Global Forest Biodiversity: Current State, Trends, and Threats

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Contents

Abstract Human activities, especially forest conversion and degradation, are causing global declines in forest biodiversity. This review quantifies the current extent of the major forest biomes on earth and their area losses in historical and recent time. The importance of global forests for the earth's terrestrial biodiversity is explored and the role of forest degradation, fragmentation, defaunation, and forest fires for

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forest biodiversity analyzed based on the comparison of managed and unmanaged forests and reported forest biodiversity trends. The outstanding role of the remaining primary forests for global forest biodiversity is highlighted, the imprint of millenia of forest use on forest biodiversity explored using Germany's forests as an example, and a brief assessment of the impact of climate change on forest biodiversity given. We conclude that conserving the last remaining primary forests is of paramount importance for the future of biodiversity on earth. When a substantial part of the earth's forest-related biodiversity is to be inherited to future generations, a global effort to establish at least ten effectively managed forest mega-reserves in the tropical and boreal forest biomes is urgently needed.

Keywords Biodiversity trends, Boreal forest, Defaunation, Forest degradation, Forest fragmentation, Forest loss, Forest management, Species numbers, Temperate forest, Tropical forest

1 Review Scope

Forests are of paramount importance for the future of biodiversity on earth. This is particularly true for tropical forests with their enormous species richness, but also for the other forest biomes, which are less species-rich, but are home to a large number of specialist taxa. This review attempts to summarize our knowledge about the current state of biodiversity in the forests on earth. The focus is on plant life, but the status of forest-dwelling animals and fungi is also addressed. Much attention is paid to deforestation and the different forms of forest degradation and their impact on forest biota. Even though the proportion of secondary forests in the global forest stock is continuously increasing, and secondary forests should therefore unquestionably be included in conservation concepts, we focus in this review on primary forests and their degradation stages due to their outstanding importance for the characteristic biodiversity of forests.

2 Definitions of Forest and Forest-Use Categories

Forests are defined very differently worldwide (Lund 2018). With regard to biodiversity, it makes sense to differentiate between closed forest (canopy closure >70%), open forest (40–70%), forest landscapes (20–40%, i.e., mosaics of forest and treeless ecosystems), and tree savannah (5–20%). The FAO Forest Resources Assessment (FRA) uses somewhat different definitions that lead to varying estimates of forest extent: closed forest (>40%) and open forest (10–40%). In forest censuses based on the FRA, all woodlands with >10% canopy closure are counted as forests, whereby the area colonizable by species bound to closed forests is significantly overestimated (Chazdon et al. 2016). With regard to forest use, the following categories are distinguished (Putz and Redford 2010): (1) degraded forest (primary forest, which has lost its characteristic structure and species composition due to human use), (2) managed forest (forest that is purposedly domesticated for production of forest products), (3) secondary forest (forest that grew naturally after complete forest destruction), and (4) plantations (stands resulting from tree planting or artificial seeding).

3 Original Forest Extent

Approximately 47% of the earth's land surface was covered by forest 8,000 years ago before humans began clearing large areas. This corresponds to an estimated total area of 62 million km^2 (Billington et al. 1996). In the following, the four most important forest biomes in terms of area are looked at: The tropical forests (with moist and dry forests), the subtropical forests (with ever-moist subtropical laurel forests and summer-dry subtropical, sclerophyllous hardwood forests), the temperate forests (with nemoral deciduous, mixed and coniferous forests), and the boreal forests.

Tropical moist forests are believed to have originally existed on approximately 16–17 million km^2, temperate and boreal forests each on 15–16 million km^2 (Kuusela 1992; Schultz 1995; Wright 2010; Martin 2015). For the subregions of the tropical moist forest, Asner et al. (2009) give original areas of 8.83 (South America), 0.69 (Central America and the Caribbean), 2.92 (Africa), and 7.19 million km^2 (Asia and Oceania); that is slightly more than mentioned above (total: 19.62 million km^2). The natural extent of the subtropical forest biome was significantly smaller (approx. 8.8 million km^2). The global extent of dry forests (>40% canopy closure) was estimated at 7.77 million km^2 in 2015 (Bastin et al. 2017), with most of the area in tropical and subtropical regions.

Already millenia ago, man has begun to transform the temperate forests of East Asia (in China since the second millennium BC) and Europe (since the Neolithic and increasingly from the early Middle Ages onwards) into agricultural land, excepting only small parts. The large-scale transformation of the subtropical hardwood forests of the Mediterranean region started in Greek and Roman times. In the temperate forests of North America, large-scale forest destruction has happened only in the course of European settlement since 1,500. This long-ago destruction of temperate and Mediterranean forests was undoubtedly associated with biodiversity losses, which can be at least partially reconstructed through biodiversity inventories in the few remaining primary forest areas. However, large parts of the forest-dwelling herbivorous and carnivorous megafauna in temperate, tropical, and boreal forests have been decimated by hunters already in early prehistoric times, with consequences for forest structure, food webs, and biogeochemical cycles (Malhi et al. 2016; Galetti et al. 2018). It has to be kept in mind that most forests of the world have been subject to more or less intense human influence since several thousands of years, often altering forest structure and species composition in the distant past, long before forest destruction started (Ellis et al. 2021).

In contrast, large-scale forest loss in the tropical moist and dry forests has only occurred in the last five decades. This is also valid for the subtropical forests outside of the Mediterranean region, the southern hemispheric temperate forests, and the boreal forests.

4 Recent Forest Area and Deforestation Rates

4.1 Forest Area

More or less systematic surveys of global forest area and its changes have been carried out only since the 1980s and 1990s with the advent of remote sensing technology and the national forest inventories stimulated by the FAO (Forest Resources Assessments; FRA 2020). Despite groundbreaking advances in the quality of satellite data, there are still inconsistencies in the determined areas of different forest categories and their cover changes over time, which make it difficult to estimate primary forest losses. The causes are a lack of uniform standards with regard to the differentiation of forest and tree-covered open land, the often insufficient distinction between primary forest, secondary forest and tree plantations, the handling of forest fragmentation and the smallest forest patches, as well as constant cloud cover in some regions (FRA 2020; Global Forest Watch 2021).

The FAO census gives for 2020 a global forest area of 40.6 million km^2 (i.e., 31% of the global land area), with 10.09 million km^2 in the boreal, 6.65 million km^2 in the temperate, 4.49 million km^2 in the subtropical, and 18.34 million km^2 in the tropical forest biome (including dry forest) (FRA 2020; Fig. 1). According to the FRA classification, 45% of the remaining forest area in 2020 was tropical forest, 27% boreal forest, 16% temperate forest, and 11% subtropical forest (Fig. 2). Considering only the tropical moist forest, the area was estimated in 2012 to 10.95 million km^2 according to high-resolution satellite images (Hansen et al. 2013). Mangrove forests covered 148,000 km^2 in 2020 (FRA 2020).

4.2 Forest Loss

The net forest loss is estimated by the FAO at around 4.2 million km^2 in the period 1990–2020, with more than 90% of it having occurred in tropical forests (FRA 2020). Global forest loss has decreased by a third from on average 158,000 km^2 per year in 1990–2000 to 102,000 km^2 per year in 2015–2020 (and from 138.000 to 92,800 km^2 year^{-1} in the tropics alone) (Fig. 3).

