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Drivers and ecological impacts of deforestation and forest degradation in the Amazon

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ABSTRACT

Deforestation (the complete removal of an area's forest cover) and forest degradation (the significant loss of forest structure, functions, and processes) are the result of the interaction between various direct drivers, often operating together. By 2018, the Amazon forest had lost approximately 870,000 km^2 of its original cover, mainly due to expansion of agriculture and ranching. Other direct drivers of forest loss include the opening of new roads, construction of hydroelectric dams, exploitation of minerals and oil, and urbanization. Impacts of deforestation range from local to global, including local changes in landscape configuration, climate, and biodiversity, regional impacts on hydrological cycles, and global increase of greenhouse gas emissions. Of the remaining Amazonian forests, 17% are degraded, corresponding to 1,036,080 km^2. Forest degradation has various anthropogenic drivers, including understory fires, edge effects, selective logging, hunting, and climate change. Degraded forests have significantly different structure, microclimate, and biodiversity as compared to undisturbed ones. These forests tend to have higher tree mortality, lower carbon stocks, more canopy gaps, higher temperatures, lower humidity, higher wind exposure, and exhibit compositional and functional shifts in both fauna and flora. Degraded forests can come to resemble their undisturbed counterparts, but this depends on the type, duration, intensity, and frequency of the disturbance event. In some cases this may impede the return to a historic baseline. Avoiding further loss and degradation of Amazonian forests is crucial to ensuring that they continue to provide valuable and life-supporting ecosystem services.

KEYWORDS: deforestation, forest degradation, wildfires, edge effects, logging

Causadores e impactos ecológicos do desmatamento e degradação florestal na Amazônia

RESUMO

O desmatamento (a remoção completa da cobertura florestal) e a degradação florestal (a perda significativa de estrutura, funções e processos florestais) são o resultado da interação entre vários fatores causadores diretos, frequentemente operando em conjunto. Até 2018, a floresta amazônica perdeu aproximadamente 870.000 km^2 de cobertura florestal original, principalmente devido à expansão da agricultura e pecuária. Outros impulsionadores diretos da perda florestal incluem abertura de novas estradas, construção de barragens hidrelétricas, exploração de minerais e petróleo e urbanização. Os impactos do desmatamento variam de local a global, incluindo mudanças locais na configuração da paisagem, clima e biodiversidade, impactos regionais nos ciclos hidrológicos, e aumento global das emissões de gases de efeito estufa. Das florestas amazônicas remanescentes, 17% estão degradadas, correspondendo a 1.036.080 km^2. A degradação florestal tem várias causas antropogênicas, incluindo incêndios no sub-bosque, efeitos de borda, extração seletiva de madeira, caça e mudanças climáticas. Florestas degradadas têm estrutura, microclima e biodiversidade significativamente diferentes em comparação com as não perturbadas, tendedo a maior mortalidade de árvores, menor estoque de carbono, mais aberturas no dossel, temperaturas mais altas, menor umidade, maior exposição ao vento e mudanças de composição e funcionais na fauna e na flora. Florestas degradadas podem se assemelhar a florestas não perturbadas, dependendo do tipo, duração, intensidade e frequência do evento de perturbação. Em alguns casos, isso pode impedir o retorno a uma linha de base histórica. Evitar mais perdas e degradação das florestas amazônicas é crucial para garantir que elas continuem a fornecer serviços ecossistêmicos valiosos e de suporte à vida.

PALAVRAS-CHAVE: desmatamento, degradação florestal, incêndios florestais, efeitos de borda, exploração madeireira

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INTRODUCTION

Across the Amazon, deforestation and forest degradation are the result of the interplay between various underlying and direct drivers acting at global, regional, and local scales (Rudel *et al.* 2009; Barona *et al.* 2010; Armenteras *et al.* 2017a; Clerici *et al.* 2020). Underlying drivers are factors that affect human actions (IPBES 2019), such as lack of governance and variation in both the price of commodities and the price of land (Garrett *et al.* 2013; Nepstad *et al.* 2014; Brandão *et al.* 2020). Conversely, direct drivers represent the human actions that impact nature (IPBES 2019), including the expansion of pastures and croplands, opening of new roads, construction of hydroelectric dams, or exploitation of minerals and oil (Ometto *et al.* 2011; Fearnside 2016; Sonter *et al.* 2017). Drivers often act simultaneously. For example, road construction and paving leads to the creation of new urban centers and the advance of the agricultural frontier (Fernández-Llamazares *et al.* 2018; Nascimento *et al.* 2021). Although each of these drivers (road building, urbanization, and agricultural expansion) will increase deforestation rates, it is very difficult to estimate their isolated impacts on ecosystems processes and functions.

The impacts of deforestation and forest degradation can be direct or indirect and have local, regional, or global consequences (Davidson *et al.* 2012; Spracklen and Garcia-Carreras 2015; de Magalhães *et al.* 2019). The most obvious direct impact of deforestation is biodiversity loss – species-rich forested areas are converted to species-poor agricultural lands. However, there are more-cryptic impacts resulting from deforestation and forest degradation, such as changes in local temperatures or regional precipitation regimes, or from increased global greenhouse gas emissions (Mollinari *et al.* 2019; Longo *et al.* 2020). These impacts can interact with others, amplifying their individual effects. For instance, changes in precipitation patterns can increase plant mortality, leading to more greenhouse gas emissions, which in turn contribute to further changes in climate (Nepstad *et al.* 2007; Esquivel-Muelbert *et al.* 2020).

