ANNUAL REVIEWS **Further**

Click here for quick links to Annual Reviews content online, including:

- Other articles in this volume
- Top cited articles
- Top downloaded articles
- Our comprehensive search

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

Tropical Forests in the Anthropocene

Yadvinder Malhi,[1] Toby A. Gardner,[2,3,4] Gregory R. Goldsmith,[1] Miles R. Silman,[5] and Przemyslaw Zelazowski[1,6]

[1]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, United Kingdom; email: yadvinder.malhi@ouce.ox.ac.uk

[2]Stockholm Environment Institute, Stockholm 104 51, Sweden; email: toby.gardner@sei-international.org

[3]Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, United Kingdom

[4]International Institute for Sustainability, Rio de Janeiro, 22460-320, Brazil

[5]Center for Energy, Environment, and Sustainability and Department of Biology, Wake Forest University, Winston-Salem, North Carolina 27109; email: silmanmr@wfu.edu

[6]Earth Observation Group, Space Research Centre, Polish Academy of Sciences, Warsaw 00-716, Poland; email: p.zelazowski@gmail.com

Annu. Rev. Environ. Resour. 2014. 39:125–59

First published online as a Review in Advance on September 3, 2014

The *Annual Review of Environment and Resources* is online at environ.annualreviews.org

This article's doi: 10.1146/annurev-environ-030713-155141

Copyright © 2014 by Annual Reviews. All rights reserved

Keywords

climate change, conservation, deforestation, hunting, logging, resilience

Abstract

The Anthropocene is characterized as an epoch when human influence has begun to fundamentally alter many aspects of the Earth system and many of the planet's biomes. Here, we review and synthesize our understanding of Anthropocene changes in tropical forests. Key facets include deforestation driven by agricultural expansion, timber and wood extraction, the loss of fauna that maintain critical ecological connections, the spread of fire, landscape fragmentation, the spread of second-growth forests, new species invasion and pathogen spread, increasing CO_2, and climate change. The patterns of change are spatially heterogeneous, are often characterized by strong interactions among different drivers, can have both large-scale and remote effects, and can play out through ecological cascades over long timescales. As a consequence, most tropical forests are on a trajectory to becoming altered ecosystems, with the degree of alteration dependent on the intensity and duration of the current bottleneck of human-induced pressures. We highlight the importance of this understanding to develop the strategies necessary for shaping the transition of tropical forests through the early Anthropocene, as well as highlight the opportunities and challenges for the tropical forest science community in the coming decades.

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

Contents

1. INTRODUCTION 126
2. TROPICAL FORESTS BEFORE THE ANTHROPOCENE 127
2.1. Change in Tropical Forests in Geological Time 127
2.2. Antecedents to the Anthropocene in Tropical Forests 129
3. TROPICAL FORESTS IN THE EARLY ANTHROPOCENE: FACETS OF CHANGE 130
3.1. Forest Conversion 131
3.2. Timber and Wood Extraction 132
3.3. Defaunation 133
3.4. Fire 134
3.5. Fragmentation and Isolation of Tropical Forest Landscapes 135
3.6. Second-Growth Forests 136
3.7. Biotic Mixing 137
3.8. Rising Temperature 138
3.9. Rising Atmospheric Carbon Dioxide 139
3.10. Changes in Tropical Precipitation and Cloudiness 140
4. TROPICAL FORESTS IN THE ANTHROPOCENE: TRAJECTORIES OF ENVIRONMENTAL CHANGE 141
4.1. Divergence and Convergence of Tropical Forests in the Anthropocene 142
4.2. Shaping the Transition of Tropical Forests Through the Early Anthropocene 145
4.3. The Challenges Facing Tropical Forest Science 148

1. INTRODUCTION

Human influence on the planet and its functioning is all-pervasive and spreading, such that no biome of Earth's surface is free from interactions with humanity. The growing scale and intensity of our influence have modified the functioning of the Earth system, leading to the suggestion that Earth has entered a new geological epoch, the Anthropocene (1, 2). This term has recently gained widespread usage as a descriptor of the current state of the planet. Some key features of the Anthropocene include recognition that (*a*) human-altered processes are of comparable magnitude to natural processes in many aspects of the global biosphere; (*b*) human influence has multiple dimensions, and this influence is occurring at scales ranging from local to global; (*c*) there has been a pronounced surge in human influence and the pace of change since the mid-twentieth century, the so-called Great Acceleration (*sensu* 2), which is continuing and expanding in the twenty-first century (see also the sidebar, When Did the Anthropocene Begin?); (*d*) the magnitude and spatial scale of change may reach tipping points and regional or planetary boundaries, which will result in major shifts in Earth system functioning when passed; and (*e*) the degree of human influence is such that shifts in ecosystem function and the emergence of increasingly altered ecosystems are likely to be occurring in even the most remote and protected regions.

Tropical forests are arguably the most significant biomes on the planet, accounting for one-third of land-surface productivity and evapotranspiration (5), and are estimated to host over half of all global terrestrial biodiversity (6). Humans have been interacting with and modifying tropical

WHEN DID THE ANTHROPOCENE BEGIN?

The start of the Anthropocene is open to debate (3) with some arguments for a start at the dawn of agriculture (5,000–10,000 years ago) or even with the Pleistocene megafaunal extinctions 10,000–50,000 years ago, but its start is frequently ascribed to the early Industrial Revolution (~1800) or to the start of the Great Acceleration (~1950). In this review, we follow the suggestion of Steffen et al. (4) and adopt 1800. The Anthropocene is likely to be a feature of the Earth system for at least millennia (see main text), and hence we adopt the term early Anthropocene to describe the past few centuries, while recognizing that humans have also had appreciable impacts on the biosphere throughout the Holocene.

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

forests for tens of thousands of years, but the intensity of this interaction has been increasing substantially in the Anthropocene. As with other biomes, tropical forests have experienced effects of the Anthropocene that are multifaceted and include conversion to agricultural use, logging and other resource extraction, increased fire incidence, hunting and wildlife trade, global interconnectivity and its associated spread of introduced species and pathogens, altered biogeochemical cycles, and climate change.

This article reviews our understanding of the prospects for tropical forests in the Anthropocene. It presents a synthesis from the natural sciences of the multifaceted drivers of ecological change and compares the present and potential future significance of these drivers in each tropical forest region, with an eye to identifying opportunities for maintaining diverse and functional tropical forests in the future, as well as the pressing research needs necessary for capitalizing on such opportunities. Although the complex array of social, political, and economic factors that determine how forests are governed falls beyond the scope of this review, our assessment of the natural science of Anthropocene changes in tropical forests provides a basis for understanding the likely success or failure of attempts to conserve and manage the tropical forest biome.

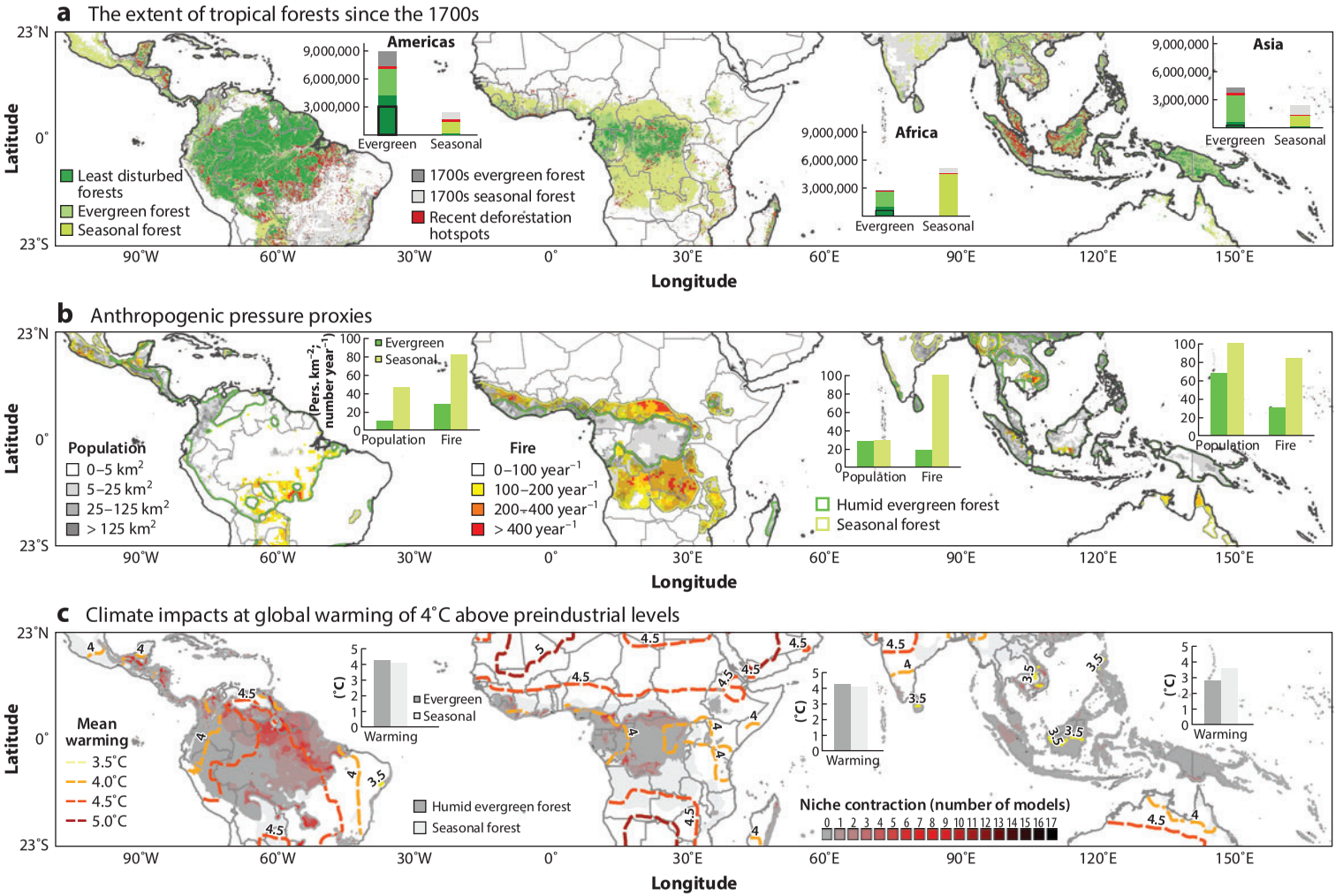
There are many reasons to be concerned about tropical forests in the Anthropocene, but we intend this review to be neither a gloomy catalog of threats nor a paean of resilience optimism. Instead, our approach is to (*a*) recognize and describe the reality of the Anthropocene for tropical forests and of the altered tropical forest ecosystems that are emerging and (*b*) identify the major challenges, unknowns, and opportunities that can assist in navigating the tropical forest biomes through the early Anthropocene.

2. TROPICAL FORESTS BEFORE THE ANTHROPOCENE

2.1. Change in Tropical Forests in Geological Time

Recognizable tropical forests probably appeared in the early Cenozoic (50–65 Mya), centered on the fragments of the continent of Gondwanaland. Today, they span five major tropical rainforest regions, mainly isolated progeny of Gondwanaland for most of the period of evolution of modern tropical flora and fauna. These regions can arguably be considered distinct biogeographical and ecological entities (tropical Americas, Africa, Southeast Asia, Madagascar, and New Guinea) (**Figure 1**), with small outliers in Australia, south Asia, and many tropical islands (7). Because of this peculiarity of Earth history, and despite occasional transoceanic species dispersal, tropical forests on different continents can be quite divergent in their floristic and particularly faunal composition, a little-recognized factor that may contribute to divergent responses to Anthropocene change.

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.



Earth has been on a long-term cooling trend for most of the Cenozoic, and by the Pleistocene (0.01–2 Mya) the mean state of tropical climate was colder and drier than present. In Africa, the forest biome probably contracted during glacial periods into distinct refugia surrounded by grasslands and savannas. In Asia, by contrast, tropical forests probably increased in area over the expanded continent of Sundaland and large portions of Australasia exposed by lower sea levels. In Amazonia, the forest likely remained largely continuous, albeit in a drier state, with forest changes concentrated at the periphery. In the Holocene (the last 10,000 years), as in previous interglacial periods, tropical forests have generally become more humid and expanded (where tropical land masses were not drowned by rising sea levels, as in about 2 million km^2 of Sundaland and 1.5 million km^2 of tropical Australasia) but still carry the ecological signatures of such recent and dramatic environmental changes. For example, the lower plant diversity of African forests probably reflects their more variable environmental history (8), compared with the high diversity and stable climatic history of northwestern Amazonia.

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

2.2. Antecedents to the Anthropocene in Tropical Forests

Clear antecedents to the Anthropocene can be observed in many biomes as hominid and modern human influence and impacts spread throughout the Pleistocene and Holocene through hunting, use of fire, and agricultural activities. *Homo sapiens* originated in African savannas 100–200 thousand years ago (kya) but had colonized Central African forests by ~60 kya and arrived in Southeast Asia ~50 kya, New Guinea and Australia ~50 kya, the American tropics ~10–15 kya, Madagascar ~2 kya, and Pacific islands ~0.8–3.5 kya (9). Probably the earliest major human influence on tropical forests was through the extinction of medium and large vertebrates (megafauna) in the late Pleistocene and early Holocene. Tropical forests possessed diverse megafauna, as they still do in parts of Africa and Asia, and the largest of these may have included elephant relatives, such as stegodonts in Asia and gomphotheres in the Neotropics, and other large animals such as the hippopotamus-sized diprotodontids in Australasia (10). The synchrony of megafaunal extinction with differing times of human arrival in different regions and the absence of extinctions in similar climatic fluctuations in the prehuman Pleistocene suggest a significant role for humans (11), although this remains the subject of some controversy (e.g., 12). In regions where human arrival

Figure 1

Facets of Anthropocene change in tropical forests. (*a*) Presents the extent of evergreen tropical forests and other dense broadleaf forests within the tropics. Gray shading represents the extent of forest in the 1700s before the onset of the Anthropocene (based on Reference 196). Green shading represents current extent; dark green represents the least disturbed areas, which consist almost entirely of evergreen forests (95%) (67). Red shading represents the most intense clearance over the period 2000–2012 (≥10% per 10 km^2), using Landsat data (27). Inset plots summarize data (area shown in km^2) for the tropical Americas, Africa, and Southeast Asia with Australasia ("Asia"), and also employ a more conservative definition of undisturbed forests (black outline), using a 5-km buffer from any high-intensity human influence, which is assumed to give a more reliable representation of areas with robust faunal assemblages. (*b*) Human population density (within forest mask only) and fire intensity as two proxies for the overall anthropogenic pressures on tropical forests. Fire intensity in seasonal forests includes both natural fire dynamics as well as anthropogenic pressure. (*c*) Potential future impacts of climate change and enhanced CO_2 concentration at 4°C global warming on humid tropical forests (data from 137). Dark gray areas mark the climatological niche of these forests derived from the current climatological conditions (water stress and annual precipitation) and are predicted to remain in such a niche by all climate models assessed in this analysis. The gray-red-black scale indicates the risk of climate change–induced dieback: the number of climate models reviewed that predict humid rainforests would no longer be viable under a global warming of 4°C. Isoclines represent the average local warming in degrees Celsius for a mean global warming of 4°C. Light gray areas show the current extent of seasonal forests. A high-resolution version of the figure and underlying data are available at **http://dx.doi.org/10.6084/m9.figshare.1018766**.

is more recent and precisely known (e.g., tropical islands), the causal link between human arrival and faunal extinction is uncontested. For example, in Pacific island ecosystems, the arrival of early settlers over the period 3,500–700 BP is estimated to have resulted in the extinction of ~1,300 bird species, 10% of global bird diversity, marking the largest known extinction event of the Holocene (13). Extinction of fauna is likely to have had effects on forest composition and structure by altering seed dispersal, tree recruitment and mortality patterns (14, 15), and forest biomass and structure (16), and likely also affected nutrient cycling (17).