Recent forest loss is by far greatest in the tropical biome. Compared to the assumed original area of around 16 million km^2 (Martin 2015), it is estimated that around 28% of the tropical moist forest area was already lost before 1990: Four

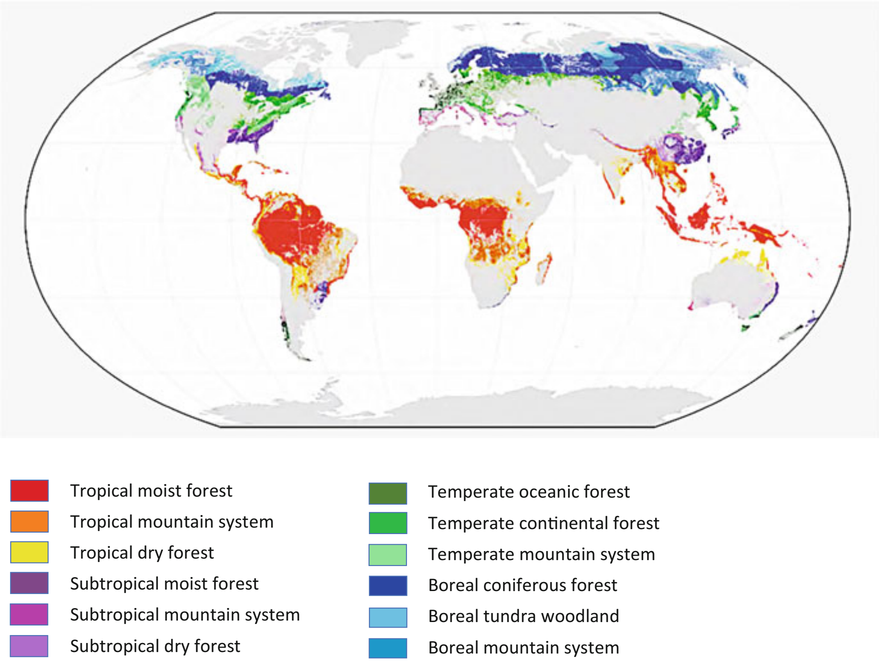

Fig. 1 Distribution of the four major forest biomes (tree cover >30%) with subtypes in 2015 according to Copernicus moderate-resolution (100 m) land cover map. Source: FAO based on Buchhorn et al. (2020)

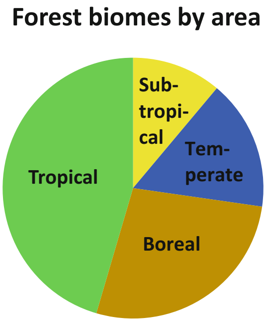

Fig. 2 Global extent of the four main forest biomes in 2020. The tropical biome includes tropical moist and dry forests. Prepared by FAO based on FAO global ecological zone map (FAO 2012) and global Copernicus Land Cover Map for 2015 (Buchhorn et al. 2020)

different surveys estimated the tropical moist forest area in the early 1990s to 11.50–11.72 million km^2; the numbers for the continents differed more widely (Latin America: 6.52–6.93 million km^2; Africa: 1.98–2.18 million km^2; South and Southeast Asia/Oceania: 2.71–3.02 million km^2). An evaluation of the Hansen et al. (2013) data by Martin (2015) gave an annual gross loss of tropical moist forest area

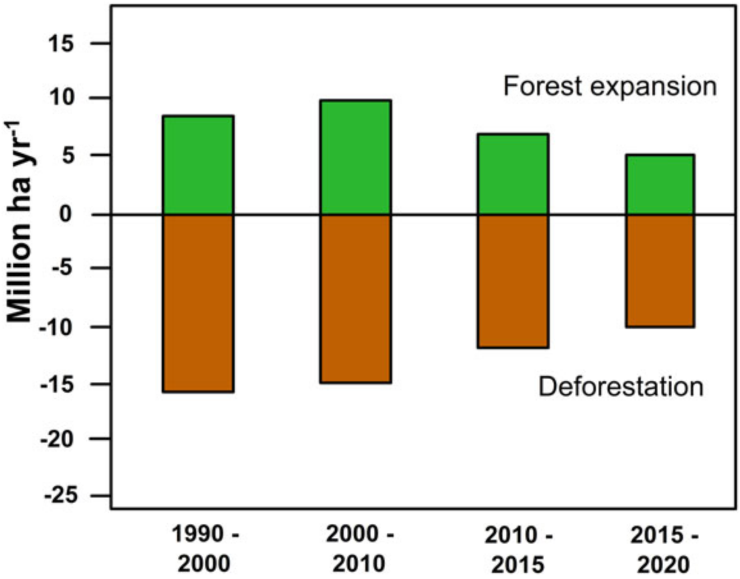

Fig. 3 Global deforestation and forest expansion between 1990 and 2020. After FAO and UNEP 2020

of 49,000 km^2 (0.43% per year) for forests with more than 50% canopy cover in the years 2000–2012. If the area gains through reforestation or afforestation of 0.08% per year (14,000 km^2) are included in the calculation, the net loss accounts to 0.31% per year. The three tropical forest regions differ significantly in their deforestation trends: In Brazil, deforestation peaked in 2004 and then declined as a result of the government's action plan to curb deforestation (Silva Jr et al. 2020). Since then it has varied between <10,000 and 20,000 km^2 per year (Curtis et al. 2018) and amounted to 182–187,000 km^2 in the period 2001–2013 (Tyukavina et al. 2017), with a recent upward trend in 2019 and 2020 (Silva Jr et al. 2020). Deforestation in the Atlantic rainforest region of Brazil has been particularly dramatic. It originally covered an area of 1.5 million km^2 and was reduced to 164,000 km^2 (11.7%) today with only small fragments remaining (Ribeiro et al. 2009). The rate of deforestation in Southeast Asia, particularly in Indonesia, rose continuously in the period 2000–2016 to more than 7,500 km^2 per year. It includes large primary forest losses (95,000 km^2 in the period 2002–2019; Global Forest Watch 2021), to a considerable extent also in protected areas (Curran et al. 2004; Margono et al. 2014). Since 2017, rates have decreased in Malaysia and Indonesia due to legal action. In the Congo Basin, there was a forest loss of 166,000 km^2 (most of it in the Democratic Republic of Congo) in the period 2000–2014 with an increasing trend (Tyukavina et al. 2018); 44% of them were primary and old secondary forests (compare also the forest loss data provided continuously by World Resources Institute: www.wri.org/initiatives/global-forest-watch and https://research.wri.org/gfr/global-forest-review).

5 Biodiversity in Forests

Forests are crucial for the conservation of biodiversity. Projections assume that 50–80% of all terrestrial organism species live in forests, which is considerably exceeding the global area share of the forest (Wilson 1988; FAO and UNEP 2020). However, biodiversity is unequally distributed, with major differences among and within the forest regions of the world.

About two thirds of the species described so far (approx. 1.9 million taxa, Régnier et al. 2015) occur in the tropics, most of them in tropical moist forests (Pimm and Raven 2000; Groombridge and Jenkins 2003). In fact, many organism groups reach their highest diversity in tropical forests. About two thirds of all land plant species are native to the tropics, probably more than 250,000 species (Antonelli and Sanmartín 2011; Pimm et al. 2014; Pimm and Joppa 2015). All five global megadiversity centers with >5,000 vascular plant species on 10,000 km^2 are located in tropical forest areas (Barthlott et al. 2005). About 20% of all tropical plant species are trees (~ 50,000 species, Fine et al. 2008; Beech et al. 2017), of which 19,000 to 25,000 each occur in Latin America and Southeast Asia, while the African tropical forest is home to only 4,500 to 6,000 tree species (Slik et al. 2015). The tree species numbers in the temperate (~1700) and boreal zone (~160; Fine et al. 2008) are by magnitudes lower.

At the local scale, almost as many tree species may exist in a single tropical forest patch as are occurring in all temperate forests of the world combined (Wright 2002). This is demonstrated by the larger tropical lowland plots of Lambir in Sarawak (52 ha: 1175 tree species $\geq$1 cm BHD) and Yasuni in Ecuador (25 ha: 1104 species). Certain 1 ha-plots in the tropical moist forest can harbor more than 300 tree species with diameters >10 cm (Valencia et al. 1994: Ecuador). Vascular plant species richness can be enormous even on small areas (0.01 ha: 233 species, Whitmore et al. 1985; 0.1 ha: 300–400 species, Duivenvoorden 1994; Galeano et al. 1998; 1 ha: 942 species, Balslev et al. 1998).

Most tropical tree species are locally rare and have small distribution ranges, but some are widespread and dominant. For example, ter Steege et al. (2013) estimated that of the approximately 16,000 tree species in the Amazon, 227 can be considered hyper-dominant and account for half of all tree trunks in the region. Another 11,000 species are so rare that together they make up only 0.12% of the stems. Nearly 58% of all tree species on earth are single-country endemics (Beech et al. 2017), many of them in tropical forests.