Although both the direct drivers and the impacts of deforestation and forest degradation do not necessarily occur in isolation, we will discuss them separately, trying to acknowledge the role of different drivers across the Amazon, as well as their varied impacts. We start by presenting a general discussion about deforestation, followed by a detailed presentation of its main drivers, namely expansion of agriculture, ranching, infrastructure, and mining. Whenever possible, we also try to quantify the direct and indirect impacts of each individual driver. We then present a general framework of degradation of Amazonian forests, discussing in more detail its main drivers, including understory fires, edge effects, selective logging, and hunting.

This review was originally developed as Chapter 19 of the Science Panel for the Amazon Assessment Report (https://www.theamazonwewant.org/) (Berenguer *et al.* 2021).

DEFORESTATION – AN OVERVIEW

Deforestation is defined as the complete removal of an area's forest cover (Putz and Redford 2010). In the Amazon, 867,675 km^2 had been deforested by 2018 (MapBiomas 2020), equivalent to 14% of its originally forested area (Figure 1). Most deforestation has been concentrated in Brazil, which lost 741,759 km^2 of forests (MapBiomas 2020; Smith *et al.* 2021) – an area 15 times greater than that lost by Peru, the country with the second largest deforested area (Figure 2a). In relative terms, the country that lost most of its Amazon forest was Brazil (19%), followed by Ecuador (13%). To date, French Guiana, Suriname, and Venezuela have the greatest proportion of the remaining original vegetation cover: 99.9%, 97.9%, and 97.9%, respectively (Figure 2b).

Deforestation varies not only across space, but also across time. Between 1991 and 2006, annual deforestation was consistently above 20,000 km^2, peaking in 2003 when 31,828 km^2 of forests were lost (MapBiomas 2020). From 2007 to 2018, annual deforestation in the region was much lower, ranging between 9918 km^2 and 17,695 km^2 (Figure 3). By 1990, only 5% of the forests in the basin had been lost. However, this figure reached 9% in 2000 and 12% in 2010 (MapBiomas 2020; Smith *et al.* 2021).

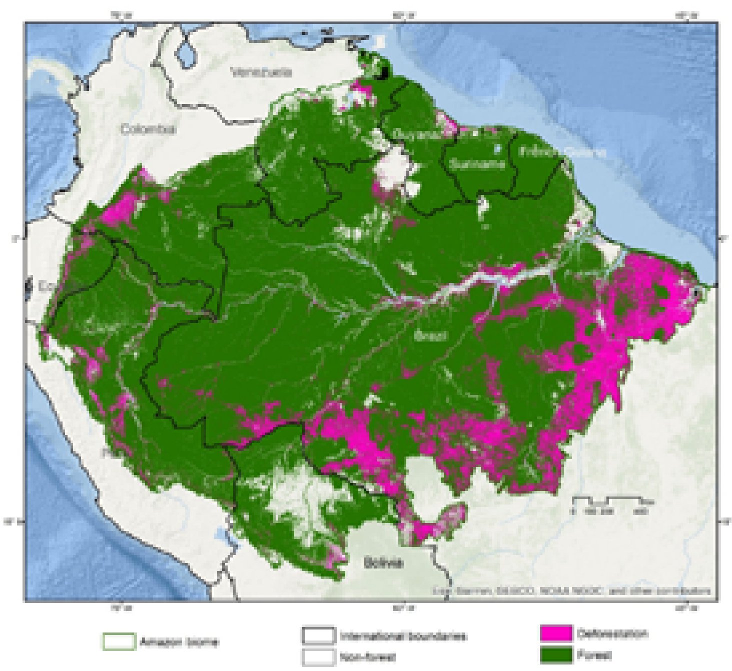

Figure 1. Current land occupied by either natural vegetation or pasture and agriculture across the Amazon biome. Cumulative deforestation data are shown up to 2018 (MapBiomas 2020).

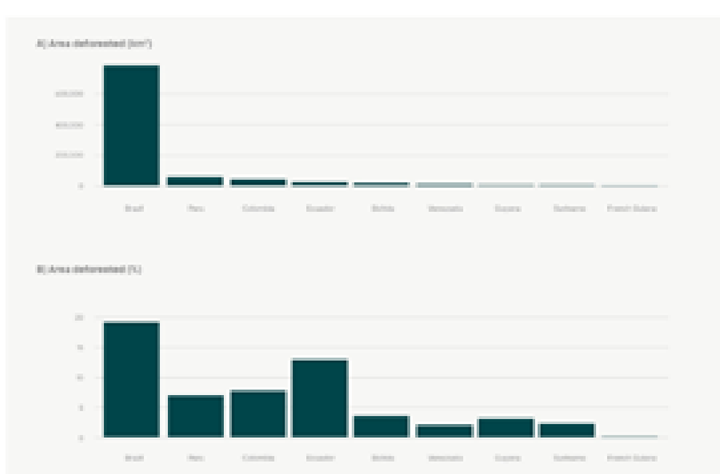

Figure 2. Country-level deforestation in the Amazon biome. **A** – Cumulative deforestation up to 2018; **B** – Percentage of the biome deforested in each Amazonian country or territory. Data obtained from MapBiomas (2020) and analyzed in accord with Smith *et al*. (2021).

