 1246752 (2014).
53. Cardinale, B. J. et al. Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67 (2012).
54. Morales-Hidalgo, D., Oswalt, S. N. & Somanathan, E. Status and trends in global primary forest, protected areas, and areas designated for conservation of biodiversity from the Global Forest Resources Assessment 2015. *For. Ecol. Manag.* **352**, 68–77 (2015).
55. Venier, L. A. et al. Effects of natural resource development on the terrestrial biodiversity of Canadian boreal forests. *Environ. Rev.* **22**, 457–490 (2014).
56. Laurance, W. F. et al. The fate of Amazonian forest fragments: a 32-year investigation. *Biol. Conserv.* **144**, 56–67 (2011).
57. Peres, C. A. Why we need megareserves in Amazonia. *Conserv. Biol.* **19**, 728–733 (2005).
58. Lortkipanidze, B. Brown bear distribution and status in the South Caucasus. *Ursus* **21**, 97–103 (2010).
59. Festa-Bianchet, M., Ray, J. C., Boutin, S., Côté, S. D. & Gunn, A. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Can. J. Zool.* **89**, 419–434 (2011).
60. Broadbent, E. N. et al. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biol. Conserv.* **141**, 1745–1757 (2008).
61. Hermy, M. & Verheyen, K. Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Ecol. Res.* **22**, 361–371 (2007).
62. Lindenmayer, D. B. et al. How to make a common species rare: a case against conservation complacency. *Biol. Conserv.* **144**, 1663–1672 (2011).
63. Ripple, W. J. et al. Collapse of the world's largest herbivores. *Sci. Adv.* **1**, e1400103 (2015).
64. Gray, T. N. E., Prum, S., Pin, C. & Phan, C. Distance sampling reveals Cambodia's Eastern Plains Landscape supports the largest global population of the endangered banteng *Bos javanicus*. *Oryx* **46**, 563–566 (2012).
65. Barlow, J. et al. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* **535**, 144–147 (2016).
66. Edwards, D. P. The rainforest's 'do not disturb' signs. *Nature* **535**, 44–46 (2016).
67. Peres, C. A. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conserv. Biol.* **15**, 1490–1505 (2001).
68. Betts, M. G. et al. Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature* **547**, 441–444 (2017).
69. Miraldo, A. et al. An Anthropocene map of genetic diversity. *Science* **353**, 1532–1535 (2016).

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.

70. Byron, N. & Arnold, M. What futures for the people of the tropical forests? *World Dev.* **27**, 789–805 (1999).
71. Lévi-Strauss, C. *The Savage Mind* (Univ. Chicago Press, Chicago, 1966).
72. Johnson, C. N., Bradshaw, C. J. A., Cooper, A., Gillespie, R. & Brook, B. W. Rapid megafaunal extinction following human arrival throughout the New World. *Quat. Int.* **308**, 273–277 (2013).
73. Hutterer, K. L. in *People of the Tropical Rain Forest* (eds Denslow, J. S. & Padoch, C.) 63–72 (Univ. California Press, Washington DC, 1988).
74. Mercader, J. Forest people: the role of African rainforests in human evolution and dispersal. *Evol. Anthropol.* **11**, 117–124 (2002).
75. Robinson, J. G. & Bennett, E. L. (eds) in *Hunting for Sustainability in Tropical Forests* 13–30 (Columbia Univ. Press, New York, 2000).
76. Bennett, E. L. & Robinson, J. G. *Hunting of Wildlife in Tropical Forests: Implications for Biodiversity and Forest Peoples* Biodiversity Studies Impact Series Paper No. 76 (World Bank, Washington DC, 2000).
77. Levis, C. et al. Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science* **355**, 925–931 (2017).
78. Schmidt, M. J. & Heckenberger, M. J. in *Amazonian Dark Earths: Wim Sombroek's Vision* (eds Woods, W. I. et al.) 163–191 (Springer, Dordrecht, 2009).