Most of the more than 31,000 known vascular epiphytes are found in tropical moist forests. This life form represents about 10% of all vascular plants on earth (Zotz and Bader 2009; Zotz et al. 2021).

It is estimated that tropical and subtropical moist forests are home to around 20,000 vertebrate species (mammals, birds, reptiles, amphibians), tropical and subtropical dry forests to about 7,000 species, temperate deciduous and mixed forests to 4,500 species and boreal forests to 1,000 species (MEA 2005). Global diversity centers are located almost exclusively in the tropical forests (Jenkins et al.

2013). The Amazon, southeastern Brazil and Central Africa together house about 50% of all vertebrate species. Almost 70% of all bird species (6,900 out of >10,000) occur in forests (Unwin 2012). Of the 6,093 tropical bird species, 53% are forest specialists and are therefore bound to forests (Sekercioglu 2012). More than 80% of the world's amphibian species are found in forests, the majority of which occur in tropical forests (Stuart et al. 2004).

While much less is known about invertebrate taxa, it appears that more than half of the estimated six to eight million terrestrial arthropod species occur in tropical moist forests (MEA 2005; Hamilton et al. 2013). In a protected area in Panama, Basset et al. (2012) detected 6,144 different arthropod species on just 0.48 ha of rainforest. They estimate the total arthropod diversity in the 6,000-ha San Lorenzo Reserve at 25,000 species. However, high arthropod species densities have also been found in near-natural temperate forests, such as 5,000–6,000 arthropod species on 60 ha of protected beech forest in Central Germany (Dorow et al. 2010).

6 Primary Forests and Their Biodiversity

Because of its outstanding importance for biodiversity, the area of intact primary forest deserves special attention (Gibson et al. 2011; Watson et al. 2018). Forests that remained largely untouched by human activities are more diverse in most organism groups than managed or degraded forests and especially agricultural transformation systems (Barnes et al. 2017). This probably also applies to the number of not yet identified species (Giam et al. 2012). Based on the information provided by the states, which, however, use non-uniform definitions, the FRA specifies a global primary forest area of 11.1 million km^2 for 2020, around 28% of the total forest area in the FRA listing (FRA 2020; see also Morales-Hidalgo et al. 2015). According to these data, more than 810,000 km^2 of primary forest have been lost between 1990 and 2020 globally, but precise data for Russia are missing (most likely >500,000 km^2 alone). According to the FRA, the global primary forest loss rate has decreased from 34,100 km^2 per year in 1990–2000 to 12,700 km^2 per year in 2010–2020 (FRA 2020); other inventories produced higher loss rates. The World Resources Institute (2020) gives average global loss rates of tropical primary forest of about 30,000 km^2 year^{-1} for the period 2002–2019, with higher figures in 2016 and 2017 (Fig. 4). Recent primary forest losses were highest in Brazil (20,000 km^2 per year in 2000–2010), in the Democratic Republic of Congo (7,230 km^2 year^{-1} in 2010–2020) and in Indonesia (7,130 km^2 year^{-1} in 2000–2010 with lower figures thereafter). An inventory based on satellite image analysis gave for 2013 an area of intact large-scale forest landscapes without human activities of 11.89 million km^2, of which about 5.6 million km^2 were in the tropical and five million km^2 in the boreal forest biome (Potapov et al. 2017). This area shrunk by 7.2% from 2000 to 2013.

The concepts of "frontier forests," "intact forest" (Watson et al. 2018) or "intact forest landscapes" (i.e., forest mosaics $\geq$500 km^2 dominated by primary forest; Potapov et al. 2017) or "hinterland forests" (i.e., late-successional tropical forests

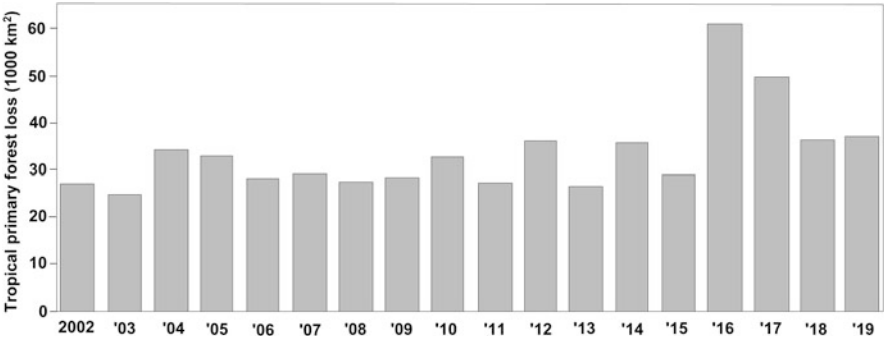

Fig. 4 Annual global loss of tropical primary forest from 2002 to 2019. After World Resources Institute (2020)

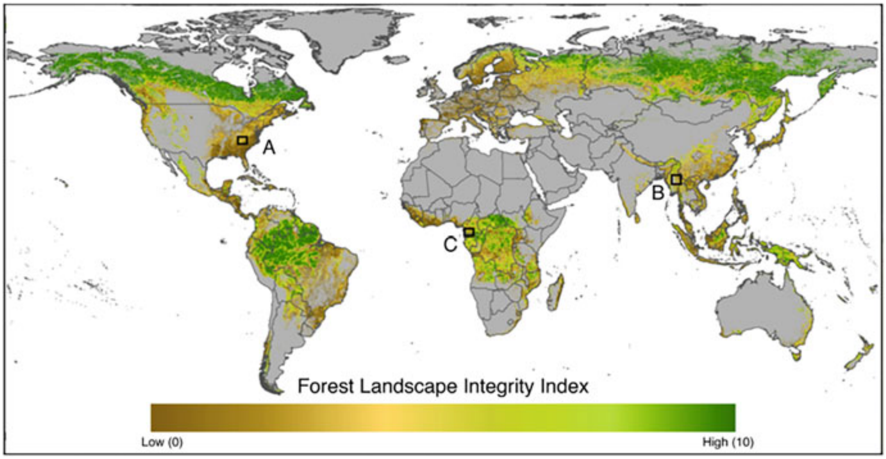

Fig. 5 Global map of forest integrity for the start of 2019. After Grantham et al. (2020). In the regions A, B, and C, case studied were conducted by the authors

$\geq$100 km^2; Tyukavina et al. 2016) consider forests that are largely uninfluenced by humans, are unfragmented and of sufficient size to maintain large-scale natural forest dynamics (Mackey et al. 2020). According to Bryant et al. (1997), in 1995 22% of the original forest area worldwide was preserved in a form that qualified it as frontier forest. This is less than the primary forest area estimated in the FRA 2020 25 years later, demonstrating inconsistent definitions. In fact, the global distribution of intact forest area can be visualized by means of different metrics (Watson et al. 2018). Here, the maps of forest landscape integrity of Grantham et al. (2020) (Fig. 5) and of forest biodiversity intactness of Hill et al. (2019) (Fig. 6) are displayed. Half of the intact forest area was in the boreal forest, only 3% in the temperate forest, and around 40% in the tropical forest. Seventy-five percent of the remaining primary forest area was constituted by three large forest blocks, i.e. in the boreal forest zones of Russia,

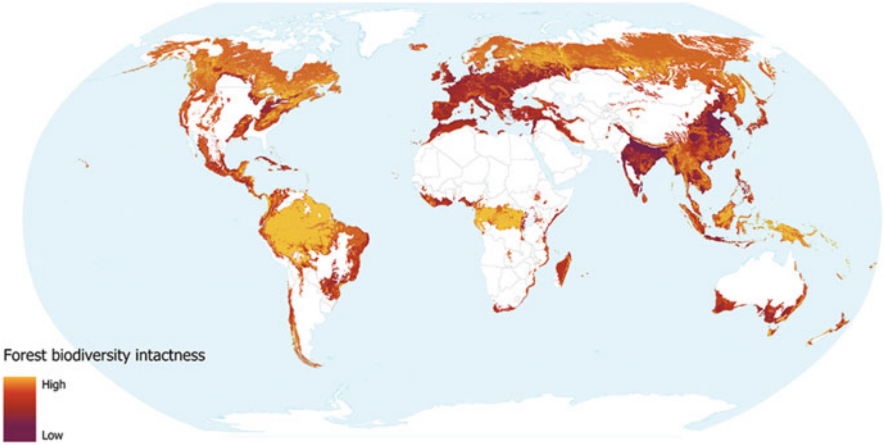

Fig. 6 Forest biodiversity intactness, showing the impacts of forest change and human population density. Yellow shows more intact areas and dark red more degraded areas. After Hill et al. (2019)

and of Canada and Alaska, and in the tropical lowland forest of the northwestern Amazon basin in connection to the Guyana shield.