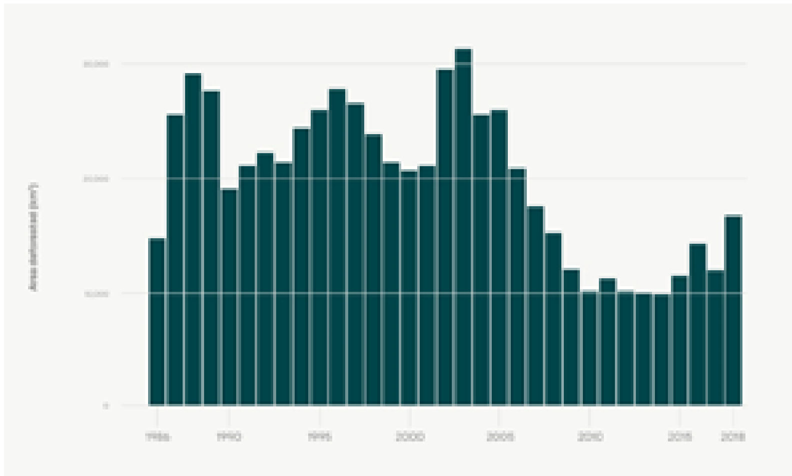

Figure 3. Annual deforestation across the Amazon biome. Deforestation data are for the period from 1986 to 2018 (MapBiomas 2020).

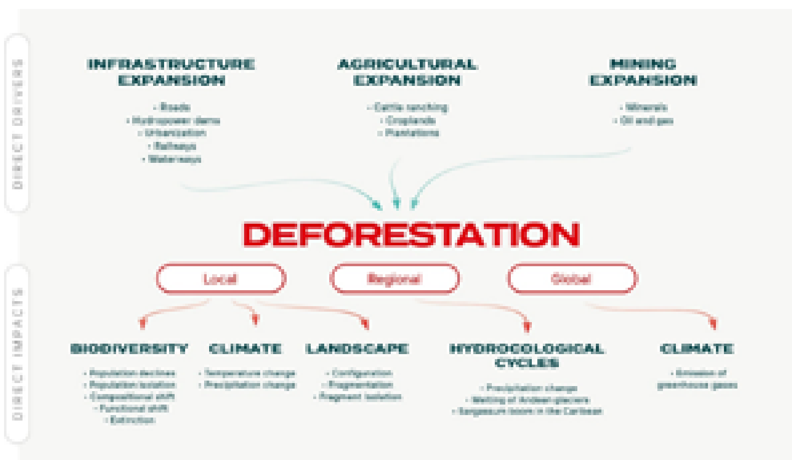

Figure 4. Direct drivers of deforestation and their direct impact at local, regional, and global scales.

Amazonian deforestation has been driven mainly by agricultural expansion (including both pastures and croplands), although other drivers also contribute, such as mining and infrastructure development, including urbanization and the building of roads, railways, waterways, and large-scale hydropower dams (Figure 4). These drivers often act together, creating positive feedbacks. For instance, after the building of large roads crossing the Brazilian Amazon, there was an influx of migrants to the region, creating new urban areas and expanding existing ones. In rural areas, numerous secondary roads branching off the main highways were constructed by agricultural settlers, leading to the well-known pattern of 'fish-bone' deforestation (Figure 5). In the sections below, we discuss each direct driver of deforestation individually, highlighting, whenever possible, how its relative importance differs across Amazonian countries.

Deforestation can lead to a wide range of direct ecological impacts that are locally, regionally, and globally relevant. Of the local impacts, biodiversity loss is extremely concerning, with various species of trees, mammals, birds, reptiles, amphibians, and terrestrial invertebrates classified as globally threatened (IUCN 2021). The number of threatened Amazonian species is highly conservative, as the majority of Amazonian species have not even had their status assessed (Supplementary Material, Appendix S1). Although to date there is no record of a regional extinction, some may have already occurred, especially in plants and invertebrates, given the large number of species yet to be described in these taxa (ter Steege *et al.* 2013; Lees and Pimm 2015; Stork 2018). Fine-scale endemism may also contribute to undetected extinctions because many species have restricted geographic distributions (Fernandes 2013), occurring in very small areas (Supplementary Material, Appendix S2).

Forest fragmentation, or the subdivision of remaining forest cover into variable-sized forest patches, is another local impact of deforestation that reshapes landscape configuration. An increase in forest fragmentation is caused by continued deforestation (Broadbent *et al.* 2008; Armenteras *et al.*

Figure 5. Deforestation driven by road building, urbanization, and agricultural expansion, resulting in a fishbone pattern of deforestation. Images from the BR-163 Highway and the Transamazon Highway in the Brazilian Amazon.

2017b; Numata *et al.* 2017; Laurance *et al.* 2018). Between 1999 and 2002, approximately 5000 new fragments were created annually due to deforestation in the Brazilian Amazon (Broadbent *et al.* 2008). Although most Amazonian forests remain in large, contiguous blocks, there are over 150,000 fragments with areas of 1-100 ha (Haddad *et al.* 2015).

The distribution of small forest fragments across the Amazon is not even; rather, fragmentation is concentrated along the southern and eastern edges, along major roads and rivers, and around urban centers (Vedovato *et al.* 2016; Montibeller *et al.* 2020). Deforestation also promotes fragment isolation, with forest patches becoming more distant from one another as well as from large contiguous forested areas (de Almeida *et al.* 2020). While fragment size affects the maintenance of viable populations of both animals and plants, fragment isolation disrupts dispersion and movement. The smaller the fragment, the smaller its chances of sustaining the original pool of forest species (Michalski and Peres 2005; Michalski *et al.* 2007; Laurance *et al.* 2011), with large-bodied animals and those that are highly dependent on forest habitat being particularly affected (Michalski and Peres 2007; Lees and Peres 2008). Fragment isolation is more harmful to species with low vagility, as these are unable to cross open, non-forest matrices (Lees and Peres 2009; Palmeirim *et al.* 2020). To date, negative impacts of fragment size and/or isolation have been detected throughout the Amazon, affecting leaf bryophytes, trees, palms, birds, carnivores, and primates (Michalski and Peres 2007; Laurance *et al.* 2011). Forest fragments also experience a whole range of edge effects, which lead to their degradation.