Through much of the Holocene, direct human alteration of tropical forests also occurred through burning for hunting and clearance for agriculture. In recent decades, there has been an increasing recognition of the long history of human interactions with tropical forests and the extensive collapse of human populations in forests from European contact (through disease and slave trade in Amazonia and Africa, respectively) or possibly through past epidemics (e.g., in the Congo Basin) or via environmental change (e.g., in the Mayan world). Key discoveries have included evidence of once complex societies in now thinly populated regions of southern Amazonia (18) and of extensive oil palm agriculture in the now virtually unpopulated regions of the western Congo Basin (19). The extent of prehistoric human alterations of tropical forests has been intensively debated, with some arguing that much of the tropical forest biome was a human-created cultural parkland (e.g., 20). However, available evidence, albeit still limited, suggests that truly extensive human modification was limited and was only prevalent in the seasonal dry fringes of tropical forests, which include many of the iconic tropical civilizations: the Maya in Central America, the Khmer in Southeast Asia, and the forest kingdoms of West Africa.

Understanding prehistoric human interactions with tropical forests adds an important nuance to understanding contemporary change, challenges notions of intactness, and may help assess the resilience of different tropical forests to disturbances of the Anthropocene (21)—while noting that such disturbances are invariably distinct from modern disturbances in the extent, intensity, and speed with which they occurred (22). Although the extent of prehistoric human modification continues to be debated and remains an important area of research, it is important to remember that agriculture is a recent Holocene phenomenon; on no continent was there agricultural clearing before 10 kya, and most evidence of agriculture commences after 6 kya.

3. TROPICAL FORESTS IN THE EARLY ANTHROPOCENE: FACETS OF CHANGE

The early Anthropocene has heralded myriad changes to tropical forests (**Figure 1**). Although the most evident change is the widespread clearance of forests for agriculture and human habitation, large swaths of remaining tropical forests have been subject to pervasive disturbances from logging, defaunation, wildfire, and fragmentation. These impacts often occur together and in sequence. Their separate and combined effects can result in marked forest degradation through the loss of biodiversity and impairment of ecological processes, with many cascading and indirect effects that can be hard to detect through short-term studies. Many human-modified tropical forest landscapes exist as complex mosaics of primary- and second-growth forest, with a patchwork of regenerating areas on fallow or abandoned agricultural land. Indeed, second-growth forests make up the majority of remaining native vegetation in the most densely inhabited areas of the tropics. Overarching such landscape-level changes is the effect of increased global connectivity leading to widespread biotic mixing and the introduction of new species and pathogens, coupled with changes in the global climate and atmosphere that include changing temperatures, CO_2 concentrations, and precipitation patterns. This combination of large-scale and remote human influences on the biosphere sharply illustrates how the early Anthropocene has affected even the

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

most remote tropical forests, often in ways that may have profound and lasting impacts on the composition and function of these forests that we are only now beginning to understand.

In the following sections, we review 10 interrelated ways in which tropical forests are changing as we enter the early Anthropocene. A common theme that emerges from this review is that the combined effects of human activities on tropical forests can result in highly variable changes to forest diversity, structure, and function, depending on the intensity and type of impacts, the past and ongoing indirect and feedback effects from altered species composition, and the underlying differences in the composition and ecological resilience of regional biota. The emergent mosaic of landscapes, from relatively undisturbed areas removed from direct impacts to both highly variegated and highly simplified landscapes, has profound implications for how we study these dynamic systems and how we manage them more sustainably now and in the future. We start with some of the most direct and intense Anthropocene processes of change, such as forest conversion and timber extraction, and conclude with cryptic yet pervasive agents of change, such as increasing atmospheric CO_2 and climate change.

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

3.1. Forest Conversion

Rates of conversion of tropical forests to agriculture or other nonforest habitats increased in the nineteenth century and reached an apparent global peak in the late twentieth century. There are many proximate and underlying causes of conversion (23). At one end of the spatial scale is small-scale farming by low-income smallholders for subsistence or cash crops. This is driven by rural population expansion, through either local population growth or immigration into frontier regions. At the other extreme of scale is the expansion of large-scale agro-industrial agriculture and pastoralism (e.g., cattle, soybeans, oil palm), driven by capital investments and transport infrastructure into previously remote frontier regions and by the economic connection of these regions to regional and global markets (24). In addition to agriculture, myriad other factors converge to drive forest clearance, often in relatively remote areas of forest, including road building, fossil-fuel and mineral extraction, mining, and hydroelectric dams. Mining, in particular, both large and small scale, can be a direct agent of forest clearance with particularly strong pollution impacts on soils, biota, and freshwater.

Exact rates of deforestation are hard to quantify because of inconsistent definitions and reporting, yet most new agricultural land is coming from tropical forest regions (25). Deforestation pressure is particularly intense in tropical dry forests and woodlands, which are more flammable and easy to clear, and these also have a climate more suitable for many arable crops. Indeed, about half of tropical dry forest areas have already been cleared. Although country-level assessments of deforestation are problematic (26), new and more consistent satellite-based analyses are beginning to benefit from the free availability of high-resolution imagery at a global scale. The first global, high-resolution analysis of forest change (27) identified that, over the period 2000–2012, the mean rate of clearance of tropical dense forests (defined as with >50% tree cover) was 74,400 km^2 $year^{-1}$ (0.45% $year^{-1}$) and for tropical dense forests and open woodlands together was 91,400 km^2 $year^{-1}$ (0.25% $year^{-1}$). Of the major tropical forest regions, absolute loss rates for dense forests over this period were highest in the tropical Americas (39,900 km^2 $year^{-1}$), followed by tropical Asia (22,300 km^2 $year^{-1}$) and Africa (11,000 km^2 $year^{-1}$). Relative rates were highest in Asia (0.62% $year^{-1}$), followed by the Americas (0.45% $year^{-1}$) and Africa (0.28% $year^{-1}$). Large-scale conversion is particularly prominent in the Americas (cattle ranching and soybean farms) and Southeast Asia (logging, both legal and illegal, and oil palm and wood pulp plantations). In contrast, deforestation in Africa, Madagascar, and New Guinea is currently dominated by smallholder activity (28).

In the past few decades, Southeast Asia has been characterized by particularly widespread forest clearance, mainly driven by large-scale establishment of oil palm plantations. Insular Southeast Asia lost a striking 8.7% of its remaining forest cover in the period 2000–2012 alone (27), with relative losses highest in Malaysia (16%) and Indonesia (10%). Borneo and Sumatra, large islands that until recently epitomized the exuberance and vastness of tropical forests, have had vast areas converted to oil palm monoculture in recent decades.

In contrast, humid tropical forest cover has remained surprisingly static in much of Africa, with declining deforestation rates from 1990 to 2010 (29). In Africa, deforestation has been driven mostly by smallholder farming, and the observed decline can be partly linked to the economic growth of mineral and fossil-fuel sectors in many Central African countries, as well as significant rural-urban migration (30). The expansion of agro-industrial farming has also been constrained by limited infrastructure and political instability in key regions, such as the Democratic Republic of the Congo, which hosts about 54% of Africa's rainforests (29), approximately 10% of global rainforest cover. If these obstacles can be overcome, there is strong potential for a rapid wave of agro-industrial expansion and accompanying forest clearance in Central Africa (31).

One of the most striking global environmental trajectories of the past decade has been the decline in deforestation in the Brazilian Amazon. Over the decade 1996–2005, Brazilian Amazonia had an average deforestation rate of 19,500 km^2 $year^{-1}$, accounting for about half of the global tropical deforestation. Then, from 2004–2012, the rate declined by 82% and stabilized at ~5,000–7,000 km^2 $year^{-1}$, with a relative increase of 28% between 2012 and 2013 (32). The reduction has been driven almost entirely by a large decline in deforestation on larger properties (33), resulting in part from major policy interventions, supported by monitoring technologies. Nevertheless, deforestation has continued to increase in many other Amazonian countries and also in the drier subtropical biomes of Bolivia and Paraguay, such that half of all current Amazonian deforestation now occurs outside Brazil (27).

3.2. Timber and Wood Extraction

Population growth and increased global affluence have led to a rising and almost insatiable demand for tropical timber. Even though much tropical timber is consumed within national markets, and is therefore hard to monitor, an increasing amount is exported, especially to emerging economies with few remaining native forests, such as China. In 2006, member nations of the International Tropical Timber Organization exported over 13 million m^3 of tropical nonconiferous logs worth US$2.1 billion, making a substantial contribution to the economies of these nations (34). As a consequence, many of the world's remaining tropical forests have been through at least one cycle of logging, with only 19 of 106 (18%) tropical nations reporting more primary than regenerating forest (consisting mostly of logged forest) (35). Although it is difficult to make accurate comparisons, between 2000 and 2005 logging in humid tropical forests had approximately 15 times the geographic footprint of direct deforestation (36). Moreover, rates of timber extraction have recently accelerated. For example, in Brazilian Amazonia, the area of forest disturbed by fire and/or logging increased by 20% between 2000 and 2010, despite a simultaneous 46% decrease in deforestation (37). Logging intensities have been particularly high across Southeast Asia, where forests are dominated by commercially valuable dipterocarp tree species that enable timber extraction rates more than 10 times higher than those in Africa or the Americas. Between 1990 and 2009, some 80% of Malaysian Borneo was affected by previously undocumented high-intensity logging or clearing operations, with large areas being logged multiple times (38).

The collection of fuelwood, distinct from logging for timber, is another pervasive driver of forest degradation across the tropics and accounts for the vast majority (often over 90%) of wood

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

removals for many densely populated countries in sub-Saharan Africa, south Asia, and parts of Southeast Asia (39). Intensive charcoal production often predictably follows an initial wave of high-value timber extraction (40), can drive a marked shift in the composition of understory tree species (e.g., 41), and may (like logging) ultimately result in complete forest clearance (29).

Our understanding of many of the effects of logging on the ecology of tropical forests remains limited because most studies to date lack prelogging baseline data (42) and samples are often very closely spaced together (43). Moreover, the uneven distribution of economically important tree species, coupled with the highly variable levels of collateral damage associated with logging (e.g., in conventional logging nearly half of nonharvest trees may be felled or severely damaged) (44), means that logged forests can be highly spatially heterogeneous and cannot be readily classified in terms of logged and nonlogged forest (45). Nevertheless, comparative work has demonstrated that logging can be a relatively benign form of disturbance if well managed (e.g., compared with fragmentation and fire) (46), with logged forests commonly hosting at least 50% of the biomass and more than 75% of the species relative to undisturbed primary forest (47, 48). The extent of degradation, whether through changes in biotic composition or forest structure and function, is determined primarily by the number, timing, intensity, and extent of past logging events, as well as by the presence of other disturbances that often accompany logging, including forest fragmentation, hunting, and differences in forest type.

Although the species richness of tropical forest biota appears relatively resilient to even multiple logging cycles (49) and the responses of taxa vary widely (47), the vast majority of studies to date have reported clear shifts in the species composition of flora and fauna in response to logging. Negative impacts have been clearly demonstrated following even relatively low-impact timber extraction (e.g., bats in the Amazon and large mammals in Afrotropical forests) (50, 51); these impacts may appear either to dissipate after only a few decades (e.g., amphibians in West Africa) (52) or to persist for much longer (e.g., large vertebrates in Central African forests, ants in Sri Lanka) (53, 54). Logging can also precipitate delayed and cascading effects on the ecology of a forest following the removal of keystone species, such as large emergent or dominant trees. For example, many bird species in tropical forests nest in tree cavities, and larger cavities are relatively rare and found only in the largest trees—the same trees that are most vulnerable to human exploitation.

3.3. Defaunation

Although the loss of trees may show a more immediate and jarring picture of forest disturbance, changes in faunal communities within remaining areas of forest, and the resulting changes in ecological interactions, can also have far-reaching effects on tropical forest biodiversity, ecosystem function and structure, biomass dynamics, and evolutionary dynamics (55, 56). Disruption of faunal communities in forests can occur by hunting (57), habitat fragmentation (58, 59), disturbance (60), epidemic disease (61), and the synergies among them (62).

Hunting for bushmeat is a major driver of defaunation, as hunters preferentially target large-bodied species (>2 kg), which account for over half of all animal biomass removed from forests (63, 64). Hunting pressure shows great geographical variation across the tropical forest realm, linked to availability of fauna, variation in rural human population density, distance to access points, and cultural preferences or taboos around bushmeat consumption. Defaunation can be pervasive even in areas remote from deforestation or logging pressure. In a study of protected areas in 36 countries throughout the tropics, Laurance et al. (65) showed that the trend is toward degradation and that external conditions, particularly hunting intensity but also fires, logging, and forest clearing, were key drivers of that transition. If a forest is within 5 km of a road, river, or settlement, the mammal

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

and bird communities are likely to be altered (66). Under this assumption, minimally disturbed dense forest ecosystems with low defaunation [defined as in Potapov et al. (67)] constitute just 12% of all dense tropical forests. Total animal biomass removal rates are highest in Africa (68) and in large parts of Southeast Asia, with bushmeat harvests of ~4,900 tonnes year^{-1} (2.7 kg km^{-2} year^{-1}) in Central African forests (69), which are some 90 times higher per unit area than in Amazonian forests (~150 tonnes year^{-1}; 0.03 kg km^{-2} year^{-1}). Despite such differences, faunal communities have still been altered in all but the most remote areas of the Amazon, with populations of targeted species being reduced by up to 90% in hunted areas (45, 70, 71). Hunted forests on all continents show decreases in population sizes of targeted taxa, with sites in Central Africa and Amazonia showing decreases of 13–100% in population size, with typical values of 40–60% in Central Africa (72, 73). Defaunation intensity is broadly correlated with human population pressure, with Asian forests being affected through the latter part of the twentieth century, a bushmeat crisis currently occurring in West and Central Africa, and defaunation predicted to extend throughout tropical South America, corresponding to population densities within or near remaining forests (522 people km^{-2}, 99 people km^{-2}, and 46 people km^{-2}, respectively) (**Figure 1**) (74, 75).

The loss of the most vulnerable, i.e., large-bodied, vertebrates has the disproportionate effect of removing species with important ecological interactions, including keystone roles in herbivory, dispersal, and seed predation (76, 77). The combined effects of hunting and forest fragmentation can also cause surprising losses of small-bodied species (78, 79). The fact that most tropical plants require animals to complete their life cycles, with some 90% of species obligately dispersed or pollinated by animals, means that disruptions to faunal composition can have cascading effects on forest community structure and ecosystem functions, including large compositional changes in tree communities (80, 81). Changes in both seed predators and seed dispersers have been shown to have effects that translate into population- and community-level changes in forests (e.g., 82). Ultimately these combined changes to animal communities can affect the basic ecological mechanisms that maintain diversity and determine relative abundances in tropical forests (83, 84), with potentially profound consequences for the structure of forests, with possible decreases in stem number and biomass, and even with collapses in canopy cover (16, 85, 86). Results from a study of defaunated African forests show an ~34% decrease in biomass carbon storage through compositional change effects on forest structure and wood density (16).