7 Extent of Forest Degradation

Primary forest losses arise not only from forest destruction in the course of conversion to other land use systems, but also from the continuing degradation of the remaining forests through human activity. The diversity of forest-dwelling species decreases with the extraction of timbers and wood fuel, with forest fragmentation and the occurrence of surface fires, through the decimation of large vertebrates (defaunation), and it may shrink after the invasion of non-native species (Pauchard and Shea 2006). Many of the processes that cause forest degradation are interrelated, and secondary effects are often more destructive than the degradation itself (Zimmerman and Kormos 2012). For example, the frequency of fires increases with the intensity of timber use and the degree of forest fragmentation.

The extent to which forests have been degraded can usually only be approximated, even with modern LIDAR and radar techniques. For the tropical moist forest, it was assumed in 2000 that degraded forests and secondary forests accounted for up to 8.5 million km^2 (more than 75%) of the 11 million km^2 of forest area remaining in that time (ITTO 2002).

The FRA counts 28% of the global forest area as intact primary forest (FRA 2020), and Bryant et al. (1997) 22% as frontier forests; the remaining forest area must be considered as more or less degraded. Woodcock et al. (2015) estimate that globally roughly half of the remaining forests are primarily used for timber production, i.e. around 20 million km^2. According to Mercer (2015), 24% of the remaining tropical forests must be considered intact, 46% as fragmented and the remaining 30% as degraded through human use (e.g., timber extraction, fire). In the Amazon basin, around a quarter of the forest area is used for logging (Bongers et al. 2015). In Africa, around 30–40% of the remaining tropical forests are granted as concessions for timber extraction (Laporte et al. 2007).

Fires are important drivers of forest degradation, especially in the boreal forest, but also in tropical dry and moist forests. In the Brazilian Amazon (4.1 million km^2), 27.5% of the forest is <10 km from areas where it has burned (Peres et al. 2006); the frequency of fire has significantly increased in recent time (Aragao and Shimabukuro 2010).

In the temperate forest biome, the majority of the remaining forest area, in central and western Europe more than 95%, is allotted to managed forests, predominantly even-aged forests with more or less regular thinning operations, which have lost part of their biodiversity. This applies in a similar way to large parts of the subtropical forest biome.

During the last decades, large tracts of the boreal forest have been degraded and fragmented by logging activities and mining and infrastructure projects. More than 50% are subject to more or less intense human interference (Potapov et al. 2008). In Canada's boreal forest, almost a third of the area is destined for forestry (Carlson et al. 2015); 730,000 km^2 are affected by timber use and other human activities (Badiou et al. 2013). Mineral resources are mined in additional forest areas or infrastructure has been established (Carlson et al. 2015). Around 10,000 km^2 of Canada's total forest area of 4.2 million km^2 have been cleared annually in 2010–2020, 21,800 km^2 in 2019 alone (Schindler and Lee 2010; Global Forest Watch 2021). In the southern boreal zone of Canada, only 36% of the forest is intact (Lee et al. 2006).

In the Eurasian taiga, Achard et al. (2006) documented a rapid change in forest cover on 400,000 km^2 due to clearing and on 700,000 km^2 due to increased fire frequency in the 10–20 years before 2005. From 2001 to 2019, about 640.000 km^2 of forest were cut in Russia; part of it is left for natural regeneration (Global Forest Watch 2021). In European Russia alone, 22,100 km^2 (1.5%) of forest were lost in the period 2000–2005 (Potapov et al. 2011). In the boreal forests of Scandinavia, disturbance intensity has markedly increased since 2016, partly due to the recent increase in harvesting intensity (Ceccherini et al. 2020).

8 Drivers of Forest Degradation and Deforestation

Forest degradation can lead to the partial or complete loss of biota with close affinity to the structural elements that are characteristic for old-growth forests, without the loss being reflected in the forest area statistics. The factors driving forest degradation and deforestation vary widely among the forest biomes and forest regions. By far the most important driver in the tropical forest is agricultural expansion, both traditional small-scale shifting cultivation and subsistence farming, and modern marketoriented agriculture (Hosonuma et al. 2012; FAO and UNEP 2020). While oil palm and tree plantations as well as commercial logging are the most important drivers in Southeast Asia's tropical forests (Seymour and Harris 2019; Qaim et al. 2020), this is small-scale farming and firewood extraction in Africa. Commercial logging plays an additional role here. In South America, the expansion of cattle pastures and the cultivation of soy for meat production for urban and international markets are key drivers (deFries et al. 2010; Laurance et al. 2014a, b; Martin 2015; Sloan and Sayer 2015; Curtis et al. 2018; Seymour and Harris 2019).

In the temperate forest biome, agricultural expansion has been the main driver of forest transformation in the past. Historical forest management forms such as coppicing have locally increased forest biodiversity by favoring light-demanding and disturbance-tolerant taxa. In recent time, the most important disruptive factors are widespread forest management for timber production together with atmospheric nitrogen deposition (Nordén et al. 2008; Wallenius et al. 2010; Leuschner and Ellenberg 2017). Modern forest management has nearly completely eradicated the senescence phase of forest dynamics with its large deadwood stocks, and habitat diversity has decreased due to the introduction of largely uniform management regimes, often in form of conifer plantations. Nitrogen deposition, often in combination with artificially high game densities, is increasingly impacting forest biota and tree regeneration in the temperate zone. However, eutrophication is of growing importance also in tropical forests (Homeier et al. 2017).

In the boreal forest, forest degradation is mainly caused by expanding logging activities, frequently on large clear cuts, to supply international markets. Anthropogenic and natural fires and large infrastructure and mining projects have a growing influence on the Eurasian and North American boreal forest (Achard et al. 2002; Potapov et al. 2011; Badiou et al. 2013).

Widespread logging activities and infrastructure establishment in the boreal forest have an impact on the occurrence of large mammals such as woodland caribou, grizzly, wolverine, lynx, wolf and others, which withdraw mostly to the intact forest blocks.

9 Impact of Forest Degradation on Biodiversity

The extent to which selective timber extraction and silvicultural management regimes are reducing the forest-dwelling biodiversity depends on the intensity of the interventions and the resulting changes in forest structure (Putz et al. 2012). Interventions of very low intensity, by which only a few logs per hectare are removed, can even promote the diversity of early-successional taxa, the occurrence of which in old-growth forests is restricted to canopy gaps. In tropical moist forests, the diversity of mammals only started to decrease with a wood removal of 10 m^3 ha^{-1}, that of the amphibians at a threshold of 23 m^3 ha^{-1}, and that of the insects of 41 m^3 ha^{-1}. With a harvest of 38 m^3 ha^{-1} (mammals) and 63 m^3 ha^{-1} (amphibians), the diversity dropped to half of the richness of the primary forest

(Burivalova et al. 2014). After two rounds of selective timber extraction, disturbed forests in Borneo still held 75% of the original diversity of birds and dung beetles at a local scale (Edwards et al. 2011). Carefully executed low-impact logging can therefore leave tropical forest stands with a relatively high diversity, which can play important roles for biodiversity conservation (Bicknell et al. 2014). This is valid especially, when sufficiently large primary forest remnants with intact flora and fauna are left in close neighborhood, and forest access is difficult. However, it must be taken into account that extinction events often only occur with a delay (extinction debt), and that these losses can lead to the progressive impoverishment of exploited forests, particularly in terms of primary forest species with narrow niches (Wilcove et al. 2013). Depending on the organism groups, 5–57% of the forest species in Amazonia occur exclusively in primary forests (Barlow et al. 2007). In addition, exploited forests have a significantly higher fire risk, and forest access tracks increase the hunting pressure with the threat of defaunation (Clark et al. 2009).