79. Foley, J. A. et al. Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin. *Front. Ecol. Environ.* **5**, 25–32 (2007).
80. Rozzi, R. Biocultural ethics: recovering the vital links between the inhabitants, their habits, and habitats. *Environ. Ethics* **34**, 27–50 (2012).
81. Southgate, D., Wasserstrom, R. & Reider, S. Oil development, deforestation, and indigenous populations in the Ecuadorian Amazon. *Lat. Am. Stud. Assoc.* **11**, 1–38 (2009).
82. Bedoya Garland, E. in *The Social Causes of Environmental Destruction in Latin America* (eds Painter, M. & Durham, W. H.) 217–248 (Univ. Michigan Press, Ann Arbor, 1995).
83. Demmer, M. J. & Overman, J. P. M. *Indigenous People Conserving the Rain Forest? The Effect of Wealth and Markets on the Economic Behaviour of Tawahka Amerindians in Honduras* (Tropenbos Foundation, 2001).
84. Godoy, R. et al. Household determinants of deforestation by Amerindians in Honduras. *World Dev.* **25**, 977–987 (1997).
85. Reyes-García, V. et al. Indigenous land reconfiguration and fragmented institutions: a historical political ecology of Tsimane'lands (Bolivian Amazon). *J. Rural Stud.* **34**, 282–291 (2014).
86. Sirén, A. *Changing Interactions Between Humans and Nature in Sarayaku, Ecuadorian Amazon*. PhD thesis, Swedish Univ. Agricultural Sciences (2004).
87. Sirén, A. H. Population growth and land use intensification in a subsistence-based indigenous community in the Amazon. *Hum. Ecol.* **35**, 669–680 (2007).
88. Luz, A. C. et al. How does cultural change affect indigenous peoples' hunting activity? An empirical study among the Tsimane'in the Bolivian Amazon. *Conserv. Soc.* **13**, 382–394 (2015).
89. Gross, D. R. et al. Ecology and acculturation among native peoples of central Brazil. *Science* **206**, 1043–1050 (1979).
90. Sheil, D. et al. *The Impacts and Opportunities of Oil Palm in Southeast Asia: What do We Know and What do We Need to Know?* (Center for International Forestry Research, Bogor, 2009).
91. Finer, M., Jenkins, C. N., Pimm, S. L., Keane, B. & Ross, C. Oil and gas projects in the western Amazon: threats to wilderness, biodiversity, and indigenous peoples. *PLoS ONE* **3**, e2932 (2008).
92. Olivero, J. et al. Distribution and numbers of pygmies in Central African forests. *PLoS ONE* **11**, e0144499 (2016).
93. Parlee, B. L. Avoiding the resource curse: indigenous communities and Canada's oil sands. *World Dev.* **74**, 425–436 (2015).
94. Barraclough, S. & Ghimire, K. *Forests and Livelihoods: The Social Dynamics of Deforestation in Developing Countries* (Springer, London, 1995).
95. Oliveira, P. J. C. et al. Land-use allocation protects the Peruvian Amazon. *Science* **317**, 1233–1236 (2007).
96. Colfer, C. J. P. *Human Health and Forests: A Global Overview of Issues, Practice and Policy* (Routledge, London, 2012).
97. Karjalainen, E., Sarjala, T. & Raitio, H. Promoting human health through forests: overview and major challenges. *Environ. Health Prev. Med.* **15**, 1–8 (2010).
98. Shanley, P. & Luz, L. The impacts of forest degradation on medicinal plant use and implications for health care in eastern Amazonia. *Bioscience* **53**, 573–584 (2003).
99. Koplitz, S. N. et al. Public health impacts of the severe haze in equatorial Asia in September–October 2015: demonstration of a new framework for informing fire management strategies to reduce downwind smoke exposure. *Environ. Res. Lett.* **11**, 94023 (2016).
100. Laurance, W. F. Forest–climate interactions in fragmented tropical landscapes. *Phil. Trans. R. Soc. Lond. B* **359**, 345–352 (2004).