3.4. Fire

Humans are estimated to have altered fire regimes during the Anthropocene across nearly two-thirds of terrestrial habitats through the expansion of agriculture, forest fragmentation, and timber harvesting and the effects of increased climate variability (87). Some of the most marked changes have occurred in tropical forests, particularly in seasonally dry tropical forests (**Figure 1**). In preindustrial times, large-scale fires in tropical forests were unlikely to have occurred more than once or twice per millennium in many humid forest areas (e.g., in the western Amazon) (88), and even Amazonian savannas appear to have been largely fire free (89). Wildfires are now commonplace in some tropical forests, particularly in areas with a high human population density, extensive road networks, and proximity to agricultural frontiers. For example, the drought caused by the 1997–1998 El Niño event resulted in some 16 million hectares (ha) of tropical forest being burned in Southeast Asia and Latin America, contributing an amount of CO_2 to the atmosphere equivalent to half of the world's fossil-fuel emissions for that period (90). Between 2000 and 2006, the average carbon emissions from fires in equatorial Asian countries (Indonesia, Malaysia, Papua New Guinea), including the burning of extensive tropical peat lands, was comparable to all fossil-fuel emissions in the same countries (91). Fires are particularly prevalent along forest edges, as

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

demonstrated by Langner et al. (92) in their analysis of land-cover change in Borneo between 2002 and 2005, where 98% of fires were within 5 km of the forest edge, underlining their role as a dominant driver of both deforestation and forest degradation.

Because moist tropical biotas are not preadapted to withstand fire, even relatively low-intensity fires can transform the ecology of a forest. Field observations both in the Amazon (93, 94) and in Southeast Asia (95) demonstrate how understory fires can kill the majority of trees and large lianas. The combined effects of drought and fire can be particularly destructive and have a profound effect on the subsequent species composition of a forest (95, 96). Changes in vegetation, combined with direct mortality, can lead to marked and lasting changes in faunal assemblages that are often more severe than the effects of logging or forest fragmentation (46). Additionally, there are often time lags in forest responses, with evidence of delayed tree mortality (97) and continued divergence in species composition more than a decade after the fire (98).

The natural heterogeneity of tropical forests, coupled with spatial variability in the spread of fire through a forest, means that once-burned and lightly burned forest landscapes often appear as heterogeneous mosaics of varyingly disturbed patches (71). By contrast, repeated burns can drive cascading shifts in the structural, functional, and compositional characteristics of the forest that converge on an early successional system, dominated by increasingly short-lived pioneer species—a process commonly termed secondarization (71, 99). Such repeatedly burned systems can be highly resilient to further change owing to the combined effects of continuing post-fire mortality, reduced growth rates, susceptibility to fire of regenerating pioneer trees and resprouting stems, buildup of more flammable fuel loads (including drier litter and an increased dominance of understory grasses), and the loss of many large-bodied vertebrate seed dispersers (99).

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

3.5. Fragmentation and Isolation of Tropical Forest Landscapes

Significant parts of the world's remaining tropical forests exist as relatively small, isolated patches, embedded within dynamic agricultural landscapes. In a global analysis of intact forest landscapes, defined as areas larger than 500 km^2 and well connected to other areas of forest, Potapov et al. (67) found that in 2000 only 30% of dense tropical and subtropical forests could be defined as intact, compared with 44% for boreal forests (**Figure 1**). The situation is most severe in densely populated parts of the tropics, such as West Africa, East Africa, Madagascar, Mesoamerica, the Atlantic Forest of Brazil, the western Ghats of India, and much of Southeast Asia. For example, in the Atlantic Forest of Brazil, >80% of remaining forest areas are smaller than 50 ha (100). The rapid proliferation of forest edges is also characteristic of more recent agricultural frontiers in areas with relatively few people. By 2002, more than half of the 1.1 million km^2 of forest that comprise the arc of deforestation in the Brazilian Amazon was <2 km from an edge (101). The process of deforestation is not random, with forest remnants often confined to steeper slopes and hilltops unsuitable for agriculture, particularly in older landscapes.

Less visibly, logging operations leave behind an extensive mosaic of soft forest edges where the canopy has been perforated by a network of logging roads and timber storage areas. This network in turn provides access for hunters and new settlers (62).

The ecological effects of forest fragmentation have been a focus of intensive research for the past three decades. At the scale of individual forest patches, the composition of biological assemblages can be strongly determined by the effects of both patch size and isolation through their influence on local extinction and colonization processes (e.g., 102). These effects can often be quite subtle. Lees & Peres (103) demonstrated that gaps as small as 4 m created by roads and power lines can become territorial barriers, restricting home-range movements of many forest birds. Forest fragmentation also influences the nature and frequency of species interactions with unknown cascading effects on

long-term biodiversity persistence (104). Both patch size and isolation effects are also intrinsically linked to edge effects, which have been repeatedly shown to be a dominant driver of changes to the ecological integrity of forest remnants, including forest microclimate, plant productivity and mortality, and the composition of flora and fauna, with some effects, such as fire and increased hunting pressure, extending up to 5 km from an edge (101, 105).

Despite such clear evidence of local scale effects, the ecological consequences of forest fragmentation can only be properly understood at the scale of entire landscapes (106), meaning that spatial heterogeneity in landscape-scale characteristics can strongly influence or override any local effects. There are at least four sets of interrelated reasons for this. First, forest clearance rarely, if ever, occurs in isolation from other pressures that influence human-modified forest landscapes, and an increasing number of studies have demonstrated the exacerbating and often synergistic effects of logging, wildfires, and hunting. Second, the total amount and distribution of remnant native habitat, and the associated landscape-level species pool, strongly moderate local patterns of biodiversity. Working in the Atlantic Forest, Pardini et al. (107) convincingly demonstrated that the species-area relationship, a central tenant of ecological theory, is entirely dependent on the total amount of forest (and hence level of ecological connectivity) remaining in a fragmented landscape. Third, landscape-wide gradients of diversity, driven by underlying environmental heterogeneity (e.g., soil, topography) and biotic dispersal processes, mean that differences in the spatial distribution of forest loss and fragmentation can have profound influences on the resultant biodiversity dynamics. Finally, the type and management of the matrix of production and fallow areas between remnant forest patches are critical in determining the extent of biological fluxes (e.g., dispersal and foraging) across the wider landscape mosaic.

Despite strong theoretical expectations that many extant species in fragments are committed to extinction (the so-called extinction debt) because of depleted numbers and small ranges (108), the apparent persistence of some entire faunas in the face of widespread landscape change illustrates the tremendous difficulty in making accurate predictions about how much of this debt will actually be paid (e.g., limited butterfly extinction in West Africa to date, despite extensive forest loss and fragmentation) (109).

The fragmentation of freshwater aquatic systems invariably occurs in parallel with forest clearance and fragmentation, with often devastating yet poorly studied and even more poorly appreciated consequences. Aquatic biota are highly susceptible to effective isolation of water channels, not only from the obvious effects of damming but also from bridges, roads, and land-use change that can markedly alter the physical and chemical characteristics of the water, presenting effective barriers to species dispersal. Large-scale dam-building projects continue to present one of the major threats to the integrity of some of the world's remaining contiguous expanses of tropical forest, with more than 200 new dams planned in the Brazilian Amazon alone (110). Such massive disruption of the world's largest freshwater system would have far-reaching ramifications, including severance of nutrient connectivity with aquatic communities and marine processes thousands of kilometers away.

3.6. Second-Growth Forests

Second-growth tropical forests, i.e., those forests regenerating on land that has once been cleared, are an increasingly dominant feature of many tropical landscapes. In some regions, they comprise the vast majority of remaining native vegetation [e.g., the Atlantic Forest of Brazil (100) and Puerto Rico (111)]. Estimating the extent of second-growth forest in the tropics is fraught with difficulty owing to confounding interpretations of both primary and plantation forests in satellite imagery and their highly dynamic nature in agricultural landscapes (112).

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

Second-growth forests can recover aboveground biomass relatively quickly, with rapid rates of recovery in the first few decades, and biomass has been estimated to reach levels comparable to that of undisturbed primary forests in 80 years or less (113). However, biotic recovery occurs over considerably longer timescales than structural recovery. Although species richness may reach levels comparable to a primary forest in only a few decades, the reestablishment of old-growth specialist species (e.g., canopy trees and associated fauna) is likely to take centuries (114, 115) and the recovery of ecological dynamics, such as trophic interactions and seed dispersal, even longer.

The conservation of old-growth species in second-growth forests is maximized in areas where (*a*) extensive tracts of old-growth forest remain within the wider region; (*b*) post-conversion land use was of limited duration and low intensity; (*c*) post-abandonment anthropogenic disturbance is relatively low, and older regenerating forests have persisted; and (*d*) seed-dispersing fauna are protected (116). By contrast, multiple studies have reported that long periods of intensive use can significantly impede or arrest succession. In a Bornean rainforest landscape under long-term, shifting cultivation, biomass accumulation was significantly lower in sites cultivated six times or more because of a loss in regenerative capacity from seed banks and a loss of resprouting species (117). In the most disturbed landscapes, invasive species may come to dominate the forest canopy (118).

Despite such generalized patterns and instructive case studies, recovery trajectories of second-growth forests are anything but deterministic. Convergent trends may be apparent in changes in structural features and functional groups, but an array of unmeasured or seemingly stochastic factors can lead to idiosyncratic differences in trajectories of species composition for similarly aged stands (119, 120), undermining the generalizations that we are often tempted to draw from chronosequence work (112). Moreover, and on a more practical note, second-growth forests are highly ephemeral phenomena across much of the tropics, and many exist only as short-lived patches of fallow land (the average age of second-growth forests in the Brazilian Amazon is less than five years) (121). The difficulty of predicting processes that drive decisions around vegetation clearance makes it hard to estimate their contribution to the maintenance of viable populations of long-lived species (122).

3.7. Biotic Mixing

There has always been some transfer of species across continents through wind, water, and flying animals, and most modern tropical forest flora and fauna include descendants of individuals that have dispersed across oceans and continents over millions of years. However, the Anthropocene is leading to greatly increased connectivity and much more rapid transfer and mixing of species between previously largely isolated regions. This sometimes deliberate process also often occurs as a by-product of the sheer volume and extent of human travel and of goods transferred around the world. It has been suggested that the long-term consequences of such shifts may mark the creation of a new Pangaea (123). For the foreseeable future, however, the flora and fauna of most major tropical continents will be determined more by biogeographical history than by Anthropocene biotic mixing.

Small-island tropical forest communities are particularly susceptible to biotic invasion, given that their unique forest communities have developed from slow rates of immigration and subsequent diversification. Such forests can have high levels of endemic diversity, but a smaller breadth of ecological interactions (e.g., they lack natural enemies to keep invaders in check). A notable example is the introduction of the brown tree snake (*Boiga irregularis*) into Guam (124), probably inadvertently though cargo from Australia. Freed from predation pressure, the snake has boomed in population, leading to the extinction of virtually all the native bird, bat, and lizard species. The

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

ensuing breakdown in mutualistic ecological interactions (e.g., loss of bird pollinators) has also had a cascading effect on the reproduction of native plant species (125).

Continental and large-island tropical forest communities, with a broader range of ecological interactions, are less susceptible to invasion. Old-growth humid tropical forests have been relatively unaffected by plant invasion to date, perhaps because most introduced species tend to lack the shade tolerance necessary to invade closed-canopy forests (126). The effects of plant invasion are most evident in disturbance-prone systems, such as the dry and fire-susceptible peripheries of forests, forest edges, hurricane-prone forests in the Caribbean, and areas of secondary growth and road expansion (e.g., 76, 127, 128). Land-use intensification is likely to enhance the spread and impact of exotic species on the mainland (129), such as the case of the yellow crazy ant (*Anoplolepis gracilipes*) in oil palm plantations and agroforests (130) in Southeast Asia.

The Anthropocene has also heralded a marked increase in the dispersal of pathogens into new regions with naïve populations. This increased connectivity has also increased the potential for mixing of previously isolated strains to create new, hypervirulent strains. Fungi are particularly potent pathogens because of their broad host range and flexibility in their ability to undergo genetic recombination (131). A particularly striking example of this is the case of the skin-infecting fungus *Batrachochytrium dendrobatidis*, which has played a major role in amphibian declines worldwide, including in remote regions removed from any direct anthropogenic pressures (e.g., 132). It has probably been spread by worldwide trade in infected but disease-tolerant species, such as African clawed frogs (*Xenopus laevis*), which were used for early pregnancy tests, and North American bullfrogs (*Rana catesbeiana*), followed by spillover into susceptible species. Population genomics analyses suggest its spread has been facilitated by the generation of a globalized hypervirulent lineage (133). Effects of *B. dendrobatidis* have been particularly devastating in the tropical montane regions of Australia and the Americas. A study of an infected tropical montane region in Panama showed a loss of 40% of the amphibian species following the arrival of *B. dendrobatidis* (134). Such losses have cascading effects on stream ecosystems, driven by the loss of tadpoles that graze and restrict algal biomass (135).

3.8. Rising Temperature

One of the defining features of the current phase of the Anthropocene is the long-term rise in surface temperature, caused by the increased concentration of atmospheric greenhouse gases. Land-surface temperatures in tropical rainforest regions have risen by ~0.25°C decade^{-1} since the mid-1970s (136) and are expected to increase by 3–6°C this century (137), depending on greenhouse gas emissions scenarios and the degree of global biosphere feedback through carbon absorption or emission. In deforesting regions, warming is also exacerbated by the direct loss of tree cover, which results in a decrease in land-surface evapotranspiration and in changes in cloud formation, persistence, and reflectance (138, 139). Tropical continental regions will likely experience higher rates of warming than maritime regions, such as Southeast Asia (**Figure 1**).

An emerging area of debate and concern is the suggestion that many tropical organisms appear to have narrow thermal niches (a consequence of the stable climate of the tropics on seasonal to millennial timescales) and may be close to a thermal threshold where a moderate degree of warming would lead to a marked decline in fitness (140). Indeed, this becomes a major source of uncertainty in predicting tropical forest biodiversity responses to the Anthropocene under scenarios of warming exceeding 2°C. Simple application of climate envelope models predicts large declines of tropical diversity in a warming world, leading to biotic attrition of the lowland tropics (141, 142). Such an interpretation is potentially misleading, however, because the observed upper thermal boundary for tropical lowland species may simply reflect the maximum observed

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

temperature, rather than provide any insight into fundamental niche boundaries (143). That said, if many tropical forest species are indeed close to a thermal limit, lowland tropical forests could be set to experience widespread species losses. Indeed, laboratory studies of the thermal fitness curves of insects, lizards, and birds suggest that many tropical organisms do have narrower thermal niches than closely related temperate organisms and would likely exhibit declines in fitness as a result of a few degrees of warming (144). By contrast, paleoecological evidence shows that tropical forests clearly persisted and, in at least some cases, had higher biodiversity in warmer periods of the Cenozoic (145). In fact, many modern tropical tree taxa have their origin in the mid-Miocene (15 Mya) when temperatures were ~3°C warmer, suggesting that they may be able to tolerate higher temperatures than they currently experience (146).

A critical aspect of the effect of rising temperatures is the pace of warming (2–4°C century^{-1}), which is thought to be one to two orders of magnitude faster than previous periods of rapid tropical warming. Such previous periods include the Paleocene-Eocene thermal maximum warming event, when the world warmed by ~5°C over 10,000–20,000 years (145), and the end of the last glaciation, when the tropics warmed from a cooler state at about 1°C per millennium (147). The anticipated Anthropocene pace of warming means that long-lived organisms, such as trees, will experience several degrees of warming within a single lifetime. Organisms and communities can respond to warming through physiological acclimation, behavioral change (for fauna), evolutionary adaptation (for high generation turnover species), or, if these previous responses are insufficient, through migration and dispersal. However, migration and dispersal are challenged by the high velocity of climate change (~1–10 km decade^{-1}) (148) in the lowland tropics, where latitudinal temperature gradients are particularly shallow or even nonexistent (149). As a consequence, tropical montane regions may play a particularly important role as potential refugia for heat-intolerant species, although low mountains may also be potential traps as retreating islands of cool in a warming tropical world. Field studies in tropical mountain transects suggest that there has been an upward shift in mean species distributions of trees and insects (142, 150), although this may be driven more by attrition at low elevations than by immigration at high elevations (151). Ultimately, the realized thermal niche of many organisms is probably determined more by biotic interactions (e.g., competition, predation, pollination) than by direct ecophysiological thresholds. For example, if a plant pollinator cannot adapt to higher temperatures, the host plant would undergo a decline in fitness irrespective of its ability to acclimate its own physiology. The long-term consequences of such changes in ecological interactions remain poorly understood.