Local temperature and precipitation are also affected by deforestation. Land surface temperature is 1.05-3.06°C higher in pastures and croplands than in nearby forests, with this difference becoming more pronounced during the dry season (Maeda *et al.* 2021). Furthermore, as forest cover decreases at landscape scales, the landscape becomes hotter; landscapes with a lower number of remaining forest patches can be up to 2.5°C hotter than those with greater forest cover (Silvério *et al.* 2015). Forest loss also leads to reduced precipitation (Werth 2002; Spracklen *et al.* 2012) because 25-50% of Amazonian rainfall is recycled by the forest (Eltahir and Bras 1994). Therefore, forest loss causes a decrease in rainfall, increasing the risk of large-scale forest dieback. It is estimated that deforestation has already decreased precipitation by 1.8% across the Amazon (Spracklen and Garcia-Carreras 2015), although changes in rainfall patterns vary across the basin and between the wet and dry seasons (Costa and Pires 2010; Bagley *et al.* 2014). Additionally, widespread deforestation negatively influences precipitation outside the Amazon Basin, influencing regional hydrological cycles. The percentage of annual precipitation in the La Plata Basin (located in Argentina, Bolivia, Brazil, Paraguay, and Uruguay) that depends on recycled moisture transported by winds from the Amazon has been estimated at 16% (Yang and Dominguez 2019), 18-23% (Zemp *et al.*, 2014), 23% (Martinez and Dominguez 2014) and 70% (van der Ent *et al.* 2010). Even the lowest of these estimates would be catastrophic for the city of São Paulo, where severe droughts in 2014 and 2021 indicate that the city has no leeway to lose the water delivered to southeastern Brazil from Amazonia via the winds known as “flying rivers” (Fearnside 2021).

Regionally, Amazonian deforestation has surprising and very diverse impacts, such as accelerating glacier melting in the Andes and contributing to *Sargassum* blooms in the Caribbean. The burning of recently felled forests as part of the deforestation process (Supplementary Material, Appendix S3) releases black carbon to the atmosphere. Smoke plumes then transport black carbon to the Andes, where it can be deposited on glaciers, speeding up glacier melt. This process is highly seasonal, peaking during high-fire months (de Magalhães *et al.* 2019). Thousands of kilometers away, in the Caribbean Sea, recent *Sargassum* blooms are likely influenced by anomalous nutrient inputs into the Atlantic resulting from Amazonian deforestation (Wang *et al.* 2019). *Sargassum* blooms negatively impact tourism and fisheries and cause community shifts in seagrass meadows and increased coral mortality (van Tussenbroek *et al.* 2017).

At a global scale, greenhouse gas emissions are the most-pronounced impact of forest loss in the Amazon. Between 1980 and 2010, the Amazon lost an estimated 283.4 Tg C annually due to deforestation, resulting in yearly emissions of 1040.8 Tg CO_2 (Phillips *et al.* 2017). Deforestation-related emissions are not homogeneous in space or time; for example, Brazil's annual emissions from Amazonian deforestation are eight times greater than those of Bolivia, the second largest emitter in the basin (Table 1). Overall, emissions have decreased in the region, being higher in the 1980s than in the 2000s (Phillips *et al.* 2017).

Table 1. Estimated annual carbon loss due to deforestation in the Amazon between 1980-2010 (Phillips *et al.* 2017).

Country	**Carbon loss** (Tg C year–1)
Bolivia	28.6
Brazil	223.9
Colombia	6.5
Ecuador	2.5
French Guiana	1
Guyana	1
Peru	17.9
Suriname	1
Venezuela	1

AGRICULTURAL EXPANSION

Across the Amazon, deforestation has been driven mainly by agricultural expansion, particularly cattle ranching (Nepstad *et al.* 2009), due to a variety of public policies. In the Brazilian Amazon alone, it is estimated that 80% of the deforested area is occupied by pastures (MMA 2018). In the early 2000s, large-scale cropland expansion, principally soy, became increasingly important as a driver of deforestation. This pattern reversed in the late 2000s, partly due to extensive conservation policies, including the soy moratorium and the creation of protected areas (Soares-Filho *et al.* 2010; Macedo *et al.* 2012; Nepstad *et al.* 2014). Currently, soy expansion in the Brazilian Amazon occurs mostly on areas that were previously pastures instead of directly replacing forests (Song *et al.* 2021). Ranchers, for example in Mato Grosso, sell their pasturelands to soy planters and use the proceeds of the sales to buy much larger areas of cheap forest land in Pará to establish new ranches (Arima *et al.* 2011; Richards *et al.* 2014). This indirect effect means that conversion of a hectare of pasture to soy can have a greater impact on deforestation than directly clearing a hectare of forest to plant soy.