101. Murray, C. J. L. et al. Disability-adjusted life years (DALYs) for 291 diseases and injuries in 21 regions, 1990–2010: a systematic analysis for the Global Burden of Disease Study 2010. *Lancet* **380**, 2197–2223 (2012).
102. Jones, K. E. et al. Global trends in emerging infectious diseases. *Nature* **451**, 990–993 (2008).
103. Myers, S. S. & Patz, J. A. Emerging threats to human health from global environmental change. *Annu. Rev. Environ. Resour.* **34**, 223–252 (2009).
104. Fornace, K. M. et al. Association between landscape factors and spatial patterns of *Plasmodium knowlesi* infections in Sabah, Malaysia. *Emerg. Infect. Dis.* **22**, 201–208 (2016).
105. Dunn, R. R. Global mapping of ecosystem disservices: the unspoken reality that nature sometimes kills us. *Biotropica* **42**, 555–557 (2010).
106. Murray, K. A. & Daszak, P. Human ecology in pathogenic landscapes: two hypotheses on how land use change drives viral emergence. *Curr. Opin. Virol.* **3**, 79–83 (2013).
107. Vasilakis, N., Cardosa, J., Hanley, K. A., Holmes, E. C. & Weaver, S. C. Fever from the forest: prospects for the continued emergence of sylvatic dengue virus and its impact on public health. *Nat. Rev. Microbiol.* **9**, 532–541 (2011).
108. Ali, S. et al. Environmental and social change drive the explosive emergence of Zika virus in the Americas. *PLoS Negl. Trop. Dis.* **11**, e0005135 (2017).
109. Jonsson, C. B., Figueiredo, L. T. M. & Vapalahti, O. A global perspective on hantavirus ecology, epidemiology, and disease. *Clin. Microbiol. Rev.* **23**, 412–441 (2010).
110. Norris, D. E. Mosquito-borne diseases as a consequence of land use change. *Ecohealth* **1**, 19–24 (2004).
111. Hahn, M. B., Gangnon, R. E., Barcellos, C., Asner, G. P. & Patz, J. A. Influence of deforestation, logging, and fire on malaria in the Brazilian Amazon. *PLoS ONE* **9**, e85725 (2014).
112. Chazdon, R. L. Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* **320**, 1458–1460 (2008).
113. Putz, F. E. & Redford, K. H. The importance of defining 'forest': tropical forest degradation, deforestation, long-term phase shifts, and further transitions. *Biotropica* **42**, 10–20 (2010).
114. Laurance, W. F., Goosem, M. & Laurance, S. G. W. Impacts of roads and linear clearings on tropical forests. *Trends Ecol. Evol.* **24**, 659–669 (2009).
115. Asner, G. P. et al. Condition and fate of logged forests in the Brazilian Amazon. *Proc. Natl Acad. Sci. USA* **103**, 12947–12950 (2006).
116. Giam, X., Clements, G. R., Aziz, S. A., Chong, K. Y. & Miettinen, J. Rethinking the 'back to wilderness' concept for Sundaland's forests. *Biol. Conserv.* **144**, 3149–3152 (2011).
117. Berry, N. J. et al. The high value of logged tropical forests: lessons from northern Borneo. *Biodivers. Conserv.* **19**, 985–997 (2010).
118. Barlow, J. & Peres, C. A. Fire-mediated dieback and compositional cascade in an Amazonian forest. *Phil. Trans. R. Soc. B* **363**, 1787–1794 (2008).
119. Thompson, J. R., Spies, T. A. & Ganio, L. M. Reburn severity in managed and unmanaged vegetation in a large wildfire. *Proc. Natl Acad. Sci. USA* **104**, 10743–10748 (2007).
120. Taylor, C., McCarthy, M. A. & Lindenmayer, D. B. Nonlinear effects of stand age on fire severity. *Conserv. Lett.* **7**, 355–370 (2014).