3.9. Rising Atmospheric Carbon Dioxide

In addition to its role as a greenhouse gas, atmospheric CO_2 is a direct agent of Anthropocene change. Atmospheric CO_2 has risen from preindustrial concentrations of 280 parts per million (ppm) (and Ice Age concentrations of ~230 ppm) to ~400 ppm in 2014 and is expected to rise to 600–1,000 ppm by 2100 under the most likely emissions scenarios. CO_2 is a raw material for photosynthesis, and a key question in understanding Anthropocene change is whether plants, and which types of plants, will be able to take advantage of CO_2 fertilization to enhance productivity and also to act as a global sink of atmospheric carbon.

Most global biosphere models assume a CO_2 fertilization response and predict enhanced tropical productivity in a high-CO_2 world (152). Such a response may be greater in the tropics than at high latitudes because of greater sensitivity of photosynthesis to CO_2 at high temperatures (153). First-order ecophysiological sensitivity studies suggest that high atmospheric CO_2 has increased tropical forest productivity by 18% from preindustrial values and would increase it by a further 60% under a scenario of 800 ppm atmospheric CO_2 in 2100 (5). High atmospheric CO_2 may

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

offset other climate change factors and enhance the resilience of the tropical biome as a whole (152). However, a key uncertainty is whether plants can sufficiently use such an abundance of CO_2 by increasing availability and access of other limiting factors such as nutrients. Phosphorus, in particular, is thought to be limiting in many tropical forest soils, and phosphorus supply is not yet incorporated in any global biosphere model. In addition, some model studies suggest that elevated CO_2 may not increase net rates of photosynthesis but rather merely compensate for the effects of higher leaf-to-air vapor pressure deficits that occur at higher temperatures (154, 155). By contrast, elevated CO_2 may also increase water-use efficiency and decrease seasonal water stress (156, 157).

Field observations from long-term plot networks across Amazonia and Africa have suggested increases in tree growth rates and biomass in recent decades, potentially caused by increasing CO_2 (158, 159), although the influence of recovery from both stochastic and past large-scale disturbances on observed increases of biomass has been debated (160, 161). Such an increase in tropical forest biomass carbon has consequences for global climate by slowing down by about 15% the annual rate of atmospheric CO_2 increase (162). A key additional feature of these results has been the observation of increasing turnover (decreasing tree life span), suggesting that the most significant long-term consequence of any CO_2-driven increase in growth rates may be increased ecosystem dynamism rather than increased biomass (163).

Increased CO_2 may alter the competitive balance of forest communities, as some taxa or functional groups are able to exploit higher CO_2 at the expense of other taxa, thus changing the reproduction, recruitment, and mortality patterns that ultimately drive forest species composition (164). One notable instance of such a change is the observed increase in dominance of tropical lianas (also linked to fragmentation, fire, overhunting, and other disturbances) and the accompanying increase in tree mortality as canopies struggle to compete for light (165). Shifts in dynamism and community composition would also cascade through higher trophic levels to affect patterns of plant defense, herbivory, frugivory, and forest habitat quality. Our understanding of the effects of increased CO_2 on ecological interactions (as opposed to directly on ecophysiology alone) remains very poor, yet changes to such interactions may be more important than changes in ecophysiology in shaping the composition of tropical communities in a high-CO_2 world.

In addition to changes in CO_2, other changes in atmospheric composition and chemistry are likely to have effects, especially in areas close to urban, industrial, transport, or fire activity. For example, increases in nitrogen dioxide concentrations lead to increased nitrogen deposition and supply, possible acidification, and ozone formation near forest canopies (166). Although potentially important, the effects and scale of such changes on tropical biogeochemistry, physiology, and competitive balance are very poorly understood.

3.10. Changes in Tropical Precipitation and Cloudiness

The two primary Anthropocene drivers for changes in patterns of tropical precipitation and cloudiness are changing atmospheric composition and changing regional vegetation cover. Global climate change is increasing the moisture and convective energy in atmospheric circulation because of enhanced evaporation from warmer oceans. Climate models consistently predict a net increase in global precipitation but also intensified spatiotemporal variability of rainfall, with more intense dry seasons and stronger, more frequent droughts. There is less climate model agreement on which regions will see net reductions in total rainfall, as such patterns are driven by regional patterns of change in tropical sea surface temperatures, which are hard to predict. Rainforest regions susceptible to reductions in dry-season rainfall include Central America, eastern Amazonia, West Africa, and peninsular Southeast Asia (**Figure 1**) (137). Vegetation cover change affects

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

precipitation patterns by altering the amount of water returned to the atmosphere via transpiration through deeper-rooted trees (167). Such recycling can account for >50% of rainfall in western Amazonia and western tropical Africa (168). Additionally, forest loss tends to increase the dustiness, smoke haze, and aerosol content in the atmosphere, leading to a decrease in cloud droplet size and changes in the duration of clouds and the intensity and frequency of precipitation. There is already direct, observational evidence of changes in the tropical hydrological cycle: The tropics as a whole have become more seasonal and unpredictable in rainfall patterns (169), and Amazonia has experienced intensified wet and dry years (170), as well as a long-term increase in the dry season along its southern fringe (171). Because the tropics are the engines of the global atmospheric circulation, changes in tropical land cover can also feed back to affect global atmospheric circulation and precipitation patterns in midlatitudes—an example of the global entanglement that is characteristic of the Anthropocene.

There is significant concern regarding the response of tropical forests to severe drought. Possible Amazon forest dieback has become one of the iconic tipping points in the Earth system, although recent studies have suggested that such a scenario is based on oversensitive climate and vegetation models (152) and that any tipping point in the Amazon system is likely to come only from the synergistic effects of climate and land-use (particularly fire) change (96, 136). Research on drought has benefited from a range of observational and experimental approaches from the scale of the plant to that of the landscape. Two large-scale rainfall exclusion experiments in Brazil have demonstrated that large trees are particularly vulnerable to drought (172), and field surveys across Amazonia following the 2005 drought demonstrated a widespread increase in tree mortality and a decrease in rates of carbon sequestration (158). The extent to which tree mortality during drought is driven directly by hydraulic failure, by access to carbon (e.g., nonstructural carbohydrates) for metabolic processes, or by the interaction of the two is poorly understood (173). Although the mechanisms are unresolved, changes at the individual and community scales clearly affect ecosystem processes, particularly with respect to above- and belowground components of biogeochemical cycling: Drought reduces carbon sinks (158), changes aboveground nutrient cycling (174), and alters stand transpiration and thus the return of water to the atmosphere (175). Cloud cover patterns also affect ecosystem processes by mediating changes in both the quantity and quality (direct versus diffuse) of light (176). Even though much research has focused on trees, it is also important to consider the direct effects of drought on other tropical biota and on key biotic interactions, such as herbivory, pollination and pathogen pressure (177).

4. TROPICAL FORESTS IN THE ANTHROPOCENE: TRAJECTORIES OF ENVIRONMENTAL CHANGE

None of the world's tropical forests are free of human influence. Large swaths of tropical dry and wet forests have already been converted to agriculture, and frontier forests across the world are highly fragmented and typically subject to high levels of extraction of both timber and nontimber resources, as well as being increasingly susceptible to fire and invasion by exotic species. Even the more remote forests typically lack their full complement of large vertebrates and associated ecosystem processes such as large seed dispersal. Pervading the entire tropical realm is a process of ongoing and projected atmospheric change and its cascading influence on species growth, mortality, and distribution through changes in temperature, rainfall patterns, and atmospheric chemistry. As we navigate the early Anthropocene, we bear witness to a world where the effects of human activities on the tropical biosphere are undergoing a rapid change not only in their extent and rapidity, but also in their interconnectedness—with the legacy of human influence in one place being borne out in distant places as well as over decades and centuries to come.

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

In the context of such pervasive human influence, the future of tropical forests, like so many elements of the Earth system (178), stands at something of a crossroads. Choices made regarding the local, regional, and global stewardship of these biomes in the coming few decades are likely to be critical in determining the efficacy and feasibility of future management and, hence, longer-term trajectories of environmental change. Understanding what choices are available first requires understanding the complex interplay of multiple drivers that have been reviewed here.

4.1. Divergence and Convergence of Tropical Forests in the Anthropocene

As the preceding sections have demonstrated, human influence is resulting in myriad environmental responses in tropical forests worldwide. Understanding the combined and interacting effects of these different drivers, operating heterogeneously across different scales, is aided by consideration of five emergent observations.

Observation 1: Drivers of environmental change manifest very differently in different parts of the tropics. This is the result of several factors. Biogeographical history matters. For example, logging intensities are particularly high in Southeast Asia, where the dominance of high timber-yielding dipterocarps is a peculiarity of Earth's tectonic and ecological history. Also, previously isolated tropical islands are particularly susceptible to biotic invasion. Human prehistory and history matter because differences in human history (population collapse and colonial history) have resulted in lower present-day rural population densities in Amazonia than in Africa and Asia, and differences in prehistory (hominid and human dispersal from Africa) may have resulted in higher remaining pre-Anthropocene animal biomass in Africa and Asia than in other regions. The resulting variation in rural population density and animal biomass is largely responsible for higher levels of fuelwood and animal biomass extraction in much of Africa and rural Asia than, for example, in Amazonia. Human cultural factors matter as these vary geographically, with some traditional and modern cultures placing higher value than others on maintaining forest cover and placing taboos or cultural preferences on consuming bushmeat. Physical geography matters because increased spatial and temporal rainfall variability and land-atmosphere feedback effects from changing patterns of land use have resulted in uneven patterns of both drought and flooding. Finally, economic and political factors matter inasmuch as economic drivers, governance, conflict, and management responses themselves are highly variable in space, as evidenced, for example, by the uniquely rapid decline of deforestation rates in Brazil during the past decade and the lack of extensive deforestation to date in the Congo Basin.

Observation 2: Drivers of environmental change rarely, if ever, operate in isolation. Feedbacks, dependencies, and synergistic effects among drivers are commonplace. In more severely modified forest landscapes, they may be the norm rather than the exception (179). Logged forests are frequently also hunted, and fragmented forests are invariably more prone to fire, logging, and hunting. Because of the spatially and temporally heterogeneous nature of such interaction effects, the impact of a particular driver is likely to be especially pronounced in specific landscapes or moments in time. For example, tropical forest wildfires very rarely occur in isolation from other drivers. Instead, increases in fire frequency and intensity commonly result from the juxtaposition of multiple exacerbating pressures, including increased flammability owing to selective logging and fragmentation, the spread of ignition sources from agricultural expansion and road building, and increased forest flammability and physiological stress during periods of severe drought (96, 180).

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

Observation 3: Regional differences in historic forest conditions can strongly mediate biotic resilience to forest disturbance, land use, and climate change. Such regional differences have emerged over evolutionary timescales and can result in similar disturbances having strikingly divergent ecological consequences (181). The resilience of regional biota can be conditioned by a variety of factors, including differences in the relative stability of biome extent during the Pleistocene and Holocene; the frequency of natural disturbance events, such as hurricanes and fire; and seasonality. As such, species from areas that have been subject to high levels of past climate variability (e.g., Central Africa compared with Amazonia), frequent disturbances, and/or distinct seasons may be more tolerant to the increasing human-induced variability in climate and land use during the early Anthropocene (31). Other emergent properties of historical differences in biophysical and climate conditions are that some areas are more species rich (e.g., northwest Amazonia or Borneo) and that some have higher levels of endemism (e.g., Madagascar or small tropical islands, and montane tropical forests, such as the Andes and Eastern Arc Mountains in Africa) than others. By simple virtue of having more species and/or more endemic species such areas may suffer concomitantly higher biodiversity impacts.

Observation 4: Drivers of environmental change, and responses to such change, can often have larger-scale and distant effects. It is well known that changes in socioeconomic conditions in one location can have marked consequences for land use elsewhere (182). Similarly, the modification of one area of tropical forest can have cascading effects on biophysical processes and biodiversity persistence in another. This can happen at multiple scales. Locally, the persistence of many forest species in fragmented landscapes depends on access to key food resources and breeding habitat that, owing to high spatial heterogeneity in habitat, may exist only in separate patches (183). At larger scales, tropical forest cover can have a pronounced effect on regional and even global climates through changes in energy balance, transpiration, and atmospheric aerosol load. For example, extensive forest and savanna clearance around eastern Amazonia can affect rainfall patterns across Amazonia, and vegetation-atmosphere feedbacks could decrease rainfall in some regions past a tipping point to a permanently drier state (184).

Observation 5: The full ecological consequences of environmental change and disturbance are never immediate and instead play out through cascading effects on species interactions that can last for centuries, if not millennia. Such delayed effects can have severe mediating or exacerbating consequences for the implications of any future disturbance or management intervention (181). Yet we are only starting to understand the long temporal shadow of many human impacts on the ecology of tropical forests, including impacts from changes in fragmentation, logging, faunal communities, and fire (68, 185, 186). A multitude of subtle changes in species interactions can have potentially severe legacy effects on myriad biological interactions and ecological processes, such as herbivory, predation, dispersal, productivity, and decomposition. These cascading effects resound across all areas of forest ecology and can lead to profound and long-term shifts in species composition (16, 68, 79). It is possible that many tropical forests and drier biomes are still responding to the distant echo of megafaunal extinctions in the late Pleistocene following potentially drastic reductions in the nutrient transport and large seed dispersal functions once performed by these animals across tropical landscapes (17). If such predictions are true, then this loss of nutrient transport could have had cascading effects on nearly all aspects of forest ecosystems, from composition and productivity to interactions in soil and communities of natural enemies (61, 79). If we consider a different aspect of Anthropocene-induced changes, the response of tropical forests to atmospheric change has been treated and modeled primarily as an issue of ecophysiological response to abiotic climate and CO_2 drivers. In fact, it is likely that biotic interactions

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

(e.g., tree and liana competition for light and the consequent effects on tree turnover rates, or the impact of higher temperature and drought on predation, pollination, and dispersal, as well as on pathogen and soil microbial communities) will play a more important role in determining long-term shifts in forest structure, function, and species composition.

Taken together, these observations give rise to several implications regarding the opportunities and challenges facing the future stewardship of these biomes.

Implication 1: The heterogeneity of many partially disturbed tropical landscapes can help maintain critical ecological resilience. The manifold human influences acting on forests, coupled with differences in underlying environmental gradients, have resulted in many modified tropical forest landscapes being best characterized as highly heterogeneous mosaics. Indeed, it is often impossible to talk meaningfully about logged versus nonlogged or burned versus unburned forest because the effects of disturbance vary enormously in extent, timing, and intensity and very rarely occur in isolation (e.g., 45, 71). Even small initial differences in disturbance regimes can precipitate marked and cumulative divergences in species composition and ecosystem functioning of different landscapes through time (72). The consequence of such heterogeneity is that ecological resilience can be temporarily maintained (pending further and more severe disturbances): Different compositional and functional tropical forest elements may be locally impaired or extinct yet persist in other places—thus providing opportunities for both ecological recovery, through either natural (passive) processes or strategic interventions, and adaptation to a changing climate.

Implication 2: Multiple, severe, and compounding disturbances can lead to highly simplified and homogeneous landscapes. Such landscapes can become highly resilient to further changes, thus impeding attempts to promote recovery. Tropical forests abound with examples of such shifts toward alternate and often highly stable states, including changes in faunal communities (74), severe fragmentation and prolonged edge effects (76), repeat burnings (99), domination by pioneer species in logging gaps (187), landscape-wide deforestation and the loss of connectivity (107), domination by invasive plant and animal species (127), and the overextraction of fuelwood (41). Common to all these situations is the presence of positive feedback dynamics driving a system from one state to another and of the additional feedbacks that hold the system in a state of persistent degradation, such as the invasion by highly flammable understory trees and grass species in burned areas or the disruption of key interactions (e.g., the erosion of recolonization processes) in highly deforested landscapes. Feedbacks can also operate at regional and even global scales; e.g., regional deforestation can reduce downwind precipitation to a degree that precludes persistence of humid forest vegetation. Many severely degraded landscapes are typically dominated by early successional species and lack functionally important elements that are necessary to support any future attempts to promote ecological recovery. As such, the management effort needed to turn around positive feedback cycles and reintroduce depleted elements can quickly become prohibitively expensive.