Fires occur more often in exploited and fragmented forests because more deadwood is available, the stand microclimate is drier and people setting fires may enter (Aragao and Shimabukuro 2010). In tropical, subtropical, and boreal forests in particular, fire is likely the main driver of forest degradation, causing fundamental change in the communities. Even light surface fires can kill more than 40% of the thin-barked trees in tropical moist forests and trigger a succession toward secondary forests with higher light penetration, in which shorter-lived, fast-growing pioneer tree species dominate, and the primary forest fauna is replaced by stress-tolerant species of secondary forests (Barlow and Peres 2004, 2008). Secondary forests burn more rapidly than primary forests. Repeated fires can eventually lead to the formation of tree savannas, causing the almost complete loss of the characteristic primary forest flora and fauna.

Tropical secondary forests become increasingly diverse with growing age, but the species pool of primary forests is not reached even after several decades (Chazdon et al. 2009). The re-immigration of many primary forest species can take centuries. Transformation systems such as oil palm and rubber plantations, which largely replace the lowland forest in Southeast Asia, have a much lower biodiversity than the primary forest (Barnes et al. 2017). More than 70 or 80%, respectively, of the forest species among birds and butterflies no longer exist in these intensively managed habitats (Koh and Wilcove 2008). A global comparison of the effects of disturbance on ten animal groups and trees showed that, averaged over all organism groups, 41% of the species were dependent on the undisturbed tropical forest (Alroy 2017). Tropical forests are also much richer in symbiontic fungi than tree plantations or other land use systems, in which pathogenic and saprophytic fungi are more common (Brinkmann et al. 2019). This illustrates the irreplaceability of tropical primary forests for biodiversity conservation.

10 Defaunation

Bushmeat hunting has been a serious threat to many tropical forests in recent time (Wilkie et al. 2011; Dirzo et al. 2014; Ripple et al. 2015); larger mammals are particularly affected. This form of degradation is not detected by remote sensing and therefore underestimated. Defaunation due to both chasing and indirect species loss with land use change has multiple implications for forest communities and ecosystem functions (Gardner et al. 2019). One consequence of defaunation is poor dispersal of large-seeded, endozoochorous species and the accumulation of seedlings under the mother tree. In many cases, herbivory and predation patterns change, certain tree species become more abundant, and species diversity generally decreases (Kurten 2013).

Eighty to ninety-six percent of tropical tree species produce fleshy, vertebrate-dispersed fruits, and many Amazonian tree species rely on large frugivore vertebrates as dispersers. Simulation models show that a decrease in this group of animals leads to a reduction in above-ground biomass in tropical forests, since many of the affected, animal-dispersed, large-seeded tree species have high wood densities and achieve large maximum tree heights (Peres et al. 2016). Accordingly, a recent study predicts a decrease in carbon storage capacity of the Brazilian Atlantic rainforest, if defaunation leads to a decrease in vertebrate-distributed tree species with high C stocks (Bello et al. 2015). In Nigeria's lowland forest, the decimation of large primates by hunting has led to changes in the species composition of tree regeneration (Effiom et al. 2013). Changes in regeneration and an increase in tree species with low wood density and in lianas have also been found with intensive hunting of mammals and birds in forests in Panama (Kurten et al. 2015) and Borneo (Harrison et al. 2013). This factor has a major impact on the biodiversity of forests, because the areas affected by defaunation are much larger than the areas only impacted by deforestation or timber extraction (Benítez-López et al. 2019). Remote and protected forest areas are often affected, too.

11 Forest Fragmentation

Habitat fragmentation also contributes to the erosion of forest biodiversity and it may threaten the functionality of forest ecosystems. According to a global meta-analysis, Haddad et al. (2015) reported decreases in forest biodiversity by 13–75% due to fragmentation. The ongoing opening-up of previously untouched forest areas through road construction (Ibisch et al. 2016; Laurance et al. 2017) and the building of access tracks for oil and gas exploration (Finer et al. 2008; Laurance and Arrea 2017) and for the construction of dams (Benchimol and Peres 2015) is a main driver of forest fragmentation. Road construction has resulted in 70% of the remaining global forest area being <1 km distant to the nearest road (Haddad et al. 2015) and almost 20% of the forest area being <100 m from the forest edge (Brinck et al. 2017).

In the three large tropical forest realms, the forest has now been split up into 50–130 million forest fragments (Brinck et al. 2017; Taubert et al. 2018), with the number of fragments increasing with decreasing size (Tapia-Armijos et al. 2015). More than half of the remaining forest in Brazil's Atlantic rainforest is <100 m away from the forest edge (Ribeiro et al. 2009). Many tropical forest reserves that were embedded in a forest matrix at the time of their establishment have now become isolated forest fragments (DeFries et al. 2005; Martínez-Ramos et al. 2016), in which signs of degeneration are increasing.

Various long-term studies have shown that species losses are highest in small, highly isolated fragments and that loss rates depend on fragment size and the mobility of the organisms (Haddad et al. 2015; Gibson et al. 2013: small mammals, Didham et al. 1998: beetles, Feraz et al. 2003: birds). Hansen et al. (2020) showed for tropical forests that the likelihood of further size decrease is highest in the smaller forest fragments. A consequence of fragmentation can be fundamental changes in plant species composition and shifts between different plant functional groups, notably the increase in disturbance-tolerant pioneer tree species at the expense of slower-growing, animal-dispersed late-successional tree species, and increases in lianas (Laurance et al. 2014a, b; Benchimol and Peres 2015; Magnago et al. 2017).

The fringes of tropical forests, estimated at a total length of ca. 50 million km worldwide (Brinck et al. 2017), are exposed to pronounced edge effects, which negatively affect species composition and ecosystem functions up to several hundred meters into the forest (Haddad et al. 2015; Laurance et al. 2002; Pfeiffer et al. 2017). This has been studied, for example, for neotropical rainforest amphibians and reptiles (Schneider-Maunoury et al. 2016). Of 1,673 vertebrate species, 85% showed their frequency to be affected by forest edges (Pfeiffer et al. 2017): Typical forest species (forest core species) only reach their highest abundances several hundred meters from the edge of the forest. Heavily fragmented forests with a high proportion of forest edges are also more frequently exposed to fires (Armenteras et al. 2013).

12 Current Trends in Forest Biodiversity and Species Losses

12.1 Tropical and Subtropical Forests

Tropical forests are home to numerous species with small distribution ranges, which makes them particularly vulnerable. Accordingly, 85% of vertebrate species that have recently become extinct are taxa living in the tropics or overwintering there (IUCN 2018), many of them in forests. The estimated number of 130,000 recently extinct insect species refers mainly to tropical species (Régnier et al. 2015). At least a quarter of all Amazonian tree species are already classified as threatened with extinction according to IUCN criteria (ter Steege et al. 2015).