In Bolivia soy is expanding directly into forest; the region of Santa Cruz has been identified as the largest deforestation hotspot in the Amazon, mainly due to forest conversion to soy fields (Redo *et al.* 2011; Kalamandeen *et al.* 2018). Since the mid-2000s, oil palm has become a growing threat to Amazonian forests, especially in Colombia, Ecuador, Peru, and the eastern part of the Brazilian Amazon (Furumo and Aide 2017). Although oil palm plantations often replace other agricultural land uses, especially cattle ranching, it has also been documented directly replacing primary forests (Castiblanco *et al.* 2013; Gutiérrez-Vélez and DeFries 2013; de Almeida *et al.* 2020). For example, between 2007 and 2013, 11% of the deforestation in the Peruvian Amazon was driven by oil palm plantations (Vijay *et al.* 2018). Planting illicit crops, more specifically coca, is also a driver of deforestation, especially in Colombia, but also in Bolivia, Ecuador, and Peru (Armenteras *et al.* 2006; Dávalos *et al.* 2016). However, its impact on forest loss is much smaller than that caused by licit commodities (Armenteras *et al.* 2013a). Since 2016, following the peace agreement between the Colombian government and the Revolutionary Armed Forces of Colombia (FARC), the role of coca-driven deforestation has decreased, with areas previously in conflict being deforested for pasture, including inside protected areas (Clerici *et al.* 2020; Prem *et al.* 2020).

Direct impacts – Although croplands and pastures hold some animal species, the ecological communities in these areas are dramatically different from those of forests, both in terms of taxonomic and functional composition (Barlow *et al.* 2007a,b; Bregman *et al.* 2016), and almost all forest-dependent species are lost. Among agricultural land uses, pastures hold significantly more taxonomic diversity than areas of mechanized agriculture (*e.g.*, soy fields) for various taxa (Solar *et al.* 2015). Tree plantations also harbor an impoverished subset of forest species. For example, in an oil palm plantation in Peru, <5% of bird species were also found in forests (Srinivas and Koh 2016). In summary, the contribution of agricultural lands to Amazonian biodiversity conservation is negligible (Moura *et al.* 2013), highlighting the irreplaceable value of forests (Barlow *et al.* 2007a,b).

Indirect impacts – In addition to GHG emissions during the deforestation process, pastures further contribute to emissions due to regular burning (Supplementary Material, Appendix S3) and bovine enteric fermentation (Bustamante *et al.* 2012). Significant changes in the physical and chemical properties of the soil, such as soil compaction and changes in nutrient concentration (de Souza Braz *et al.* 2013; Fujisaki *et al.* 2015; Melo *et al.* 2017), are also a result of forest conversion to pastures and croplands in the Amazon. Pesticide and herbicide use in agricultural systems is often excessive in the region (Schiesari *et al.* 2013; Bogaerts *et al.* 2017). Little has been done to describe or quantify the impacts of this in terrestrial ecosystems, but some impacts are evident. Near a pasture treated with herbicides near Manaus, Amazonas, Brazil, frogs were found to have unusually high incidence of malformations and some formerly common species disappeared from locations nearest the site of herbicide use (Ferrante and Fearnside 2020).

INFRASTRUCTURE

Roads

Major official roads and highways (*i.e.*, those built by the government) extend deep into the Amazon; only the western part of the basin is largely road free (Figure 6). Official roads, even if unpaved, often spawn networks of unofficial roads (*i.e.*, those built by local actors), providing further access to previously inaccessible forests, resulting in the classic 'fishbone' deforestation pattern (Figure 5). In terms of total length, the network of unofficial roads is so extensive that it greatly surpasses official ones (Nascimento *et al.* 2021).

Figure 6. Planned (yellow), paved (red), and unpaved (brown) roads across the Amazon, as well as existing (black) and planned (purple) railways. The Amazon biome is outlined in green, while the Amazon Basin is outlined in blue.

Direct impacts – The impacts of roads on terrestrial wildlife in the Amazon are diverse and multi-faceted (Laurance *et al.* 2009). Their direct effects are dwarfed by their indirect impacts, but nonetheless remain important. First, roads lead to high levels of roadkill mortality. For example, over the course of 50 days of monitoring a 15.9-km stretch of road in Napo (in the western Amazon), 593 animals were killed, including reptiles, amphibians, birds, and mammals (Filius *et al.* 2020). Occasionally, roadkill includes threatened species, such as harpy eagles, giant anteaters, giant armadillos, giant otters, red-faced spider monkeys, lowland tapirs, and red-billed toucans (de Freitas *et al.* 2017; Medeiros 2019). Given the approximately 40,000 km of official roads across the Amazon, roadkill is highly underreported and understudied. Second, roads can act as direct drivers of habitat fragmentation, isolating populations on either side (Lees and Peres 2009). Widths of just 12–25 m restrict the movements of bird species adapted to the forest understory (Laurance *et al.* 2004, 2009).

Indirect impacts – The greatest impacts of roads are indirect. The construction of official roads (and subsequently unofficial roads) increases land values because it makes agriculture and ranching more profitable, since products can be transported to urban centers and ports (Perz *et al.* 2008). In turn, higher land prices lead to land speculation that motivates deforestation to secure land possession (Fearnside 2005). Roads also induce migration, leading to invasions and settlements (Mäki *et al.* 2001; Perz *et al.* 2007). As a result, the presence of roads is strongly associated with deforestation in the Amazonian portions of Brazil (Laurance *et al.* 2002; Pfaff *et al.* 2007), Peru (Naughton-Treves 2004; Chávez Michaelsen *et al.* 2013; Bax *et al.* 2016), and Ecuador. In the case of Ecuador, road construction is linked to oil concessions (Sierra 2000; Mena *et al.* 2006). The paving of official roads provokes direct deforestation along highways (Fearnside 2007; Asner *et al.* 2010) and induces displaced deforestation by increasing land values for use for soy planting and thereby favoring land sales by ranchers to soy planters.