Implication 3: Most tropical forests of the early Anthropocene are altered ecosystems or are on a trajectory to become them. This review has demonstrated that most remaining areas of forest, save for the last tropical wildernesses, have experienced a notable loss or gain of key taxa, caused by local extinctions or invasions, the creation of dispersal barriers, or changes to system productivity that alter the relative abundance of resident biota. Given global changes in climate, CO_2, and biogeochemical cycling of key nutrients, the trajectory of forest change in even the most remote wilderness regions is toward increasing divergence from pre-Anthropocene conditions. As

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

we have seen, many disturbed forest landscapes continue to host diverse biological assemblages and support key functional processes. They also offer unquestionably better prospects for the recovery of regionally depleted and ecologically extinct biota than areas completely transformed to agriculture. Nevertheless, an increasing number of disturbed forests are characterized by species assemblages and biotic interactions that are unlikely to have evolutionary precedents, underscoring the difficulty in estimating the possible cascade effects and secondary extinctions.

In contemplating the range of diversity of human-modified tropical forests that exist today, we can identify a mosaic of (*a*) relatively undisturbed forest landscapes with a full complement of biodiversity and ecological interactions, removed from most direct anthropogenic influence yet still subject to the effects of climate and atmospheric change, the reduction of some large animal populations and the introduction of novel pathogens and species; (*b*) highly variegated landscapes where the varying impact of different disturbances has allowed much biodiversity to persist, albeit with reduced distributions and altered ecological interactions; and (*c*) highly simplified, homogeneous landscapes where multiple, severe disturbances have led to severe biodiversity loss, functional extinction, and a convergence in the biotic composition of remnant forests. Depending on the region in question and the amount of native vegetation remaining, all three systems have critical roles in safeguarding the future of tropical forests.

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

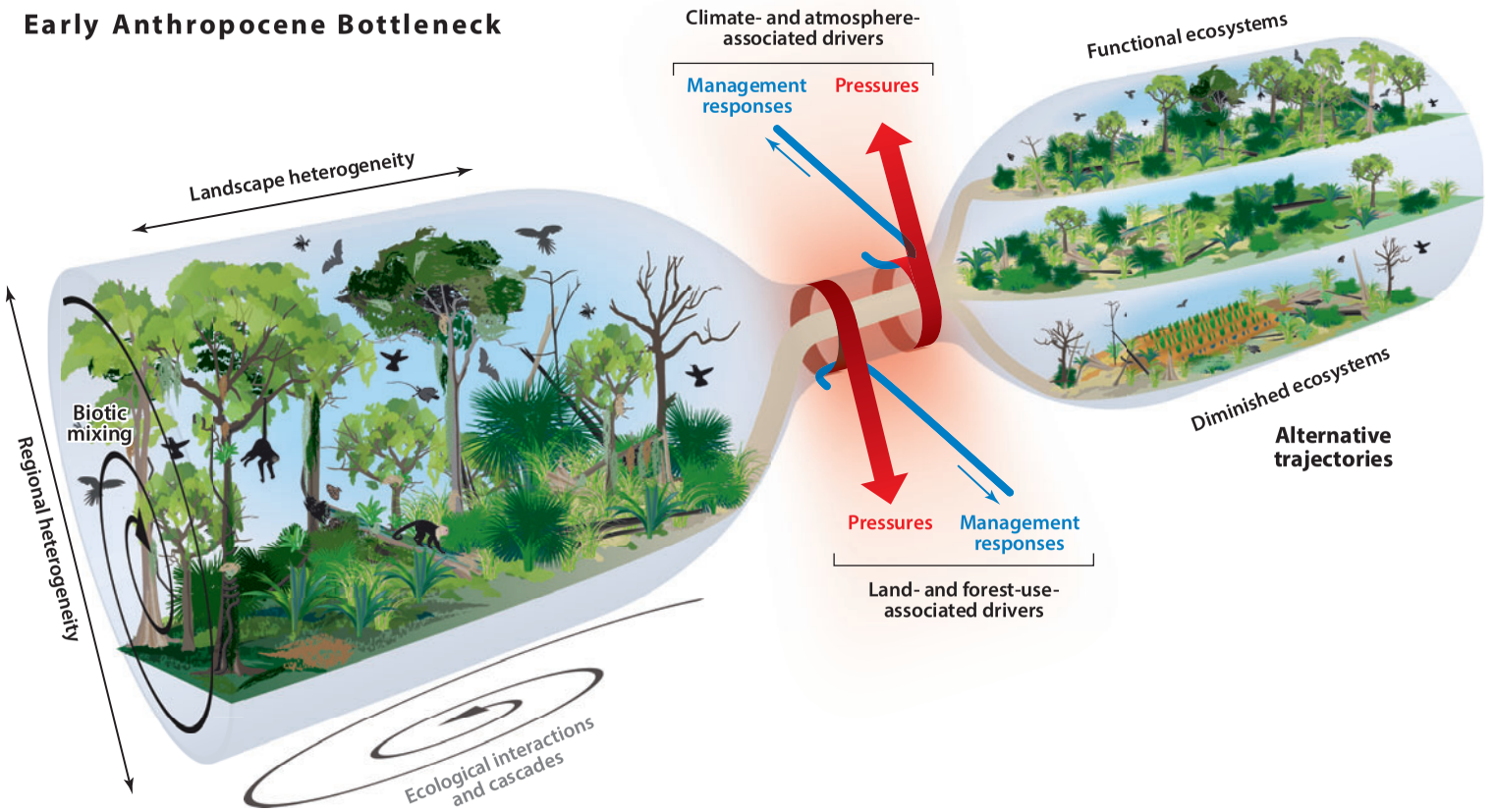
4.2. Shaping the Transition of Tropical Forests Through the Early Anthropocene

There are many utilitarian reasons for protecting tropical forests, and some of these have been outlined above. Yet we must also not lose sight of the fact that tropical forests merit attention as the most exuberant celebration of the miracle and diversity of life on Earth. This rich tapestry of life can be an incalculable source of wonder and discovery for untold generations to come. As we navigate the early Anthropocene, we are faced with a clear yet narrowing window of opportunity within which we can still play an effective role in positively influencing the future trajectories of this magnificent biome.

Despite widespread deforestation and forest degradation, relatively few tropical forest species are known to have gone globally extinct (although estimates of global extinctions are nothing more than educated guesses). Moreover, the heterogeneous nature of disturbance means that many modified forest ecosystems retain sufficient ecological resilience such that—should humanity succeed in making an eventual shift toward a stabilizing climate and atmospheric composition and a more judicious governance of natural resources—they are capable of retaining their current diversity and recovering most, if not all, of their depleted elements. Yet the potential for such a change depends critically on our ability to limit the severity and duration of the bottleneck that tropical biomes are currently passing through (**Figure 2**). The more species that are lost and the more ecological processes that are disrupted or altered, the harder and more costly it will be and the longer it will take to recover the diversity that we cherish and on which we depend. A failure to act now, and to implement a more sustainable approach to the stewardship of these ultimately fragile biomes will severely compromise the effectiveness of conservation efforts of generations to come and will precipitate unpredictable yet potentially significant consequences for the evolutionary trajectories of surviving biota.

Averting the worst effects of this bottleneck requires concerted effort across three main fronts. First, increased protection and incentives are needed to preserve the remaining areas of relatively intact forests as the only sources of recolonization for species that have been lost from elsewhere and as a vital source of comparative information for understanding the significance of changes in more disturbed areas. Second, renewed efforts are needed to stem continued deforestation

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.



through improvements in tropical agriculture and forest management systems and through improved monitoring of forest frontiers. Vast swaths of varyingly fragmented and disturbed forest in older landscapes and frontier regions urgently need proactive management to avert further pressures. Such management includes the avoidance of repeated logging cycles, wildfires, and reduction of hunting pressure, as well as efforts to rehabilitate degraded areas and avoid large-scale feedback effects, such as local and regional reductions in precipitation. These forests often provide the only serious prospect for biodiversity persistence and the maintenance of key ecosystem processes in parts of the world with little structurally intact forest remaining (e.g., West Africa or many parts of Southeast Asia). Yet they are often disregarded by conservation agencies and remain highly vulnerable to further degradation and clearance (e.g., 188). Third, opportunities for large-scale restoration of native forest on marginal and abandoned agricultural land following large-scale rural-urban migration need to be carefully nurtured. There is some evidence for such forest transitions already occurring in some tropical nations [e.g., Puerto Rico and Costa Rica (189, 190)]. However, it cannot be viewed as a passive process because continued and rising demand for agricultural commodities, such as palm oil, can drive deforestation even in areas with very low population densities and low soil fertility (191). Restoration is a particularly urgent priority for regions where tropical forests currently occupy a mere fraction of their pre-Anthropocene extent (e.g., much of Southeast Asia, the Atlantic Forest of Brazil, Mesoamerica, West Africa, and the Eastern Arc Mountains of East Africa). Moreover, in a world very likely to experience several degrees of warming, the restoration and maintenance of ecological connectivity between remnant areas of forest are critical in allowing species distributions to shift in accordance with changes in climate (192).

One consistent observation from all areas of study of tropical forest responses to Anthropocene changes is that drivers of change affect species in many different ways, with the result that future trajectories are difficult to predict. Moreover, given the complexity of the Earth system, it is unlikely that we will ever acquire the information needed to make precise predictions of ecosystem change. Therefore, it is critical that we focus investigation and conservation efforts on making forest systems resilient, even in the face of unknown changes and hidden nonlinearities (193). Central to this challenge is the need to preserve not only species but also species interactions, as well as to maintain communities with large portfolios of functional types so they are buffered against change.

Figure 2

The early Anthropocene bottleneck and the future of tropical forests. The composition, condition, and dynamics of future tropical forest landscapes will be largely determined by the size of the bottleneck that forests are experiencing. The severity and duration of this bottleneck, influenced by the current state and heterogeneity of tropical forests and ongoing pressures and management responses, will lay the groundwork for how viable and effective future management actions are likely to be in restoring and conserving native biota and ecological interactions, and hence will influence the likely trajectories of environmental change in tropical forests around the world. Pressures (*red belts*) include both interacting land- and forest-use-associated drivers (including forest clearance and fragmentation, overexploitation of natural resources, and fire), exacerbated by the effects of biotic mixing and cascading species interactions, and coupled with atmosphere- and climate-associated drivers (including increasing temperatures, CO_2 concentrations, and changes in precipitation patterns). These are offset by management interventions (*blue books*) that act to avoid and mitigate ongoing pressures (e.g., through reduced deforestation, responsible forest management, global climate change mitigation) and to rehabilitate degraded areas (e.g., through restoration and enrichment plantings, landscape connectivity, invasive species eradication) to maximize the biological and functional diversity, and therefore long-term ecological resilience, of human-modified landscapes. Our ability to maintain the resilience and diversity of tropical forests around the world depends critically on our ability to foster multiple transitions in the way in which these forests are exploited, managed, and restored—thus avoiding severe bottlenecks, turning around positive feedback cycles of environmental degradation, and facilitating the recovery of elements that have already been depleted. A high-resolution version of the figure is available at **http://dx.doi.org/10.6084/m9.figshare.1018765**.

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

Averting a severe and protracted bottleneck in the degradation of tropical forests, while ensuring that protected and restored forests are safeguarded in the long-term, requires a concerted and coordinated effort across all of these fronts and at multiple spatial scales. The continued loss of forests across the tropics (27), coupled with the pervasive threats described in this review, including climate change–induced shifts in species distributions and the specter of major new infrastructure projects in some tropical forest regions (e.g., massive dam-building plans in the Amazon Basin), illustrates that there is no room for complacency. Nevertheless, conservation success stories can be found across the tropics, including the sharp decrease in deforestation rates in Brazil since 2004, a major increase in the coverage of protected areas (with a disproportionately greater increase in tropical nations compared with richer countries in the northern hemisphere) (194), large-scale passive regeneration of forests in abandoned agricultural areas across the world (189), and a limited expansion in the area of native tropical forests that are considered to be under sustainable management (with an increase of 20% between 2005 and 2010) (195). Such evidence demonstrates that it is indeed possible to turn around historically negative trajectories.

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

4.3. The Challenges Facing Tropical Forest Science

The early Anthropocene heralds an era of profound environmental change in tropical forests that is unprecedented for possibly millions of years. Understanding the nature, dynamics, and implications of these changes—and hence where interventions through policy, conservation, and management can assist in adapting to new situations and in recovering from undesirable states—sets the challenge to which the tropical forest science community must rise. The extent of our current understanding, when confronted with such dynamic and complex systems, is severely lacking on multiple fronts. Our review has argued that there is a need to better encompass the geographical and ecological heterogeneity and history of Anthropocene tropical forests and that there are large differences across regions in both the drivers of change and the likely ecological responses to change across regions. Yet the vast majority of environmental research on tropical forests to date is focused on relatively undisturbed areas and is heavily biased toward certain regions, especially the tropical Americas, particularly Mesoamerica (**Figure 3**), although even in these areas investigative effort is typically concentrated in a small number of research stations (181). Of the major tropical forest regions, Africa especially is woefully understudied. Research that addresses an aspect of Anthropocene change (which represents just under half of papers on tropical forest science published between 2009 and 2013; see **Figure 3**), has largely focused on structural disturbance and climate change, with little attention to understanding the importance of ubiquitous interaction effects among disturbances, particularly those caused by faunal disruption. Seasonally dry tropical forests are also greatly understudied compared with humid forests, despite being more affected by most aspects of Anthropocene change. There is also a need to expand our temporal scale by incorporating a long-term understanding of the histories and prehistories of different tropical forest regions to better understand how such history influences contemporary drivers and responses to change. That said, important new advances in scientific methods and technologies, information access, and organizational capacity and vision offer the potential for significant improvements in the contributions science can make to improving our understanding, and hence ability to govern, tropical forests in the coming decades.