121. Stephens, S. L. et al. Managing forests and fire in changing climates. *Science* **342**, 41–42 (2013).
122. Wang, X. et al. Increasing frequency of extreme fire weather in Canada with climate change. *Clim. Change* **130**, 573–586 (2015).
123. Bowman, D. Ecohydrology: when will the jungle burn? *Nat. Clim. Change* **7**, 390–391 (2017).
124. Lindenmayer, D. B., Hobbs, R. J., Likens, G. E., Krebs, C. J. & Banks, S. C. Newly discovered landscape traps produce regime shifts in wet forests. *Proc. Natl Acad. Sci. USA* **108**, 15887–15891 (2011).
125. Côté, I. M., Darling, E. S. & Brown, C. J. Interactions among ecosystem stressors and their importance in conservation. *Proc. R. Soc. B* **283**, 20152592 (2016).
126. Thompson, I., Mackey, B., McNulty, S. & Mosseler, A. *Forest Resilience, Biodiversity, and Climate Change* Technical Series No. 43 (Secretariat of the Convention on Biological Diversity, Montreal, 2009).
127. Mackey, B. G., Watson, J. E. M., Hope, G. & Gilmore, S. Climate change, biodiversity conservation, and the role of protected areas: an Australian perspective. *Biodiversity* **9**, 11–18 (2008).
128. Alberto, F. J. et al. Potential for evolutionary responses to climate change – evidence from tree populations. *Glob. Change Biol.* **19**, 1645–1661 (2013).
129. Watson, J. E. M., Iwamura, T. & Butt, N. Mapping vulnerability and conservation adaptation strategies under climate change. *Nat. Clim. Change* **3**, 989–994 (2013).
130. Shoo, L. P., Storlie, C., VanDerWal, J., Little, J. & Williams, S. E. Targeted protection and restoration to conserve tropical biodiversity in a warming world. *Glob. Change Biol.* **17**, 186–193 (2011).
131. Sgro, C. M., Lowe, A. J. & Hoffmann, A. A. Building evolutionary resilience for conserving biodiversity under climate change. *Evol. Appl.* **4**, 326–337 (2011).
132. Hole, D. G. et al. Projected impacts of climate change on a continent-wide protected area network. *Ecol. Lett.* **12**, 420–431 (2009).

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.

133. Saleska, S. R., Didan, K., Huete, A. R. & Da Rocha, H. R. Amazon forests green-up during 2005 drought. *Science* **318**, 612 (2007).
134. Piao, S. et al. Footprint of temperature changes in the temperate and boreal forest carbon balance. *Geophys. Res. Lett.* **36**, L07404 (2009).
135. Rose, R. A. et al. Ten ways remote sensing can contribute to conservation. *Conserv. Biol.* **29**, 350–359 (2015).
136. Hansen, M. C. et al. High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853 (2013).
137. Kim, D.-H., Sexton, J. O. & Townshend, J. R. Accelerated deforestation in the humid tropics from the 1990s to the 2000s. *Geophys. Res. Lett.* **42**, 3495–3501 (2015).
138. Venter, O. et al. Global terrestrial Human Footprint maps for 1993 and 2009. *Sci. Data* **3**, 160067 (2016).
139. Ibisch, P. L. et al. A global map of roadless areas and their conservation status. *Science* **354**, 1423–1427 (2016).
140. Tyukavina, A., Hansen, M. C., Potapov, P. V., Krylov, A. M. & Goetz, S. J. Pan-tropical hinterland forests: mapping minimally disturbed forests. *Glob. Ecol. Biogeogr.* **25**, 151–163 (2016).
141. Steffen, W. et al. The Anthropocene: from global change to planetary stewardship. *AMBIO* **40**, 739–761 (2011).
142. Laurance, W. F. et al. A global strategy for road building. *Nature* **513**, 229–232 (2014).
143. Watson, J. E. M. et al. Catastrophic declines in wilderness areas undermine global environment targets. *Curr. Biol.* **26**, 2929–2934 (2016).