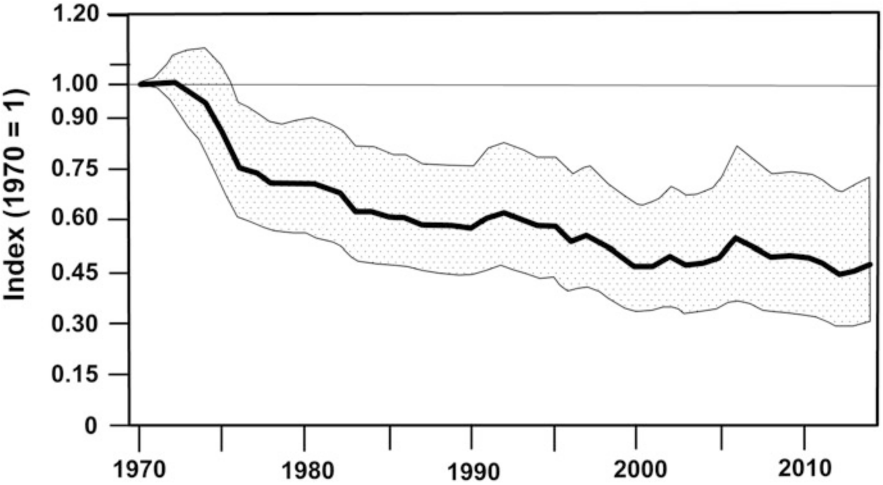

Fig. 7 Change in the Living Planet Forest Specialist Index of the population sizes of 268 vertebrate species from forests (455 populations) between 1970 (= 1) to 2014 from all over the world. Shaded area shows 95% confidence interval of the weighted mean. After WWF (2018)

The best available estimate of global population trends of forest-dwelling organisms is the WWF Living Planet Forest Specialist Index, for which population sizes of up to 268 forest vertebrate species (mammals, birds, reptiles, amphibians) have been continuously recorded since 1970 (WWF 2018). It includes some of the large iconic mammals of tropical forests such as primates and top carnivores. The index has decreased by 53% in the period 1970–2014, i.e. more than half of the vertebrate populations have been lost in <50 years (Fig. 7).

12.2 Temperate and Boreal Forests

12.2.1 Site Comparisons

Forest degradation, fragmentation and defaunation result in population declines and regional and global extinction events that have only rarely been documented precisely, because they are difficult to record and often only occur with a delay. The temperate forests of Eurasia and North America, which have long been used for logging and hunting, have lost most of their typical forest fauna of large mammals (e.g., bear, wolf, elk, European bison, aurochs) already in historical times (Vera 2000). Further, multiple studies comparing managed temperate forests to nearby primary forests (or forests with true old-growth characteristics) evidence an impoverished biodiversity with association to dead wood and old and senescent trees in most managed stands. Organism groups with observed reductions in species richness and abundance upon increasing management intensity are saproxylic insects (Müller and Bütler 2010; Jacobsen et al. 2020), saprophytic fungi (Heilmann-Clausen and Christensen 2003; Dvorák et al. 2017), ectomycorrhizal fungi (Tomao et al. 2020), and epiphytic lichens (Nascimbene et al. 2013; Kaufmann et al. 2017) and bryophytes (Friedel et al. 2006; Fritz et al. 2008).

For example, ancient beech forests in the Slovakian Carpathians are home to a 50% greater diversity of epiphytic bryophytes and twice as many epiphytic lichen species than neighboring managed beech forests (Kaufmann et al. 2017). A significant proportion of the about 1,500 species of deadwood fungi in Central European forests are lacking in managed forests with little deadwood (Dörfelt 2007; Härdtle and von Oheimb 2013). In contrast, vascular plant diversity is a poor indicator of old-growthness (Lelli et al. 2019), as diversity is generally promoted by disturbance, at least at low to moderate intensities.

The overall value of primary or old-growth forests for conserving the diversity of these forest-dwelling organisms is broadly accepted. Forest reserves with a management history in the recent past cannot fulfill this task (Meyer et al. 2021), as the biodiversity of managed forests recovers only slowly (Burrascano et al. 2018).

12.2.2 Biodiversity Trends

Biomass and species richness of forest-living arthropods have declined by 41% and 36%, respectively, between 2008 and 2017 in 30 forest sites in Germany (Seibold et al. 2019), paralleling the recently documented insect biomass decline in Central Europe’s agricultural landscape (Schuch et al. 2012; Hallmann et al. 2017). Even though the sampling interval covers only 10 years, the results point at landscape-scale drivers of arthropod decline that also impact forests.

More detailed information is available on long-term trends in forest bird populations in Europe’s temperate forests. Population monitoring of 34 forest bird species in the forests of England showed an average decrease by 28% in the period 1970–2018; specialist species (22 taxa) declined by even 41%, while generalist species (12 taxa) increased by 7% (Dept Environ. Food and Rural Affairs UK 2020; see Fig. 8). Of 53 bird species in Germany with habitat preferences for forests, 21 show long-term population increases, 12 decreases, and 20 no clear long-term population trend (Gerlach et al. 2019). As in England, increases were observed in generalist species with wide ecological niches and occurrences in non-tree habitats as well. These species seem to profit from local shifts to a more nature-oriented silviculture with more hardwoods, and from eutrophication. Long-term population declines and local extinctions have been observed in bird species adapted to old-growth features such as old trees, high small-scale structural heterogeneity, large deadwood amounts, and long forest continuity. Examples are the white-backed woodpecker, *Dendrocopos leucotos*, gray-headed woodpecker, *Picus canus*, Eurasian woodcock, *Scolopax rusticola*, and capercaillie, *Tetrao urogallus*. Similar observations were made in Switzerland’s forests (Grendelmeier et al. 2020).

A resampling study of epiphytic lichens in northwest German broadleaf forests indicated that 28–30% of the species have been lost in the past 100–150 years, likely

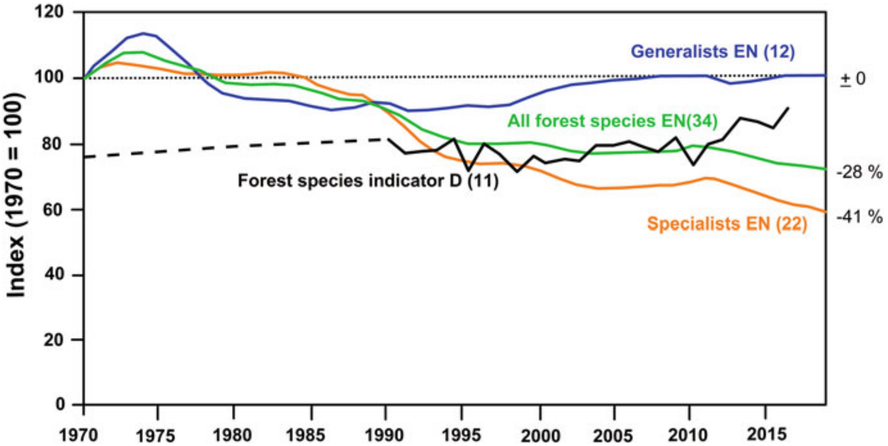

Fig. 8 Results of forest bird population monitoring in England (EN) and Germany (D) since 1970 (index values). The numbers in brackets denote the numbers of studied species. In England, generalist and specialist bird species were monitored separately. After Dept Environment, Food, and Rural Affairs UK (2020), and Bundesamt für Naturschutz 2018 (NBS-Indikator Artenvielfalt und Landschaftsqualität, Teilindikator Wälder, data of DDA 2017)

due to the reduction of deadwood amounts and senescent trees, forest drainage, and nitrogen deposition (Hauck et al. 2013). The fact that the diversity of epiphytic bryophytes is significantly lower in Central European managed forests than in unmanaged forests also points at species losses due to management intensification (Hofmeister et al. 2015). Part of the temperate tree flora is also endangered. More than half of Europe's endemic tree species are threatened (Rivers et al. 2019), notably taxa of the species-rich genus *Sorbus*.

Formerly managed forests taken out of use for conservation purposes achieve the diversity of characteristic forest biota only after many decades, if not centuries. According to a meta-analysis, the epiphytic lichen flora of temperate managed forests takes on average 180 years, the community of ECM fungi 90 years, and the saproxylic beetle fauna 60 years to recover to the state of old-growth forests (Spake et al. 2015). A modeling study based on estimated extinction rates thus assumed that the fragmented production forest landscape of Western Europe (The Netherlands) has lost, or will lose, 13–24% of its native forest-dwelling species, and about half of the original saproxylic species due to low deadwood amounts (Wallenius et al. 2010).

Decade-long nitrogen deposition, together with the abandonment of more traditional management regimes, is a key driver of recent compositional change in the herb layer composition of temperate forests (Verheyen et al. 2012; Förster et al. 2017; Heinrichs and Schmidt 2017). In general, N-demanding, disturbance-tolerant species with wider ecological niches and larger distribution ranges have increased at the expense of small-ranged, more nitrogen-efficient plants with narrower niches (Staude et al. 2020), resulting in pronounced species turnover within a few decades.