To capitalize on this momentum, the tropical forest natural science community, in partnership with colleagues across the social and political sciences and stakeholders at all levels, has both the opportunity and the need to deliver significant progress in several broad directions: (*a*) the expansion, improved coordination, and long-term support of data collection, as well as the long-term monitoring efforts across broad gradients of disturbance and environmental heterogeneity to

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

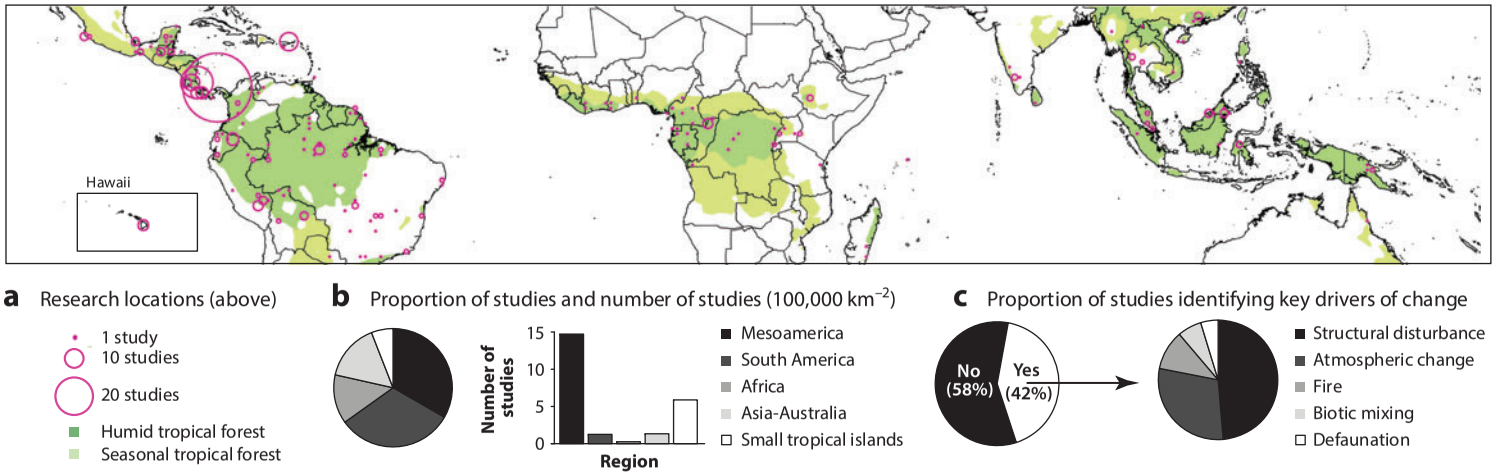


Figure 3

The location and focus of recent research in tropical forests. (*a*,*b*) A map of recent (2009–2013) field studies in the tropics reveals the dominance of research from the Americas (~65% of the studies) relative to Africa (~13%), Asia-Australia (~16%), and small tropical islands (~6%). Mesoamerica (~33%) is subject to considerably more study relative to its land area than other regions, with the 15 km^2 Barro Colorado Island in Panama accounting for ~10% of all field studies. (*c*) From a thematic perspective, most recent studies (~58%) do not possess topic words indicating a focus on key drivers of environmental change in the Anthropocene. Where they do, this research focuses largely on either structural disturbance to the forest (e.g., deforestation, logging, fragmentation; ~49%) or atmospheric change (e.g., CO_2, temperature, precipitation; ~29%). Fire, biotic mixing, and defaunation together account for ~22% of the studies. Field study locations were identified from all papers with tropical forest* in the topic words through a search on Thomson Reuters's Web of Science for the journals *Biotropica*, *Conservation Biology*, *Ecology*, *Global Change Biology*, and *Journal of Tropical Ecology* (n = 321 articles, ~7% of all possible articles) between 2009 and 2013 following the methods of Pitman (197). Research themes in panel *c* were identified from all papers with tropical forest* and other topic words related to key drivers of change in the Anthropocene through a search on Thomson Reuters's Web of Science for all available journals (n = 4,982 articles) between 2009 and 2013. Underlying data are available at **http://dx.doi.org/10.6084/m9.figshare.1018762**. A high-resolution version of the figure is available at **http://dx.doi.org/10.6084/m9.figshare.1017333**.

inform recommendations at scales relevant to management and to permit the scaling up of more detailed, site-based, and experimental work; (*b*) resolution of key uncertainties in biodiversity responses to global climate change, particularly an in-depth focus on the understandings of plant and animal responses to changes in temperature; and (*c*) improved utilization of new technologies, such as advanced airborne and space-borne remote sensing, cheap DNA sequencing, and bar coding that permits rapid species identification and deep-time evolutionary insights into responses to contemporary change. These new technologies should be integrated with ground observations, improved data access (most vitally in tropical nations themselves), and data management tools to understand change at sufficient scales and at rapid enough timescales to facilitate awareness, advocacy, policy, and management responses. Progress is also needed in following areas: (*d*) the connection of understanding and interpretations of past changes with current observations and future projections; (*e*) understanding the cascading effects on species interactions and forest ecology that are precipitated by the loss or depletion of functionally important flora and fauna; and (*f*) improved integration of individual scientists and groups into connected research networks to facilitate the rapid and effective exchange of ideas, knowledge, and technical capacities. Critical to this challenge is the need to dramatically increase opportunities for local capacity building and scientific leadership of research networks in tropical nations. The open-access Global Forest Cover Change Project is a superb example of what is becoming possible (27), bringing together the recent open availability of Landsat imagery with advances in cloud computing to provide open-access, global, high-resolution maps of forest cover change on an annual basis.

In conclusion, this review has demonstrated the multifaceted and complex nature of the changes being experienced by tropical forests. There is much that we do not know about the future state of the tropics, and we may never know as much as we would like. However, in broad terms, it is virtually inevitable that all the forest systems emerging from the early Anthropocene will be altered in their composition and functioning in some way. Yet the widespread and long-lasting loss and degradation of tropical forests are not inevitable. It is conceivable that the tide of Anthropocene pressures will begin to recede, especially where the pressures are linked to rural population density, poor governance, inadequate monitoring capacity, and unsustainable economics. At the global level, there is still an opportunity to chart a course toward less carbon-intensive economies and to mitigate against the more devastating effects of climate change. What types of tropical forest biomes emerge through this early Anthropocene bottleneck, and how narrow and protracted the bottleneck is, depend on the science, policy, and management decisions that are implemented now.

SUMMARY POINTS

1. Tropical forests across the world are changing owing to a diverse array of drivers, including clearance and fragmentation for agriculture, unsustainable exploitation and defaunation, increased prevalence and intensity of wildfires, rising temperatures and carbon dioxide concentrations, and altered precipitation patterns. Multiple drivers invariably operate in unison and play out in different combinations and intensities across the tropical realm.
2. The species composition and ecosystem functioning of many tropical forests are becoming altered in response to local and regional extinctions, shifting species abundance distributions, and the cascading effects of invasive species, including the impacts of pests and pathogens that often lack natural enemies in their new environments.

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

3. Tropical forests are highly dynamic systems. The effects of human activities today are mediated by legacy effects of past disturbance regimes that play out across ecological and evolutionary timescales to determine the nature and resilience of contemporary biota. Ongoing changes in the structure, composition, and function of forests can have profound effects on future trajectories of change.
4. The spatially discrete nature of human-associated disturbances and associated ecological cascades mean that modified tropical forests often appear as highly heterogeneous mosaics. This heterogeneity confers vital ecological resilience by maintaining connectivity and providing refugia for source populations.
5. Globally, the nature and extent of human impacts on tropical forests determine the size and longevity of a bottleneck that is central to determining the fate of tropical forest biodiversity and functioning in the Anthropocene.

FUTURE ISSUES

1. Natural sciences have vital roles to play in mitigating the severity of the Anthropocene bottleneck on tropical forests by helping prioritize and guide effective conservation strategies.
2. Addressing these challenges requires a focus on the study of disturbed and regenerating forests, neglected geographic regions, and the structures necessary to foster collaborative and multidisciplinary work across multiple scales.

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

Y.M. is supported by the Frank Jackson Foundation and an Advanced Investigator Award of the European Research Council (ERC). G.R.G. is supported by the ERC. M.R.S. is supported by the National Science Foundation Division of Environmental Biology (Grant No. 1416357) and the Blue Moon Fund. T.A.G. is supported by Formas (Grant No. 2013-1571). We are grateful to Greg Asner, Robin Chazdon, Bill Laurance, Oliver Phillips, John Terborgh, Joe Wright, Tereza Cavazos, and Tom Tomich for their thoughtful and helpful reviews of this manuscript.

LITERATURE CITED

1. Crutzen PJ. 2002. Geology of mankind. *Nature* 415(6867):23
2. Steffen W, Grinevald J, Crutzen P, McNeill J. 2011. The Anthropocene: conceptual and historical perspectives. *Philos. Trans. R. Soc. A* 369(1938):842–67
3. Smith BD, Zeder MA. 2013. The onset of the Anthropocene. *Anthropocene* 4:8–13
4. Steffen W, Crutzen PJ, McNeill JR. 2007. The Anthropocene: Are humans now overwhelming the great forces of nature? *AMBIO* 36(8):614–21

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

5. Malhi Y. 2012. The productivity, metabolism and carbon cycle of tropical forest vegetation. *J. Ecol.* 100(1):65–75
6. Pimm SL, Raven P. 2000. Extinction by numbers. *Nature* 403(6772):843–45
7. Corlett R, Primack R. 2006. Tropical rainforests and the need for cross-continental comparisons. *Trends Ecol. Evol.* 21(2):104–10
8. Parmentier I, Malhi Y, Senterre B, Whittaker RJ, Alfonso Alonso ATDN, et al. 2007. The odd man out? Might climate explain the lower tree α-diversity of African rain forests relative to Amazonian rain forests? *J. Ecol.* 95(5):1058–71
9. Eriksson A, Betti L, Friend AD, Lycett SJ, Singarayer JS, et al. 2012. Late Pleistocene climate change and the global expansion of anatomically modern humans. *Proc. Natl. Acad. Sci. USA* 109(40):16089–94
10. Corlett RT. 2013. The shifted baseline: prehistoric defaunation in the tropics and its consequences for biodiversity conservation. *Biol. Conserv.* 163:13–21
11. Koch PL, Barnosky AD. 2006. Late quaternary extinctions: state of the debate. *Annu. Rev. Ecol. Evol. Syst.* 37(1):215–50
12. Lima-Ribeiro MS, Nogués-Bravo D, Terribile LC, Batra P, Diniz-Filho JAF. 2013. Climate and humans set the place and time of Proboscidean extinction in late Quaternary of South America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 392:546–56
13. Duncan RP, Boyer AG, Blackburn TM. 2013. Magnitude and variation of prehistoric bird extinctions in the Pacific. *Proc. Natl. Acad. Sci. USA* 110(16):6436–41
14. Guimarães PR, Galetti M, Jordano P. 2008. Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. *PLOS ONE* 3(3):e1745
15. Blake S, Deem SL, Mossimbo E, Maisels F, Walsh P. 2009. Forest elephants: tree planters of the Congo. *Biotropica* 41(4):459–68
16. Poulsen JR, Clark CJ, Palmer TM. 2013. Ecological erosion of an Afrotropical forest and potential consequences for tree recruitment and forest biomass. *Biol. Conserv.* 163:122–30
17. Doughty CE, Wolf A, Malhi Y. 2013. The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia. *Nat. Geosci.* 6(9):761–64
18. Heckenberger MJ, Kuikuro A, Kuikuro UT, Russell JC, Schmidt M, et al. 2003. Amazonia 1492: pristine forest or cultural parkland? *Science* 301(5640):1710–14
19. Oslisly R, White L, Bentaleb I, Favier C, Fontugne M, et al. 2013. Climatic and cultural changes in the west Congo Basin forests over the past 5000 years. *Philos. Trans. R. Soc. B* 368(1625):20120304
20. Mann CC. 2005. *1491: New Revelations of the Americas Before Columbus*. New York: Knopf
21. Bhagwat SA, Nogué S, Willis KJ. 2012. Resilience of an ancient tropical forest landscape to 7500 years of environmental change. *Biol. Conserv.* 153(C):108–17
22. Barlow J, Gardner TA, Lees AC, Parry L, Peres CA. 2012. How pristine are tropical forests? An ecological perspective on the pre-Columbian human footprint in Amazonia and implications for contemporary conservation. *Biol. Conserv.* 151:45–49
23. Geist HJ, Lambin EF. 2002. Proximate causes and underlying driving forces of tropical deforestation. *BioScience* 52(2):143–50
24. Laurance WF, Sayer J, Cassman KG. 2014. Agricultural expansion and its impacts on tropical nature. *Trends Ecol. Evol.* 29(2):107–16
25. Gibbs HK, Ruesch AS, Achard F, Clayton MK, Holmgren P, et al. 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proc. Natl. Acad. Sci. USA* 107(38):16732–37
26. Grainger A. 2008. Difficulties in tracking the long-term global trend in tropical forest area. *Proc. Natl. Acad. Sci. USA* 105(2):818–23
27. Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, et al. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342(6160):850–53
28. Kissinger G, Herold M, de Sy V. 2012. *Drivers of deforestation and forest degradation: a synthesis report for REDD+ policymakers*. Rep., Lexeme Consult., Vancouver, Can. **https://www.forestcarbonpartnership.org/sites/fcp/files/DriversOfDeforestation.pdf_N_S.pdf**
29. Mayaux P, Pekel J-F, Desclée B, Donnay F, Lupi A, et al. 2013. State and evolution of the African rainforests between 1990 and 2010. *Philos. Trans. R. Soc. B* 368(1625):20120300

30. Rudel TK. 2013. The national determinants of deforestation in sub-Saharan Africa. *Philos. Trans. R. Soc. B* 368(1625):20120405
31. Malhi Y, Adu-Bredu S, Asare RA, Lewis SL, Mayaux P. 2013. African rainforests: past, present and future. *Philos. Trans. R. Soc. B* 368(1625):20120312
32. Coord.-Geral Obs. Terra (OBT). 2013. *Projeto PRODES: monitoramento da floresta Amazônica Brasileira por satellite* [PRODES Project: satellite monitoring of Brazilian Amazon Forest]. Rep., Natl. Inst. Space Res. (INPE), São Jose dos Campos, SP, Brazil. **http://www.obt.inpe.br/prodes/index.php**
33. Rosa IMD, Souza JC, Ewers RM. 2012. Changes in size of deforested patches in the Brazilian Amazon. *Conserv. Biol.* 26(5):932–37
34. Int. Trop. Timber Organ. (ITTO), Div. Econ. Inf. Mark. Intell. 2007. *Annual Review and Assessment of the World Timber Situation 2007.* Yokohama, Jpn.: Int. Trop. Timber Organ. (ITTO). **http://www.itto.int/annual_review/**
35. UN Food Agric. Organ. (FAO). 2010. *Global Forest Resources Assessment 2010*. Rome: UN
36. Asner GP, Rudel TK, Aide TM, Defries R, Emerson R. 2009. A contemporary assessment of change in humid tropical forests. *Conserv. Biol.* 23(6):1386–95
37. Souza CM Jr, Siqueira JV, Sales MH, Fonseca AV, Ribeiro JG, et al. 2013. Ten-year Landsat classification of deforestation and forest degradation in the Brazilian Amazon. *Remote Sens.* 5(11):5493–513
38. Bryan JE, Shearman PL, Asner GP, Knapp DE, Aoro G, Lokes B. 2013. Extreme differences in forest degradation in Borneo: comparing practices in Sarawak, Sabah, and Brunei. *PLOS ONE* 8(7):e69679
39. UN Food Agric. Organ. (FAO). 2005. *Global Forest Resources Assessment 2005: Progress Towards Sustainable Forest Management*. Rome: UN
40. Ahrends A, Burgess ND, Milledge SAH, Bulling MT, Fisher B, et al. 2010. Predictable waves of sequential forest degradation and biodiversity loss spreading from an African city. *Proc. Natl. Acad. Sci. USA* 107:14556–61
41. Furukawa T, Fujiwara K, Kiboi SK, Mutiso PBC. 2011. Threshold change in forest understory vegetation as a result of selective fuelwood extraction in Nairobi, Kenya. *For. Ecol. Manag.* 262(6):962–69
42. Laufer J, Michalski F, Peres CA. 2013. Assessing sampling biases in logging impact studies in tropical forests. *Trop. Conserv. Sci.* 6(1):16–34
43. Ramage BS, Sheil D, Salim HMW, Fletcher C, Mustafa N-ZA, et al. 2013. Pseudoreplication in tropical forests and the resulting effects on biodiversity conservation. *Conserv. Biol.* 27(2):364–72
44. Pinard MA, Putz FE. 1996. Retaining forest biomass by reducing logging damage. *Biotropica* 28(3):278–95
45. Struebig MJ, Turner A, Giles E, Lasmana F, Tollington S, et al. 2013. Quantifying the biodiversity value of repeatedly logged rainforests: gradient and comparative approaches from Borneo. *Adv. Ecol. Res.* 48:183–224
46. Barlow J, Peres CA, Henriques LMP, Stouffer PC, Wunderle JM. 2006. The responses of understorey birds to forest fragmentation, logging and wildfires: an Amazonian synthesis. *Biol. Conserv.* 128(2):182–92
47. Berry NJ, Phillips OL, Lewis SL, Hill JK, Edwards DP, et al. 2010. The high value of logged tropical forests: lessons from northern Borneo. *Biodivers. Conserv.* 19(4):985–97
48. Putz FE, Zuidema PA, Synnott T, Pinard MA, Sheil D, et al. 2012. Sustaining conservation values in selectively logged forests: the attained and the attainable. *Conserv. Lett.* 5:296–303
49. Edwards DP, Larsen TH, Docherty TDS, Ansell FA, Hsu WW, et al. 2011. Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. *Proc. R. Soc. B* 278(1702):82–90
50. Peters SJL, Malcolm JR, Zimmerman BL. 2006. Effects of selective logging on bat communities in the southeastern Amazon. *Conserv. Biol.* 20(5):1410–21
51. Poulsen JR, Clark CJ, Bolker BM. 2011. Decoupling the effects of logging and hunting on an Afrotropical animal community. *Ecol. Appl.* 21(5):1819–36
52. Adum GB, Eichhorn MP, Oduro W, Ofori-Boateng C, Rödel M-O. 2013. Two-stage recovery of amphibian assemblages following selective logging of tropical forests. *Conserv. Biol.* 27(2):354–63
53. Clark CJ, Poulsen JR, Malonga R, Elkan PW Jr. 2009. Logging concessions can extend the conservation estate for Central African tropical forests. *Conserv. Biol.* 23(5):1281–93
54. Gunawardene NR, Majer JD, Edirisinghe JP. 2010. Investigating residual effects of selective logging on ant species assemblages in Sinharaja Forest Reserve, Sri Lanka. *For. Ecol. Manag.* 259(3):555–62