144. Chazdon, R. L. et al. When is a forest a forest? Forest concepts and definitions in the era of forest and landscape restoration. *AMBIO* **45**, 538–550 (2016).
145. Penman, J. et al. (eds) *IPCC Good Practice Guidance for Land Use, Land-Use Change and Forestry* (Institute for Global Environmental Strategies, Kanagawa, 2003).
146. Venter, O. & Koh, L. P. Reducing emissions from deforestation and forest degradation (REDD+): game changer or just another quick fix? *Ann. NY Acad. Sci.* **1249**, 137–150 (2012).
147. *A Global Standard for the Identification of Key Biodiversity Areas: Version 1.0* (IUCN, Gland, 2016).
148. Watson, J. E. M., Dudley, N., Segan, D. B. & Hockings, M. The performance and potential of protected areas. *Nature* **515**, 67–73 (2014).
149. DeVelice, R. L. & Martin, J. R. Assessing the extent to which roadless areas complement the conservation of biological diversity. *Ecol. Appl.* **11**, 1008–1018 (2001).
150. Gibbs, H. K. et al. Brazil's Soy Moratorium. *Science* **347**, 377–378 (2015).
151. Azhar, B., Saadun, N., Prideaux, M. & Lindenmayer, D. B. The global palm oil sector must change to save biodiversity and improve food security in the tropics. *J. Environ. Manag.* **203**, 457–466 (2017).
152. Schleicher, J., Peres, C. A., Amano, T., Llactayo, W. & Leader-Williams, N. Conservation performance of different conservation governance regimes in the Peruvian Amazon. *Sci. Rep.* **7**, 11318 (2017).
153. Nolte, C., Agrawal, A., Silvius, K. M. & Soares-Filho, B. S. Governance regime and location influence avoided deforestation success of protected areas in the Brazilian Amazon. *Proc. Natl Acad. Sci. USA* **110**, 4956–4961 (2013).
154. Santika, T. et al. Community forest management in Indonesia: avoided deforestation in the context of anthropogenic and climate complexities. *Glob. Environ. Change* **46**, 60–71 (2017).
155. Hardner, J., Gullison, R. E. & O'Neill, E. Staying the course: how a long-term strategic donor initiative to conserve the Amazon has yielded outcomes of global significance. *Found. Rev.* **9**, 14 (2017).
156. *Final Recommended Peel Watershed Regional Land Use Plan* (Peel Watershed Planning Commission, Whitehorse, 2011).
157. Soares-Filho, B. et al. Role of Brazilian Amazon protected areas in climate change mitigation. *Proc. Natl Acad. Sci. USA* **107**, 10821–10826 (2010).
158. *Amazon Region Protected Areas Programme* (World Wildlife Fund, 2016).
159. Paquette, A. & Messier, C. The role of plantations in managing the world's forests in the Anthropocene. *Front. Ecol. Environ.* **8**, 27–34 (2010).
160. Phalan, B., Onial, M., Balmford, A. & Green, R. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* **333**, 1289–1291 (2011).
161. Edwards, D. P. et al. Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. *Glob. Change Biol.* **20**, 183–191 (2014).
162. Phelps, J., Carrasco, L. R., Webb, E. L., Koh, L. P. & Pascual, U. Agricultural intensification escalates future conservation costs. *Proc. Natl Acad. Sci. USA* **110**, 7601–7606 (2013).
163. D'Antonio, C. & Meyerson, L. A. Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restor. Ecol.* **10**, 703–713 (2002).
164. Brown, R. T., Agee, J. K. & Franklin, J. F. Forest restoration and fire: principles in the context of place. *Conserv. Biol.* **18**, 903–912 (2004).
165. Jantz, P., Goetz, S. & Laporte, N. Carbon stock corridors to mitigate climate change and promote biodiversity in the tropics. *Nat. Clim. Change* **4**, 138–142 (2014).