Roads also stimulate forest degradation, including selective logging (Asner *et al.* 2006; Amachar *et al.* 2009; Merry *et al.* 2009), as they provide machinery access (*e.g.*, logging trucks, skidders) to areas that still contain valuable timber. The opposite can also be true; often loggers open small roads to extract target trees (Uhl and Vieira 1989; Johns *et al.* 1996; Gutierrez-Velez and MacDicken 2008), which can then drive additional degradation. Proximity to roads is also highly correlated with forest fires, even in non-drought years (Alencar *et al.* 2004). This is due to the influx of migrants and agricultural expansion surrounding roads (Figure 5), thus resulting in more deforestation and pasture-related fires, which can escape into forested areas (Supplementary Material, Appendix S3).

Hydropower dams

Substantial energy resources exist in the Amazon, some actively exploited and others as potential reserves (Ferreira *et al.* 2014). There are currently 307 hydropower dams either in operation or under construction, with proposals for at least 239 more (Figure 7). Of these, some are considered mega-dams with >1 GW capacity. Hydroelectric dams not only disrupt aquatic ecosystems – they also have severe consequences for terrestrial ones.

Direct impacts – Most hydropower dams require an area to be flooded, acting as a reservoir. Both floodplain (*várzea*) and upland (*terra firme*) forests are killed by reservoir flooding (Lees *et al.* 2016), resulting in high levels of CO_2 and CH_4 emissions due to the decomposition of submerged trees (Figure 8). Although seasonally flooded forests can survive several months under water, they die if flooded year-round. Forests bordering the reservoir also suffer stress, including reductions in the rates of photosynthesis of trees (dos Santos Junior *et al.* 2015). Depending on local topography, islands containing upland forests can be formed after flooding. Newly formed islands suffer from edge effects and fragmentation, as they have been cut off from the rest of the previously contiguous forest. Reservoir islands have significantly different species composition of both fauna and flora than adjacent mainland areas (Benchimol and Peres 2015; Tourinho *et al*. 2020), a pattern particularly pronounced on small islands, where large-bodied fauna become extinct (Benchimol and Peres 2016). A recent study found that invertebrates are also negatively impacted by flooding; one study found that thirty years after the reservoir was filled, many islands completely lacked dung beetle species (Storck-Tonon *et al.* 2020). Dams also affect forests downstream; altered flood regimes can even impact forests 125 km away from the reservoir (Schöngart *et al.* 2021), resulting in large-scale tree mortality (Assahira *et al.* 2017), leading to the loss of crucial habitat for a variety of organisms (*e.g.*, arboreal mammals, birds, and plants), which can become locally extinct (Lees *et al.* 2016). Finally, dams can also affect the status of protected areas; for example, the planned São Luiz do Tapajós Dam resulted in part of Amazonia National Park being degazetted (Fearnside 2015).

Indirect impacts – The construction of hydroelectric dams also leads to indirect impacts; for example, the population attracted to the region boosts deforestation in the area surrounding the dam (Jiang *et al.* 2018; Velastegui-Montoya *et al.* 2020). Furthermore, dam construction often results in socio-economic problems, such as increases in violence and lawlessness, and the displacement and destruction of the livelihoods of both Indigenous and non-Indigenous communities (Randell 2017; Castro-Diaz *et al.* 2018; Athayde *et al.* 2019; Moran 2020).

Figure 7. Planned and active hydropower dams across the Amazon biome, as well as waterways. The Amazon biome is outlined in green, while the Amazonian Basin is outlined in blue. Sources: Venticinque *et al.* (2016), RAISG (2020).

Urbanization

Approximately 70% of Amazonians live in urban centers (Padoch *et al.* 2008; Parry *et al.* 2014), with the largest city, Manaus, hosting >2.2 million inhabitants (IBGE 2021). Urban expansion is currently concentrated in small and medium cities (Richards and VanWey 2015; Tritsch and Le Tourneau 2016) and results from various processes, from rural-urban and urban-urban migration to displacement due to armed conflict and intrinsic population growth (Rudel *et al.* 2002; Perz *et al.* 2010; Randell and VanWey 2014; Camargo *et al.* 2020).

Direct impacts – Urban and suburban sprawl increase deforestation (Jorge *et al.* 2020), especially in frontier settlements. Amazonian urban biodiversity is poorly studied but is generally taxonomically depauperate and typically dominated by a small subset of common species found in secondary habitats (Lees and Moura 2017; Rico-Silva *et al.* 2021). As observed elsewhere, urbanization also influences the local climate, which becomes hotter (de Souza *et al.* 2016; de Oliveira *et al.* 2020).

Indirect impacts – Many rural-urban migrants continue to consume forest resources, therefore playing a role in forest-use decisions (Padoch *et al.* 2008; Chaves *et al.* 2021). For example, surveys of two Amazonian cities on the Madeira River showed that 79% of urban households consumed bushmeat, including terrestrial mammals and birds (Parry *et al.* 2014). Animals hunted for urban consumption can be sourced from forests located up to 800 km away and frequently include threatened species, such as the black curassow, giant armadillo, gray tinamou, red-faced spider monkey, lowland tapir, red-billed toucan, and white-lipped peccary (Bodmer and Lozano 2001; Parry *et al.* 2010, 2014; Bizri *et al.* 2020; IUCN 2021).