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

55. Terborgh J, Lopez L, Nuñez P, Rao M, Shahabuddin G, et al. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294(5548):1923–26
56. Gibson L, Lynam AJ, Bradshaw CJA, He F, Bickford DP, et al. 2013. Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science* 341(6153):1508–10
57. Stoner KE, Vulinec K, Wright SJ, Peres CA. 2007. Hunting and plant community dynamics in tropical forests: a synthesis and future directions. *Biotropica* 39(3):385–92
58. Peres CA. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conserv. Biol.* 15(6):1490–1505
59. Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34:487–515
60. Markl JS, Schleuning M, Forget PM, Jordano P, Lambert JE, et al. 2012. Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conserv. Biol.* 26(6):1072–81
61. Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, et al. 2011. Trophic downgrading of planet Earth. *Science*. 333(6040):301–6
62. Laurance WF, Useche DC. 2009. Environmental synergisms and extinctions of tropical species. *Conserv. Biol.* 23(6):1427–37
63. Fa JE, Ryan SF, Bell DJ. 2005. Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in Afrotropical forests. *Biol. Conserv.* 121(2):167–76
64. Peres CA, Palacios E. 2007. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. *Biotropica* 39(3):304–15
65. Laurance WF, Useche DC, Rendeiro J, Kalka M, Bradshaw CJA, et al. 2012. Averting biodiversity collapse in tropical forest protected areas. *Nature* 489(7415):290–94
66. Benítez-López A, Alkemade R, Verweij PA. 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biol. Conserv.* 143(6):1307–16
67. Potapov P, Yaroshenko A, Turubanova S, Dubinin M, Laestadius L, et al. 2008. Mapping the world's intact forest landscapes by remote sensing. *Ecol. Soc.* 13(2):51
68. Abernethy KA, Coad L, Taylor G, Lee ME, Maisels F. 2013. Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. *Philos. Trans. R. Soc. B* 368(1625):20120303
69. Fa JE, Peres CA, Meeuwig J. 2002. Bushmeat exploitation in tropical forests: an intercontinental comparison. *Conserv. Biol.* 16(1):232–37
70. Peres CA. 2000. Evaluating the impact of sustainability of subsistence hunting at multiple Amazonian forest sites. In *Hunting for Sustainability in Tropical Forests*, ed. JG Robinson, EL Bennett, pp. 31–56. New York: Columbia Univ. Press
71. Xaud HAM, Martins FSRV, dos Santos JR. 2013. Tropical forest degradation by mega-fires in the northern Brazilian Amazon. *For. Ecol. Manag.* 294:97–106
72. Laurance WF, Nascimento HEM, Laurance SG, Andrade A, Ewers RM, et al. 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLOS ONE* 2(10):e1017
73. Wilkie DS, Bennett EL, Peres CA, Cunningham AA. 2011. The empty forest revisited. *Ann. NY Acad. Sci.* 1223(1):120–28
74. Terborgh JW, Feeley KJ. 2008. Ecosystem decay in closed forest fragments. In *Tropical Forest Community Ecology*, ed. WP Carson, SA Schnitzer, pp. 308–21. New York: Blackwell
75. Fa JE, Brown D. 2009. Impacts of hunting on mammals in African tropical moist forests: a review and synthesis. *Mammal Rev.* 39(4):231–64
76. Tabarelli M, Lopes AV, Peres CA. 2008. Edge-effects drive tropical forest fragments towards an early-successional system. *Biotropica* 40(6):657–61
77. Dirzo R, Miranda A. 1990. Contemporary neotropical defaunation and forest structure, function, and diversity—a sequel to John Terborgh. *Conserv. Biol.* 4(4):444–47
78. Laurance WF, Vasconcelos HL, Lovejoy TE. 2000. Forest loss and fragmentation in the Amazon: implications for wildlife conservation. *Oryx* 34(1):39–45
79. Galetti M, Dirzo R. 2013. Ecological and evolutionary consequences of living in a defaunated world. *Biol. Conserv.* 163:1–6
80. Phillips OL. 1997. The changing ecology of tropical forests. *Biodivers. Conserv.* 6(2):291–311

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

81. Terborgh JW, Feeley KJ. 2010. High functional redundancy and diffuse vertical links create multiple pathways for the trophic cascade in tropical forests. In *Trophic Cascades*, ed. JW Terborgh, JA Estes, pp. 125–40. Washington, DC: Island
82. Kurten EL. 2013. Cascading effects of contemporaneous defaunation on tropical forest communities. *Biol. Conserv.* 163:22–32
83. Wyatt JL, Silman MR. 2004. Distance-dependence in two Amazonian palms: effects of spatial and temporal variation in seed predator communities. *Oecologia* 140(1):26–35
84. Terborgh J. 2013. Using Janzen-Connell to predict the consequences of defaunation and other disturbances of tropical forests. *Biol. Conserv.* 163:7–12
85. Terborgh J, Feeley K, Silman M, Nuñez P, Balukjian B. 2006. Vegetation dynamics of predator-free land-bridge islands. *J. Ecol.* 94(2):253–63
86. Harrison RD, Tan S, Plotkin JB, Slik F, Detto M, et al. 2013. Consequences of defaunation for a tropical tree community. *Ecol. Lett.* 16(5):687–94
87. Shlisky A, Alencar AAC, Nolasco MM, Curan LM. 2009. Global fire regime conditions, threats, and opportunities for fire management in the tropics. In *Tropical Fire Ecology: Climate Change, Land Use, and Ecosystem Dynamics*, ed. MA Cochrane, pp. 65–83. Chichester: Springer Praxis
88. McMichael CH, Piperno DR, Bush MB, Silman MR, Zimmerman AR, et al. 2012. Sparse pre-Columbian human habitation in western Amazonia. *Science* 336:1429–31
89. Iriarte J, Power MJ, Rostain S, Mayle FE, Jones H, Watling J. 2012. Fire-free land use in pre-1492 Amazonian savannas. *Proc. Natl. Acad. Sci. USA* 109(17):6473–78
90. Cochrane MA. 2003. Fire science for rainforests. *Nature* 421(6926):913–19
91. van der Werf GR, Dempewolf J, Trigg SN, Randerson JT, Kasibhatla PS, et al. 2008. Climate regulation of fire emissions and deforestation in equatorial Asia. *Proc. Natl. Acad. Sci. USA* 105(51):20350–55
92. Langner A, Miettinen J, Siegert F. 2007. Land cover change 2002–2005 in Borneo and the role of fire derived from MODIS imagery. *Glob. Change Biol.* 13(11):2329–40
93. Barlow J, Lagan BO, Peres CA. 2003. Morphological correlates of fire-induced tree mortality in a central Amazonian forest. *J. Trop. Ecol.* 19(3):291–99
94. Gerwing JJ. 2002. Degradation of forests through logging and fire in the eastern Brazilian Amazon. *For. Ecol. Manag.* 157(1–3):131–41
95. Van Nieuwstadt MGL, Sheil D. 2005. Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. *J. Ecol.* 93(1):191–201
96. Brando PM, Balch JK, Nepstad DC, Morton DC, Putz FE, et al. 2014. Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *Proc. Natl. Acad. Sci. USA* 111(17):6347–52
97. Barlow J, Peres CA. 2004. Avifaunal responses to single and recurrent wildfires in Amazonian forests. *Ecol. Appl.* 14(5):1358–73
98. Adeney JM, Ginsberg JR, Russell GJ, Kinnaird MF. 2006. Effects of an ENSO-related fire on birds of a lowland tropical forest in Sumatra. *Anim. Conserv.* 9:292–301
99. Barlow J, Peres CA. 2008. Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philos. Trans. R. Soc. B* 363(1498):1787–94
100. Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biol. Conserv.* 142(6):1141–53
101. Broadbent EN, Asner GP, Keller M, Knapp DE, Oliviera PJC, et al. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biol. Conserv.* 141(7):1745–57
102. Ferraz G, Nichols JD, Hines JE, Stouffer PC, Bierregaard RO Jr, Lovejoy TE. 2007. A large-scale deforestation experiment: effects of patch area and isolation on Amazon birds. *Science* 315(5809):238–41
103. Lees AC, Peres CA. 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments. *Oikos* 118(2):280–90
104. Mokross K, Ryder TB, Côrtes MC, Wolfe JD, Stouffer PC. 2014. Decay of interspecific avian flock networks along a disturbance gradient in Amazonia. *Proc. R. Soc. B* 281(1776):20132599
105. Laurance WF, Camargo JLC, Luizão RCC, Laurance SG, Pimm SL, et al. 2011. The fate of Amazonian forest fragments: a 32-year investigation. *Biol. Conserv.* 144:56–67

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

106. Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, et al. 2012. Landscape moderation of biodiversity patterns and processes—eight hypotheses. *Biol. Rev.* 87:661–85
107. Pardini R, Bueno ADA, Gardner TA, Prado PI, Metzger JP. 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. *PLOS ONE* 5(10):e13666
108. Wearn OR, Reuman DC, Ewers RM. 2012. Extinction debt and windows of conservation opportunity in the Brazilian Amazon. *Science* 337(6091):228–32
109. Larsen TB. 2008. Forest butterflies in West Africa have resisted extinction. . .so far (Lepidoptera: Papilionoidea and Hesperioidea). *Biodivers. Conserv.* 17(12):2833–47
110. RAISG. 2012. *Amazonia Under Pressure*. São Paulo: RAISG Amazon. Netw.
111. Lugo AE, Helmer EH. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. *For. Ecol. Manag.* 190(2–3):145–61
112. Chazdon RL. 2014. *Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation*. Chicago: Univ. Chicago Press
113. Martin PA, Newton AC, Bullock JM. 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. *Proc. R. Soc. B* 280(1773):20132236
114. Dunn RR. 2004. Recovery of faunal communities during tropical forest regeneration. *Conserv. Biol.* 18(2):302–9
115. Dent DH, Joseph Wright S. 2009. The future of tropical species in secondary forests: a quantitative review. *Biol. Conserv.* 142(12):2833–43
116. Chazdon RL, Peres CA, Dent D, Sheil D, Lugo AE, et al. 2009. The potential for species conservation in tropical secondary forests. *Conserv. Biol.* 23(6):1406–17
117. Lawrence D. 2005. Biomass accumulation after 10–200 years of shifting cultivation in Bornean rain forest. *Ecology* 86(1):26–33
118. Grau HR, Aide TM, Zimmerman JK, Thomlinson JR, Helmer E, Zou X. 2003. The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. *BioScience* 53(12):1159–68
119. Chazdon RL, Letcher SG, van Breugel M, Martínez-Ramos M, Bongers F, Finegan B. 2007. Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philos. Trans. R. Soc. B* 362(1478):273–89
120. Dent DH, DeWalt SJ, Denslow JS. 2013. Secondary forests of central Panama increase in similarity to old-growth forest over time in shade tolerance but not species composition. *J. Veg. Sci.* 24(3):530–42
121. Neeff T, Lucas RM, Santos JD, Brondizio ES, Freitas CC. 2006. Area and age of secondary forests in Brazilian Amazonia 1978–2002: an empirical estimate. *Ecosystems* 9(4):609–23
122. van Breugel M, Hall JS, Craven D, Bailon M, Hernandez A, et al. 2013. Succession of ephemeral secondary forests and their limited role for the conservation of floristic diversity in a human-modified tropical landscape. *PLOS ONE* 8(12):e82433
123. Rosenzweig ML. 2001. The four questions: What does the introduction of exotic species do to diversity? *Evol. Ecol. Res.* 3(3):361–67
124. Fritts TH, Rodda GH. 1998. The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annu. Rev. Ecol. Syst.* 29:113–40
125. Mortensen HS, Dupont YL, Olesen JM. 2008. A snake in paradise: disturbance of plant reproduction following extirpation of bird flower-visitors on Guam. *Biol. Conserv.* 141(8):2146–54
126. Fine PVA. 2002. The invasibility of tropical forests by exotic plants. *J. Trop. Ecol.* 18:687–705
127. Asner GP, Hughes RF, Vitousek PM, Knapp DE, Kennedy-Bowdoin T, et al. 2008. Invasive plants transform the three-dimensional structure of rain forests. *Proc. Natl. Acad. Sci. USA* 105(11):4519–23
128. Lugo A. 2013. Novel tropical forests: nature's response to global change. *Trop. Conserv. Sci.* 6(3):325–37
129. Kupfer JA, Malanson GP, Franklin SB. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Glob. Ecol. Biogeogr.* 15:8–20
130. Bos MM, Tylianakis JM, Steffan-Dewenter I, Tscharntke T. 2008. The invasive yellow crazy ant and the decline of forest ant diversity in Indonesian cacao agroforests. *Biol. Invasions* 10(8):1399–409
131. Fisher MC, Henk DA, Briggs CJ, Brownstein JS, Madoff LC, et al. 2012. Emerging fungal threats to animal, plant and ecosystem health. *Nature* 484(7393):186–94