In addition, eutrophication together with the shift to a largely uniform forest management has resulted in many temperate forest regions in widespread homogenization of the herb layer vegetation during the last 40–70 years (Heinrichs and Schmidt 2017; Prach and Kopecky 2018). The related plant species richness has remained unchanged (Berrnhardt-Römermann et al. 2015; Staude et al. 2020) or decreased in the last decades (Prach and Kopecky 2018; see also Newbold et al. 2015). In many temperate forests, artificially high game densities have a negative influence on herb layer species richness at the plot and landscape level (Jenkins et al. 2014; Berrnhardt-Römermann et al. 2015).

13 The Biodiversity of Europe’s Temperate Forests with a Focus on Germany

Central Europe with more than 7,000 years of permanent human settlements may serve here as an example for assessing the long-term impact of man on forest biota. In Europe, as in eastern North America, only tiny remnants of primary forest remain. The FRA assessment gives for Europe only 41.800 km^2 of primary forest in 2020 (including boreal and Mediterranean forests, but excluding Russia; FRA 2020). Applying stricter criteria, Sabatini et al. (2018) report 14.000 km^2 for Europe (excluding Russia), which is 0.7% of the forest area. These small leftovers are not equally distributed to Europe’s different forest types (Sabatini et al. 2020).

In Central and Western Europe, true primary forests are virtually absent. The vast majority of the existing Central and Western Europe forests are today subjected to silviculture, with forest managers selecting tree species, conducting thinning to increase yield, and finally cutting the trees well before the age of senescence. Forests that were set aside in recent time for protecting biodiversity usually bear the legacy of the former production forest for many decades if not centuries, and their biodiversity lacks part of the characteristic old-growth species (Meyer et al. 2021).

The fundamental change in forest biodiversity that took place since humans began to utilize the forest shall be illustrated by the example of Germany’s forests. Eight thousand years ago, about 97% of Germany is thought to have been covered by forest. During the Middle Ages, forest cover shrunk to about 20% (Bork 2001), but this figure has increased through re-afforestation to 31% in recent time. Around 23% of Germany’s recent forest area represents re-afforestation on arable land and heathland (Glaser and Hauke 2004). In many regions, especially in the lowlands, only small remnants of the so-called historically-old forests have survived, i.e. forests with more than 200 years of forest continuity. Before large-scale forest destruction, about 67% of the forest area was potentially covered by forests of European beech (*Fagus sylvatica*; the rest mainly by oak, pine, and mixed mountain forests; Knapp 2007). The portion of this main native tree species has been reduced to 15.4% of today’s forest area. The 16,800 km^2 of beech forest in Germany that still exist today correspond to just 7% of the former potential beech forest area. The natural area share of coniferous forest of <1% (Suck et al. 2014) has been increased by forestry to 54.2%, including above all Norway spruce (*Picea abies* Karst., 25.4%) and Scots pine (*Pinus sylvestris* L., 22.3%) (BMEL 2012). Not only the tree species composition is far from natural, but also the age and population structure of the stands. Most of these are even-aged forests that result from planting or supported natural regeneration and that lack the vertical and horizontal heterogeneity in the canopy that is characteristic of primary forests. 73.7% of the stands are younger than 100 years, only 3.2% older than 160 years. The bulk of Germany's forests thus lack the senescence phase of forest development with dying and dead trees and large amounts of dead wood (Knapp 2007). The average deadwood stock in managed forests is 20.6 m^3 ha^{-1} (BMEL 2012), while in Slovakian primary beech forests, a 10 times higher amount was found (up to 200 m^3 ha^{-1}) (Glatthorn et al. 2017).

Although more than half of Germany was once covered with acidophytic beech forests with low tree species diversity, these forests can be species-rich habitats with a large number of habitat specialists, when management intensity is low. About 15,000 animal species, more than 3,000 macrofungal species and more than 600 lichen species are found in Swiss forests (Bollmann et al. 2009; Scheidegger et al. 2010). Thorough inventories in 60 ha of a beech forest in Hesse (Germany) show the presence of 5–6,000 animal species (Dorow et al. 2010), including numerous specialized saproxylic taxa. Such high species numbers have only been recorded from unmanaged forests.

In 2019, 2.8% of the German forest area had been set aside for the primary goal of biodiversity conservation, i.e. they were given "process protection" and management has ceased (Engel 2019). The area includes national parks, the federal natural heritage, forest protected under the nature conservation law (as far as silviculture is not permitted), and natural forest reserves, the latter often of very small size (at least 0.3 ha). In the early 2000s, beech forests without management covered in Germany 1,226 km^2, which is 2.7% of the current beech forest area or 0.18% of the potential beech forest area in Germany (Knapp 2007). Compared to the global mean of legally protected forest area (11%) and the European average (12%, excluding Russia; FRA 2020), Germany is one of the tail-lights in forest conservation.

14 Effects of Recent Climate Change on Forest Biodiversity

The five primary threats to biodiversity in the world's forests (forest conversion, forest degradation through (over-)use, fires, defaunation, and fragmentation) are exacerbated by recent and to be expected future changes in climate (Hauck et al. 2019; Pörtner et al. 2021). In most forests (apart from the cold-limited northern boreal forests and some mountain forests), a significant temperature increase combined with rising atmospheric evaporative demand exposes trees to stress. This is exacerbated regionally by long-term decreases in growing season precipitation. Atmospheric nitrogen deposition is another important driver of recent changes in forest biodiversity, currently acting mainly in the industrialized regions of the global north, but increasingly expanding to the south as well. In the following chapter, a brief overview of observed major climate change-driven alterations in forest structure and functioning in the forests on earth is given for the period 1980–2020 (for more details, see recent reviews in, e.g., Allen et al. 2010, 2015; Hauck et al. 2019; Forzieri et al. 2021; Pörtner et al. 2021). Many of the anticipated changes have the potential to destabilize forests and to negatively affect forest biodiversity, but the consequences are often not well understood.

14.1 Tropical and Subtropical Forests

In the tropical moist forests, elevated temperatures and more frequent dry spells will very likely cause reductions in tree biomass and long-term carbon sequestration in the future (Mitchard 2018; Maia et al. 2020; Sullivan et al. 2020), caused by increased tree mortality, higher respiration rates, and altered tree species composition (Clark et al. 2010; Anderegg et al. 2015; Doughty et al. 2015; McDowell et al. 2018). Accordingly, carbon storage in the above-ground biomass of tropical lowland forests seems to have increased until 2000 (Baker et al. 2004; Lewis et al. 2009; Qie et al. 2017). Yet, recent studies are indicating a decrease, for example in Amazonia in the period 1983–2011 (Brienen et al. 2015). A shift from longer-lived, slower-growing, drought-sensitive tree species to faster-growing, shorter-lived and more drought-tolerant species is expected (Butt et al. 2014; Esquivel-Muelbert et al. 2018). Some authors have registered an increase in the frequency of lianas in undisturbed tropical lowland forests (Phillips et al. 2002; Schnitzer and Bongers 2011). Possible drivers are the increased atmospheric CO_2 concentration, a higher drought frequency and increased anthropogenic disturbance levels. A higher liana frequency can change the biomass dynamics of tropical forests by influencing tree growth (van der Heijden et al. 2015). Repeated sampling of the avifauna of Amazonian tropical lowland forests in 1980–1984 and again in 2008–2016 revealed reduced abundances of terrestrial and near-ground insectivorous birds even in the absence of deforestation, edge effects, and anthropogenic disturbance, which possibly are caused by climatic change (Stouffer et al. 2021). In the mountain forests of the tropical Andes, a thermophilization of the vegetation has been observed in many places, i.e. an increasing abundance of thermophilic tree species at higher altitudes (Fadrique et al. 2018).