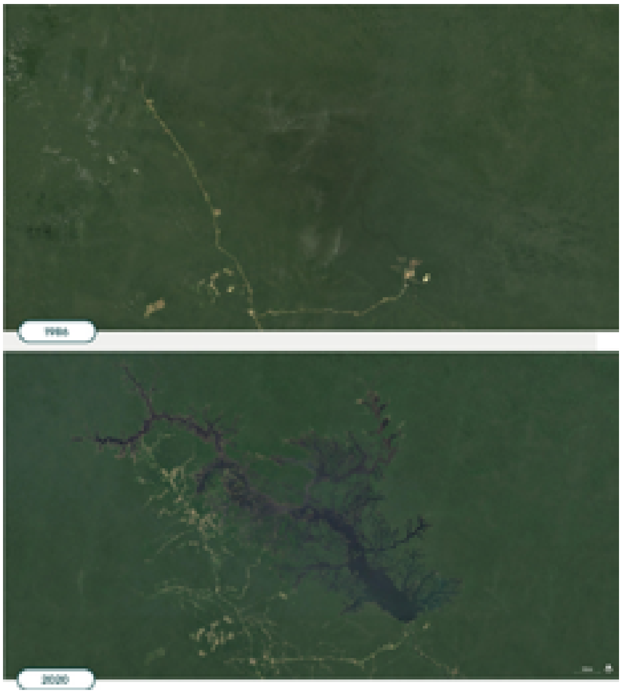

Figure 8. Flooding of the reservoir of the Balbina hydropower dam in Brazil. **A** – Before flooding (1986); **B** – after flooding (2020).

Railways and waterways

Across the Amazon, the density of railways and waterways is much lower than that of roads (Figures 6 and 7). As a result, there are few studies on the impacts of these forms of infrastructure on terrestrial ecosystems.

Direct impacts – Opening railways in the Amazon results in deforestation and fragmentation of the forest that is cut by the rail line, impacting the movement of animals that cannot cross even narrow clearings (Laurance *et al.* 2009). There is currently no published investigation into the direct impacts of waterways on Amazonian forests.

Indirect impacts – The limited movement of passengers along railways means that levels of adjacent deforestation are far lower relative to roads. However, railways can still indirectly induce deforestation. For example, between 1984 and 2014, approximately 30,000 km^2 of forests were lost in the area of influence of the Carajás Railway in the Brazilian Amazon (Santos *et al.* 2020). However, some of these impacts are hard to disentangle from that of roads built near some of the railway stations. In addition to carrying iron ore, the Carajás railway operates passenger trains from the area of São Luis, Maranhão to Marabá and Parauapebas, in central Pará; over the decades since this began in 1985 the flow of migrants arriving by train from Maranhão has been a major factor in the deforestation of central Pará (Fearnside 2001a).

Railways present important risks for the future of the Amazon. The "*Ferro Grão*" Railway, also located in the Brazilian Amazon, would link soy areas in Mato Grosso (in the southern Amazon) to the port at Miritituba on the lower Tapajós River, with access to the Amazon River (Figure 6). The lower freight costs from Mato Grosso can be expected to contribute to the conversion of pasture to soybeans, leading to displaced deforestation, as seen elsewhere when roads were paved (Fearnside *et al.* 2013). Another proposed railway would connect Mato Grosso to the port of Bayóvar in the Peruvian state of Piura (Dourojeanni 2015). This railway, known as the "Railway to the Pacific" in Brazil and the "Interoceanic Railway" in Peru, could also contribute to soy expansion and displaced deforestation in Brazil. The same pattern of displaced deforestation is expected as a result of the proposed Tapajós and Tocantins waterways, which would stimulate pasture conversion to large croplands (Fearnside 2001b).

MINING

Mining is a major source of environmental impacts in the Amazon, with 45,065 mining concessions either under operation or waiting for approval, of which 21,536 overlap with protected areas and Indigenous lands (Figure 9). While some minerals, such as bauxite, copper, and iron ore (Souza-Filho *et al.* 2021), are extracted through legal operations conducted by large corporations (Sonter *et al.* 2017), gold mining is largely illegal (Sousa *et al.* 2011; Asner and Tupayachi 2017). Despite its illegality, gold mining has become far from artisanal, and is now a semi-mechanized activity, employing large and expensive machinery such as prospecting drills and hydraulic excavators (Tedesco 2013; Massaro and de Theije 2018; Springer *et al.* 2020).

Direct impacts – Overall, the extent of mining-driven deforestation is far smaller than that caused by agricultural expansion. However, it still represents the main driver of forest loss in French Guiana, Guyana, Suriname and parts of Peru (Dezécache *et al.* 2017; Caballero-Espejo *et al.* 2018). For example, in Guyana, mining led to the loss of approximately 89,000 ha of forests between 1990 and 2019, an area 18 times larger than that lost to agricultural expansion in the same period (Guyana Forestry Commission and Indufor 2020). In Suriname, 71% of deforestation is attributed to mining (Suriname 2019). In the southeastern Peruvian Amazon, approximately 96,000 ha were deforested due to mining between 1985 and 2017 (Caballero-Espejo *et al.* 2018), including areas inside the Tambopata National Reserve and its buffer zone (Asner and Tupayachi 2017). In a single year, deforestation due to gold mining in the Madre de Dios region resulted in the direct loss of 1.12 Tg C (Csillik and Asner 2020).