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

132. Catenazzi A, Lehr E, Rodriguez LO, Vredenburg VT. 2011. *Batrachochytrium dendrobatidis* and the collapse of anuran species richness and abundance in the Upper Manu National Park, southeastern Peru. *Conserv. Biol.* 25:382–91
133. Farrer RA, Weinert LA, Bielby J, Garner TWJ, Balloux F, et al. 2011. Multiple emergences of genetically diverse amphibian-infecting chytrids include a globalized hypervirulent recombinant lineage. *Proc. Natl. Acad. Sci. USA* 108(46):18732–36
134. Crawford AJ, Lips KR, Bermingham E. 2010. Epidemic disease decimates amphibian abundance, species diversity, and evolutionary history in the highlands of central Panama. *Proc. Natl. Acad. Sci. USA* 107(31):13777–82
135. Colón-Gaud C, Whiles MR, Kilham SS, Lips KR, Pringle CM, et al. 2009. Assessing ecological responses to catastrophic amphibian declines: patterns of macroinvertebrate production and food web structure in upland Panamanian streams. *Limnol. Oceanogr.* 54(1):331–43
136. Malhi Y, Aragão LE, Galbraith D, Huntingford C, Fisher R, et al. 2009. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proc. Natl. Acad. Sci. USA* 106(49):20610–15
137. Zelazowski P, Malhi Y, Huntingford C, Sitch S, Fisher JB. 2011. Changes in the potential distribution of humid tropical forests on a warmer planet. *Philos. Trans. R. Soc. A* 369(1934):137–60
138. Bala G, Caldeira K, Wickett M, Phillips TJ, Lobell DB, et al. 2007. Combined climate and carbon-cycle effects of large-scale deforestation. *Proc. Natl. Acad. Sci. USA* 104(16):6550–55
139. Davin EL, de Noblet-Ducoudré N. 2010. Climatic impact of global-scale deforestation: radiative versus nonradiative processes. *J. Clim.* 23(1):97–112
140. Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, et al. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci. USA* 105(18):6668–72
141. Colwell RK, Brehm G, Cardelus CL, Gilman AC, Longino JT. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322(5899):258–61
142. Feeley KJ, Silman MR, Bush MB, Farfan W, Cabrera KG, et al. 2011. Upslope migration of Andean trees. *J. Biogeogr.* 38(4):783–91
143. Feeley KJ, Silman MR. 2010. Biotic attrition from tropical forests correcting for truncated temperature niches. *Glob. Change Biol.* 16(6):1830–36
144. Araújo MB, Ferri-Yáñez F, Bozinovic F, Marquet PA, Valladares F, Chown SL. 2013. Heat freezes niche evolution. *Ecol. Lett.* 16(9):1206–19
145. Jaramillo C, Cárdenas A. 2013. Global warming and neotropical rainforests: a historical perspective. *Annu. Rev. Earth Planet. Sci.* 41(1):741–66
146. Dick CW, Lewis SL, Maslin M, Bermingham E. 2013. Neogene origins and implied warmth tolerance of Amazon tree species. *Ecol. Evol.* 3(1):162–69
147. Bush MB, Silman MR, Urrego DH. 2004. 48,000 years of climate and forest change in a biodiversity hot spot. *Science* 303(5659):827–29
148. Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD. 2009. The velocity of climate change. *Nature* 462(7276):1052–55
149. Wright SJ, Muller-Landau HC, Schipper J. 2009. The future of tropical species on a warmer planet. *Conserv. Biol.* 23(6):1418–26
150. Chen I-C, Shiu H-J, Benedick S, Holloway JD, Chey VK, et al. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proc. Natl. Acad. Sci. USA* 106(5):1479–83
151. Feeley KJ, Hurtado J, Saatchi S, Silman MR, Clark DB. 2013. Compositional shifts in Costa Rican forests due to climate-driven species migrations. *Glob. Change Biol.* 19:3472–80
152. Huntingford C, Zelazowski P, Galbraith D, Mercado LM, Sitch S, et al. 2013. Simulated resilience of tropical rainforests to CO_2-induced climate change. *Nat. Geosci.* 6(4):1–6
153. Hickler T, Smith B, Prentice IC, Mjöfors K, Miller P, et al. 2008. CO_2 fertilization in temperate FACE experiments not representative of boreal and tropical forests. *Glob. Change Biol.* 14(7):1531–42
154. Lloyd J, Farquhar GD. 2008. Effects of rising temperatures and [CO_2] on the physiology of tropical forest trees. *Philos. Trans. R. Soc. B* 363(1498):1811–17

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

155. Cernusak LA, Winter K, Dalling JW, Holtum JAM, Jaramillo C, et al. 2013. Tropical forest responses to increasing atmospheric CO_2: current knowledge and opportunities for future research. *Funct. Plant Biol.* 40(6):531–51
156. Loader NJ, Walsh RPD, Robertson I, Bidin K, Ong RC, et al. 2011. Recent trends in the intrinsic water-use efficiency of ringless rainforest trees in Borneo. *Philos. Trans. R. Soc. B* 366(1582):3330–39
157. Peñuelas J, Canadell JG, Ogaya R. 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. *Glob. Ecol. Biogeogr.* 20(4):597–608
158. Phillips OL, Aragão LE, Lewis SL, Fisher JB, Lloyd J, et al. 2009. Drought sensitivity of the Amazon rainforest. *Science* 323(5919):1344–47
159. Lewis SL, Lopez-Gonzalez G, Sonké B, Affum-Baffoe K, Baker TR, et al. 2009. Increasing carbon storage in intact African tropical forests. *Nature* 457(7232):1003–6
160. Gloor M, Phillips OL, Lloyd JJ, Lewis SL, Malhi Y, et al. 2009. Does the disturbance hypothesis explain the biomass increase in basin-wide Amazon forest plot data? *Glob. Change Biol.* 15(10):2418–30
161. Espírito-Santo FDB, Gloor M, Keller M, Malhi Y, Saatchi S, et al. 2014. Size and frequency of natural forest disturbances and the Amazon forest carbon balance. *Nat. Commun.* 5(3434):1–6
162. Malhi Y. 2010. The carbon balance of tropical forest regions, 1990–2005. *Curr. Opin. Environ. Sustain.* 2(4):237–44
163. Phillips OL, Lewis SL, Baker TR, Chao KJ, Higuchi N. 2008. The changing Amazon forest. *Philos. Trans. R. Soc. B* 363(1498):1819–27
164. Lewis SL, Lloyd J, Sitch S, Mitchard ETA, Laurance WF. 2009. Changing ecology of tropical forests: evidence and drivers. *Annu. Rev. Ecol. Evol. Syst.* 40(1):529–49
165. Schnitzer SA, Bongers F. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecol. Lett.* 14(4):397–406
166. Hietz P, Turner BL, Wanek W, Richter A, Nock CA, Wright SJ. 2011. Long-term change in the nitrogen cycle of tropical forests. *Science* 334(6056):664–66
167. Spracklen DV, Arnold SR, Taylor CM. 2012. Observations of increased tropical rainfall preceded by air passage over forests. *Nature* 489(7415):282–85
168. van der Ent RJ, Savenije HHG, Schaefli B, Steele-Dunne SC. 2010. Origin and fate of atmospheric moisture over continents. *Water Resour. Res.* 46(9):WO9525
169. Feng X, Porporato A, Rodriguez-Iturbe I. 2013. Changes in rainfall seasonality in the tropics. *Nat. Clim. Change* 3(6):1–5
170. Gloor M, Brienen RJW, Galbraith D, Feldpausch TR, Schöngart J, et al. 2013. Intensification of the Amazon hydrological cycle over the last two decades. *Geophys. Res. Lett.* 40(9):1729–33
171. Fu R, Yin L, Li W, Arias PA, Dickinson RE, et al. 2013. Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. *Proc. Natl. Acad. Sci. USA* 110(45):18110–15
172. da Costa ACL, Galbraith D, Almeida S, Portela BTT, da Costa M, et al. 2010. Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytol.* 187(3):579–91
173. McDowell NG. 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiol.* 155(3):1051–59
174. Myneni RB, Yang W, Nemani RR, Huete AR, Dickinson RE, et al. 2007. Large seasonal swings in leaf area of Amazon rainforests. *Proc. Natl. Acad. Sci. USA* 104(12):4820–23
175. Jung M, Reichstein M, Ciais P, Seneviratne SI, Sheffield J, et al. 2010. Recent decline in the global land evapotranspiration trend due to limited moisture supply. *Nature* 467(7318):951–54
176. Pau S, Wolkovich EM, Cook BI, Nytch CJ, Regetz J, et al. 2013. Clouds and temperature drive dynamic changes in tropical flower production. *Nat. Clim. Change* 3(7):1–5
177. Swinfield T, Lewis OT, Bagchi R, Freckleton RP. 2012. Consequences of changing rainfall for fungal pathogen-induced mortality in tropical tree seedlings. *Ecol. Evol.* 2(7):1408–13
178. Rockstrom J, Steffen W, Noone K, Persson A, Chapin FS, et al. 2009. A safe operating space for humanity. *Nature* 461:472–75
179. Tabarelli M, Cardoso da Silva JM, Gascon C. 2004. Forest fragmentation, synergisms and the impoverishment of neotropical forests. *Biodivers. Conserv.* 13:1419–25

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

180. Nepstad DC, Veríssimo A, Alencar A, Nobre C, Lima E, et al. 1999. Large-scale impoverishment of Amazonian forests by logging and fire. *Nature* 398:505–8
181. Gardner TA, Barlow J, Chazdon R, Ewers RM, Harvey CA, et al. 2009. Prospects for tropical forest biodiversity in a human-modified world. *Ecol. Lett.* 12(6):561–82
182. Lambin EF, Meyfroidt P. 2011. Global land use change, economic globalization, and the looming land scarcity. *Proc. Natl. Acad. Sci. USA* 108(9):3465–72
183. Becker CG, Fonseca CR, Haddad CFB, Batista RF, Prado PI. 2007. Habitat split and the global decline of amphibians. *Science* 318(5857):1775–77
184. Malhado ACM, Pires GF, Costa MH. 2010. Cerrado conservation is essential to protect the Amazon rainforest. *AMBIO* 39(8):580–84
185. Metzger JP, Martensen AC, Dixo M, Bernacci LC, Ribeiro MC, et al. 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic Forest region. *Biol. Conserv.* 142(6):1166–77
186. Ewers RM, Didham RK, Pearse WD, Lefebvre VER, Rosa IMD, et al. 2013. Using landscape history to predict biodiversity patterns in fragmented landscapes. *Ecol. Lett.* 16:1221–33
187. Aoyagi R, Imai N, Kitayama K. 2013. Ecological significance of the patches dominated by pioneer trees for the regeneration of dipterocarps in a Bornean logged-over secondary forest. *For. Ecol. Manag.* 289:378–84
188. Asner GP, Broadbent EN, Oliveira PJC, Keller M, Knapp DE, Silva JNM. 2006. Condition and fate of logged forests in the Brazilian Amazon. *Proc. Natl. Acad. Sci. USA* 103(34):12947–50
189. Rudel TK, Coomes OT, Moran E, Achard F, Angelsen A, et al. 2005. Forest transitions: towards a global understanding of land use change. *Glob. Environ. Change* 15(1):23–31
190. Aide TM, Clark ML, Grau HR, López-Carr D, Levy MA, et al. 2012. Deforestation and reforestation of Latin America and the Caribbean (2001–2010). *Biotropica* 45(2):262–71
191. Melo FPL, Arroyo-Rodríguez V, Fahrig L, Martínez-Ramos M, Tabarelli M. 2013. On the hope for biodiversity-friendly tropical landscapes. *Trends Ecol. Evol.* 28(8):462–68
192. Feeley KJ, Malhi Y, Zelazowski P, Silman MR. 2012. The relative importance of deforestation, precipitation change, and temperature sensitivity in determining the future distributions and diversity of Amazonian plant species. *Glob. Change Biol.* 18(8):2636–47
193. Chapin FS III, Carpenter SR, Kofinas GP, Folke C, Abel N, et al. 2010. Ecosystem stewardship: sustainability strategies for a rapidly changing planet. *Trends Ecol. Evol.* 25(4):241–49
194. Wright SJ. 2010. The future of tropical forests. *Ann. NY Acad. Sci.* 1195(1):1–27
195. Blaser J, Sarre A, Poore D, Johnson S. 2011. *Status of tropical forest management 2011*. ITTO Tech. Ser. No. 38, Int. Trop. Timber Organ., Yokohama, Jpn. **http://www.itto.int/direct/topics/topics_pdf_download/topics_id=2660&no=0&disp=inline**
196. Ramankutty N, Foley JA. 1999. Estimating historical changes in global land cover: croplands from 1700 to 1992. *Glob. Biogeochem. Cycles* 13(4):997–1027
197. Pitman N. 2011. Volume and geographical distribution of ecological research in the Andes and the Amazon, 1995–2008. *Trop. Conserv. Sci.* 4(1):64–81

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

Annual Review of Environment and Resources

Volume 39, 2014

Contents

Introduction v

Who Should Read This Journal? vii

I. Integrative Themes and Emerging Concerns

Environmental Issues in Australia
Alistair J. Hobday and Jan McDonald 1

Gender and Sustainability
Ruth Meinzen-Dick, Chiara Kovarik, and Agnes R. Quisumbing 29

II. Earth's Life Support Systems

Implications of Arctic Sea Ice Decline for the Earth System
Uma S. Bhatt, Donald A. Walker, John E. Walsh, Eddy C. Carmack, Karen E. Frey, Walter N. Meier, Sue E. Moore, Frans-Jan W. Parmentier, Eric Post, Vladimir E. Romanovsky, and William R. Simpson 57

Modeling the Terrestrial Biosphere
Joshua B. Fisher, Deborah N. Huntzinger, Christopher R. Schwalm, and Stephen Sitch 91

Tropical Forests in the Anthropocene
Yadvinder Malhi, Toby A. Gardner, Gregory R. Goldsmith, Miles R. Silman, and Przemyslaw Zelazowski 125

Life's Bottleneck: Sustaining the World's Phosphorus for a Food Secure Future
Dana Cordell and Stuart White 161

Tropical Intraseasonal Modes of the Atmosphere
Yolande L. Serra, Xianan Jiang, Baijun Tian, Jorge Amador-Astua, Eric D. Maloney, and George N. Kiladis 189

III. Human Use of the Environment and Resources

Dynamics and Resilience of Rangelands and Pastoral Peoples Around the Globe
Robin S. Reid, María E. Fernández-Giménez, and Kathleen A. Galvin 217

Carbon Dioxide Capture and Storage: Issues and Prospects
Heleen de Coninck and Sally M. Benson 243

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

Consensus and Contention in the Food-Versus-Fuel Debate
Mark W. Rosegrant and Siwa Msangi 271

Energy for Transport
Maria Figueroa, Oliver Lah, Lewis M. Fulton, Alan McKinnon, and Geetam Tiwari 295

The Environmental Costs and Benefits of Fracking
Robert B. Jackson, Avner Vengosh, J. William Carey, Richard J. Davies, Thomas H. Darrah, Francis O'Sullivan, and Gabrielle Pétron 327

Human Appropriation of Net Primary Production: Patterns, Trends, and Planetary Boundaries
Helmut Haberl, Karl-Heinz Erb, and Fridolin Krausmann 363

Consumer End-Use Energy Efficiency and Rebound Effects
Inês M.L. Azevedo 393

IV. Management and Governance of Resources and Environment

Environmental Ethics
Clare Palmer, Katie McShane, and Ronald Sandler 419

The Psychology of Environmental Decisions
Ben R. Newell, Rachel I. McDonald, Marilynn Brewer, and Brett K. Hayes 443

The Business of Water: Market Environmentalism in the Water Sector
Karen Bakker 469

V. Methods and Indicators

Advances in Measuring the Environmental and Social Impacts of Environmental Programs
Paul J. Ferraro and Merlin M. Hanauer 495

Concepts and Methodologies for Measuring the Sustainability of Cities
María Yetano Roche, Stefan Lechtenböhmer, Manfred Fischedick, Marie-Christine Gröne, Chun Xia, and Carmen Dienst 519

Measuring the Co-Benefits of Climate Change Mitigation
Diana Ürge-Vorsatz, Sergio Tirado Herrero, Navroz K. Dubash, and Franck Lecocq 549

Networks and the Challenge of Sustainable Development
Adam Douglas Henry and Björn Vollan 583

Water Security and Society: Risks, Metrics, and Pathways
Dustin Garrick and Jim W. Hall 611

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.

Citizen Science: A Tool for Integrating Studies of Human and Natural Systems
Rhiannon Crain, Caren Cooper, and Janis L. Dickinson 641

Indexes

Cumulative Index of Contributing Authors, Volumes 30–39 667

Cumulative Index of Article Titles, Volumes 30–39 672

Errata

An online log of corrections to *Annual Review of Environment and Resources* articles may be found at http://www.annualreviews.org/errata/environ

Annu. Rev. Environ. Resourc. 2014.39:125-159. Downloaded from www.annualreviews.org
by Eidgenossische Ansalt fur Wasserversorgung on 10/21/14. For personal use only.