14.2 Temperate and Boreal Forests

In the temperate forest biome, increasing temperatures and rising evaporative demand are seen as the main drivers of widespread vitality loss and increasing mortality of drought-sensitive tree species, especially after extreme hot droughts (van Mantgem et al. 2009; Allen et al. 2010; Anderegg et al. 2013; Leuschner 2020;

Schuldt et al. 2020). Elevated tree mortality rates have been observed in various forest types on the southern and continental edges of the distribution ranges (e.g., in European beech, Penuelas et al. 2007; Lakatos and Molnár 2009), but recently after the extreme 2018/19 drought also in Central Europe (Schuldt et al. 2020; Braun et al. 2021). Widespread tree dieback has also occurred in other temperate regions, e.g., in the *Nothofagus pumilio* forests of Patagonia (Rodriguez-Caton et al. 2016). Long-term growth decline and increased climate sensitivity of growth have been observed since the 1980s in sensitive temperate tree species as European beech even in the center of the species' distribution range (Zimmermann et al. 2015; Knutzen et al. 2017), which is explained by the warming trend and the rising evaporative demand. In some natural temperate mixed forests, a change in the species composition toward more drought-tolerant tree species is taking place (Olano and Palmer 2003; Rigling et al. 2013; Martinez-Vilalta and Lloret 2014). In many North American and European temperate forests, thermophilic herb layer plants have significantly increased in recent decades (thermophilization), while cold-adapted taxa have on average declined (de Frenne et al. 2013).

In the boreal forest, warming has increased growth mainly in the northern taiga, while widespread growth declines and, regionally, increased mortality has been observed in the southern boreal forest and where water is limiting (Dulamsuren et al. 2013; Bond-Lamberty et al. 2014). On the southern edge of the North American boreal forest, *Populus tremuloides* forests have died on large areas as a result of the warming since the 1990s (Peng et al. 2011). An increase in forest fire risk is observed in many regions or is expected for the near future (Malevsky-Malevich et al. 2008). Currently, boreal forests mostly act as carbon sinks, albeit of low strength (Dolman et al. 2012). Yet, this could change with climate warming, especially in drier regions.

In the decades to come, the warming trend may lead in many forest regions on earth to profound changes in community composition, and widespread loss of forest biota with narrow niches is to be expected.

15 A Global Effort to Protect the Last Primary Forests Is Needed

Over the past 8,000 years, humans have reduced the global forest area by almost 40%; a further 40% or more have been degraded through the harvest of wood products, defaunation and fire in such a way that the characteristic forest-dwelling communities only exist in impoverished form (Watson et al. 2018). Fragmentation has resulted in 70% of the remaining forest area being <1 km distant to roads, substantially altering community structure. Today, <11.5 million km^2 of intact primary forest are left, especially in the boreal and tropical forest biome; that is ca. 18.5% of the originally existing global forest area. The remaining forest area free of significant anthropogenic degradation is rapidly declining: Around 30,000 km^2 of

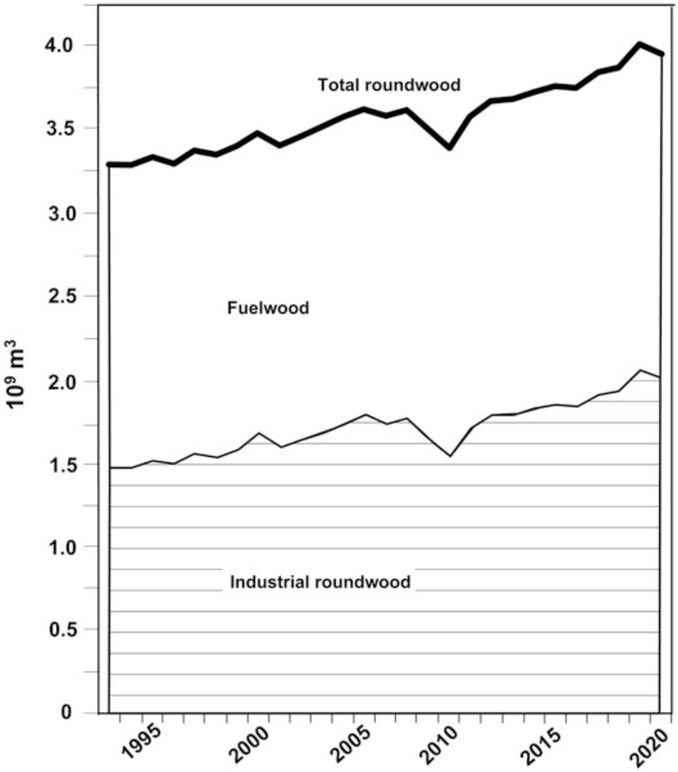

Fig. 9 Total industrial roundwood and fuelwood production on earth 1993–2020. After Forest Product Statistics, FAO. Note that the fuelwood figures likely underestimate the wood extraction for primary energy due to incomplete accounting

primary forest are lost annually through deforestation, and this rate has increased in the last years (Fig. 4). The consequences of rapid warming during the past 40 years (and locally decreasing summer precipitation) are visible in all forest biomes in the form of regionally increasing tree mortality, the thermophilization of vegetation and, in some places, decreasing carbon storage. Progressive warming will further destabilize forests and their biota with likely consequences for productivity, carbon sequestration potential, and other ecosystem functions.

During the last 20 years, the global demand for roundwood (industrial and fuelwood) has increased by on average 0.85% annually to more than 4 billion m^3 $year^{-1}$ in 2020. Demand is expected to rise to about 6 billion m^3 roundwood by 2050 due to population growth and increasing resource consumption levels (Barua et al. 2014; FAO 2021; Fig. 9). Policy recommendations to increase carbon storage in wood products, to replace energy-intensive materials by wood, and to stimulate the use of forest-based bioenergy in order to substitute fossil fuel as part of the green economy (e.g., EEA 2017; Doyle and Roche 2017) will further increase wood consumption and thus demand for roundwood (Searchinger et al. 2018). This would raise the pressure on primary forests, as a growing wood supply from expanding industrial forest plantations and managed forests is unlikely to meet the growing demand (Barua et al. 2014). Promoting the use of forest products and forest management as a pathway to reduce climate warming, as has been agreed on in the Paris Agreement and is implemented into national and supra-national policies such as the European Union's Renewable Energy Directive, is therefore inevitably conflicting with the declared goal of the global community to halt global biodiversity loss (Pörtner et al. 2021).

Currently, about 11% of the remaining forest area has been assigned primarily to biodiversity protection (4.2 million km^2, FRA 2020), but the effectiveness varies greatly from region to region, and much of the left primary forest is insufficiently protected. The future of global forest biodiversity will depend crucially on whether the 11.5 million km^2 of primary forest (i.e., 28% of the remaining forest area or 7.7% of global land surface area) can be effectively protected in the form of large reserves. When a substantial part of the earth's forest-dependent biodiversity is to be inherited to future generations, it is indispensible to establish at least ten effectively managed forest mega-reserves on earth, notably in the boreal forest of Russia, Canada and Alaska, and in the tropical moist forest of northwest Amazonia (Brazil, Peru, Colombia, Venezuela, the Guyanas), of the Congo Basin (Democratic Republic of Congo), and in the highlands of Borneo and New Guinea (PNG and Indonesia). These reserves should cover the complete elevational range of the respective areas to allow for species migration. Only such mega-reserves are suited to buffer forest biodiversity against the negative effects of degradation, fragmentation, and the looming threat of climate change (Watson et al. 2018).

Regional biodiversity hotspots outside these primary forest areas require protected area networks of at least 20% of the forest area to effectively conserve the characteristic forest biota. For forest areas designated mainly for timber production, multiple uses or without designation (i.e., 69% of the global forest area according to FRA 2020), management regimes have to be adopted that guarantee the permanent retention of small areas of intact forest with old and senescent trees and large deadwood amounts. Such a retention approach would allow achieving a certain degree of forest continuity also in logged forests. These remnants might function in the post-harvest forest generation as nuclei of recolonization for disturbance-sensitive taxa (Lindenmeier et al. 2012).

Successful conservation and management of the remaining forests also requires an effective global forest monitoring network, which merges reliable data on forest extent with up-to-date information on biodiversity, forest dynamics processes, and forest ecosystem functions in their dependence on changing environmental conditions. Such a network should link ground-based monitoring in permanent plots (e.g., Malhi et al. 2021) to remote sensing information on forest extent and forest health (as provided by, e.g., Global Forest Watch) in order to understand and control the human impact on forests.

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