166. Galetti, M., Pires, A. S., Brancalion, P. H. S. & Fernandez, F. A. S. Reversing defaunation by trophic rewilding in empty forests. *Biotropica* **49**, 5–8 (2017).
167. Pielke, R. A. et al. Interactions between the atmosphere and terrestrial ecosystems: influence on weather and climate. *Glob. Change Biol.* **4**, 461–475 (1998).
168. Spracklen, D. V., Arnold, S. R. & Taylor, C. M. Observations of increased tropical rainfall preceded by air passage over forests. *Nature* **489**, 282–285 (2012).
169. Alkama, R. & Cescatti, A. Biophysical climate impacts of recent changes in global forest cover. *Science* **351**, 600–604 (2016).
170. Bathurst, J. C. et al. Forest impact on floods due to extreme rainfall and snowmelt in four Latin American environments. 1: Field data analysis. *J. Hydrol.* **400**, 281–291 (2011).
171. Barlow, J. et al. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proc. Natl Acad. Sci. USA* **104**, 18555–18560 (2007).
172. Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P. & Lesieur, D. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. *Can. J. For. Res.* **31**, 384–391 (2001).
173. Feeley, K. J. & Terborgh, J. W. The effects of herbivore density on soil nutrients and tree growth in tropical forest fragments. *Ecology* **86**, 116–124 (2005).
174. Rosin, C. & Poulsen, J. R. Hunting-induced defaunation drives increased seed predation and decreased seedling establishment of commercially important tree species in an Afrotropical forest. *For. Ecol. Manag.* **382**, 206–213 (2016).
175. Gottdenker, N. L., Streicker, D. G., Faust, C. L. & Carroll, C. R. Anthropogenic land use change and infectious diseases: a review of the evidence. *Ecohealth* **11**, 619–632 (2014).
176. Kurz, W. A., Beukema, S. J. & Apps, M. J. Carbon budget implications of the transition from natural to managed disturbance regimes in forest landscapes. *Mitig. Adapt. Strateg. Glob. Change* **2**, 405–421 (1998).
177. Lasco, R. D. et al. Carbon stocks assessment of a selectively logged dipterocarp forest and wood processing mill in the Philippines. *J. Trop. For. Sci.* **18**, 212–221 (2006).
178. Pearson, T. R. H., Brown, S. & Casarim, F. M. Carbon emissions from tropical forest degradation caused by logging. *Environ. Res. Lett.* **9**, 34017 (2014).
179. Brown, S., Casarim, F. M., Grimland, S. K. & Pearson, T. *Carbon Impacts from Selective Logging of Forests in Berau, East Kalimantan, Indonesia* Final Report to the Nature Conservancy (Winrock International, Arlington, 2011).
180. Bryan, J., Shearman, P., Ash, J. & Kirkpatrick, J. B. Impact of logging on aboveground biomass stocks in lowland rain forest, Papua New Guinea. *Ecol. Appl.* **20**, 2096–2103 (2010).
181. Fox, J. C. et al. Assessment of aboveground carbon in primary and selectively harvested tropical forest in Papua New Guinea. *Biotropica* **42**, 410–419 (2010).
182. Putz, F. E. et al. Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conserv. Lett.* **5**, 296–303 (2012).
183. Dean, C. & Wardell-Johnson, G. Old-growth forests, carbon and climate change: functions and management for tall open-forests in two hotspots of temperate Australia. *Plant Biosyst.* **144**, 180–193 (2010).
184. Dean, C., Wardell-Johnson, G. W. & Kirkpatrick, J. B. Are there any circumstances in which logging primary wet-eucalypt forest will not add to the global carbon burden? *Agric. For. Meteorol.* **161**, 156–169 (2012).
185. Brown, S. et al. *Impact of Selective Logging on the Carbon Stocks of Tropical Forests: Republic of Congo as a Case Study* (Winrock International, Arlington, 2005).
186. Medjibe, V. D. P. *Carbon Dynamics in Central African Forests Managed for Timber.* PhD thesis, Univ. Florida (2012).
187. Vidal, E., West, T. A. & Putz, F. E. Recovery of biomass and merchantable timber volumes twenty years after conventional and reduced-impact logging in Amazonian Brazil. *For. Ecol. Manag.* **376**, 1–8 (2016).
188. Asner, G. P. et al. Selective logging in the Brazilian Amazon. *Science* **310**, 480–482 (2005).
189. Berenguer, E. et al. A large-scale field assessment of carbon stocks in human-modified tropical forests. *Glob. Change Biol.* **20**, 3713–3726 (2014).
190. Blanc, L. et al. Dynamics of aboveground carbon stocks in a selectively logged tropical forest. *Ecol. Appl.* **19**, 1397–1404 (2009).
191. Janisch, J. E. & Harmon, M. E. Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. *Tree Physiol.* **22**, 77–89 (2002).
192. Dirzo, R. et al. Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.

193. Milner-Gulland, E. J. & Bennett, E. L. Wild meat: the bigger picture. *Trends Ecol. Evol.* **18**, 351–357 (2003).
194. Peres, C. A. & Lake, I. R. Extent of nontimber resource extraction in tropical forests: accessibility to game vertebrates by hunters in the Amazon Basin. *Conserv. Biol.* **17**, 521–535 (2003).
195. Camargo-Sanabria, A. A., Mendoza, E., Guevara, R., Martínez-Ramos, M. & Dirzo, R. Experimental defaunation of terrestrial mammalian herbivores alters tropical rainforest understorey diversity. *Proc. R. Soc. B* **282**, 20142580 (2015).
196. Galetti, M. et al. Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* **340**, 1086–1090 (2013).
197. Nuñez-Iturri, G. & Howe, H. F. Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain forest in western Amazonia. *Biotropica* **39**, 348–354 (2007).
198. Abernethy, K. A., Coad, L., Taylor, G., Lee, M. E. & Maisels, F. Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. *Phil. Trans. R. Soc. B* **368**, 20120303 (2013).
199. Blake, S., Deem, S. L., Mossimbo, E., Maisels, F. & Walsh, P. Forest elephants: tree planters of the Congo. *Biotropica* **41**, 459–468 (2009).
200. Harrison, R. D. et al. Consequences of defaunation for a tropical tree community. *Ecol. Lett.* **16**, 687–694 (2013).
201. Brodie, J. F. & Gibbs, H. K. Bushmeat hunting as climate threat. *Science* **326**, 364–365 (2009).
202. Wright, I. J. et al. Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Ann. Bot.* **99**, 1003–1015 (2006).
203. Osuri, A. M. et al. Contrasting effects of defaunation on aboveground carbon storage across the global tropics. *Nat. Commun.* **7**, 11351 (2016).
204. Jansen, P. A., Muller-Landau, H. C. & Wright, S. J. Bushmeat hunting and climate: an indirect link. *Science* **327**, 30 (2010).
205. Poulsen, J. R., Clark, C. J. & Palmer, T. M. Ecological erosion of an Afrotropical forest and potential consequences for tree recruitment and forest biomass. *Biol. Conserv.* **163**, 122–130 (2013).
206. van der Heijden, G. M., Powers, J. S. & Schnitzer, S. A. Lianas reduce carbon accumulation and storage in tropical forests. *Proc. Natl Acad. Sci. USA* **112**, 13267–13271 (2015).

Acknowledgements

We thank the John D. and Catherine T. MacArthur Foundation for funding this research, and C. Holtz, A. Rosenthal, B. Mackey, D. DellaSalla, C. Kormos, J. Funk, J. Feidler, S. Lewis, B. Mercer, S. Rumsey, P. Dargusch and E. Sanderson for conversations around different ideas that have been presented within this manuscript. A special thank you to B. Simmons for creating the figure in Box 2.

Author contributions

J.E.M.W. and T.E. conceived the study. The remaining authors provided ideas and critical feedback.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-018-0490-x.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to J.E.M.W.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.