Another direct impact of mining is the potential biodiversity loss in one of the Amazon's smallest ecosystems, the cangas. This is a ferruginous savanna-like ecosystem associated with ironstone outcrops in the eastern Amazon (Skirycz *et al.* 2014). It originally occupied an area of 144

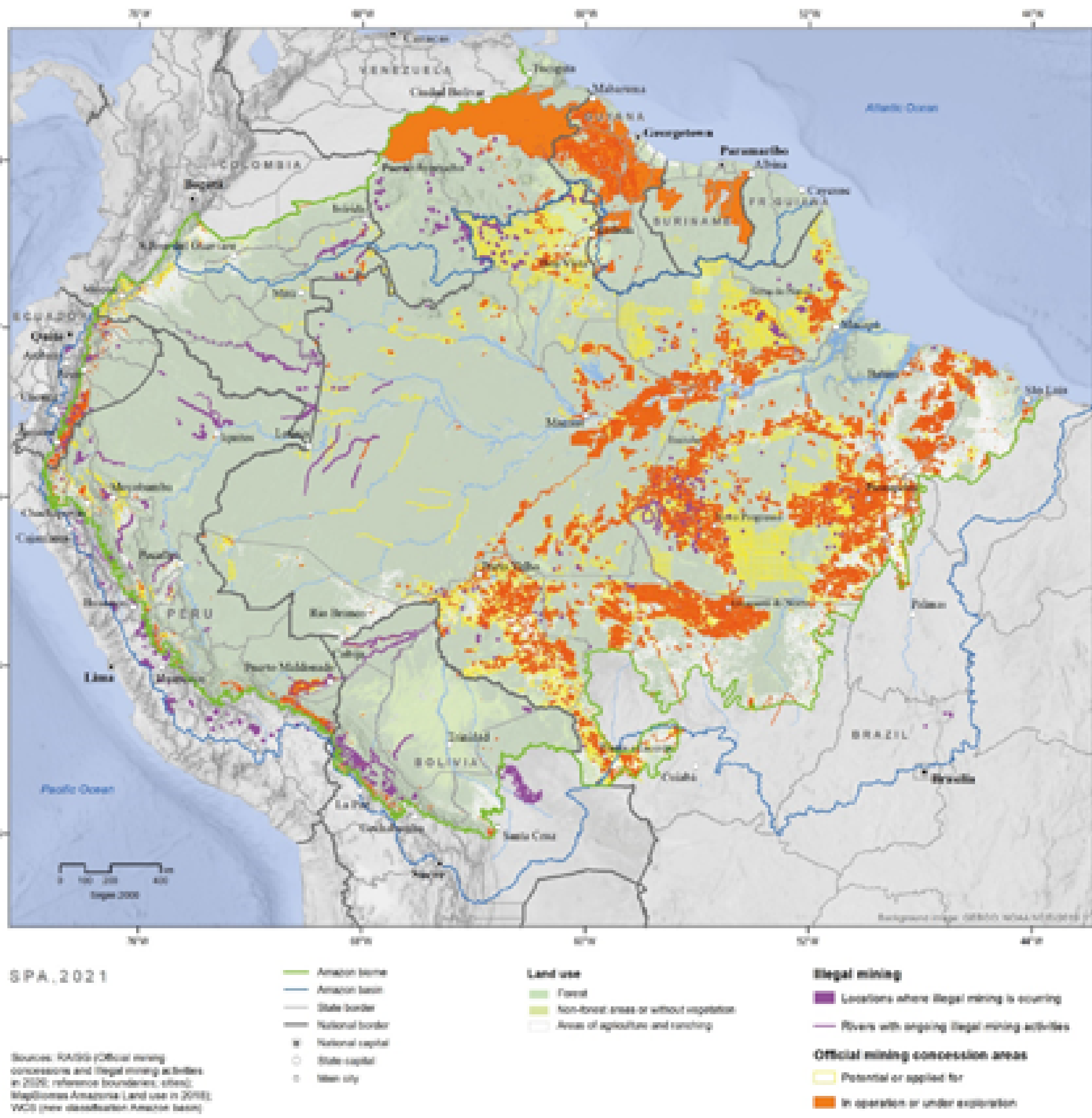

Figure 9. Illegal (purple) and legal mining that is either planned (yellow) or active (orange) across the Amazon. The Amazon biome is outlined in green, while the Amazon Basin is outlined in blue. Sources: Venticinque *et al*. (2016), RAISG (2020).

km^2, but 20% of this area has been lost to mining of iron ore (Souza-Filho *et al.* 2019). Despite the small area occupied, the Amazonian cangas has 38 endemic vascular plants, 24 of which are considered rare (Giulietti *et al.* 2019). The cangas is also rich in endemic cave-dwelling fauna (Giupponi and Miranda 2016; Jaffé *et al.* 2018). Little is known about the impacts of mining in this unique ecosystem.

Indirect impacts – Indirect impacts of mining activities are often greater than direct ones. In Brazil, for instance, mining was responsible for the loss of 11,670 km^2 of Amazonian forests between 2000 and 2015, corresponding to 9% of all deforestation in that period (Sonter *et al.* 2017), with effects extending 70 km beyond the boundaries of mining concessions. Mining also stimulates forest loss by motivating the construction of roads and other transportation infrastructure that leads to high levels of human migration and consequent deforestation (Sonter *et al.* 2017; Fearnside 2019). The Carajás Railway, in the Brazilian Amazon, is an example of this. Finally, mining can lead to increased logging and deforestation for charcoal production, especially to be used in pig iron production (Fearnside 1989a; Sonter *et al.* 2015).

OIL AND GAS

Oil and gas exploitation occur mainly in the western Amazon, where extraction of crude oil started in the 1940s, and grew substantially from the 1970s onwards (San Sebastián and Hurtig 2004; Finer *et al.* 2009). Currently, 192 oil and gas leases are under production and 33 are being prospected; some of these overlap with protected areas and Indigenous lands (Figure 10).

Direct impacts – Major threats from hydrocarbon development include deforestation and oil spills, as has occurred on numerous occasions in Colombia, Ecuador, and Peru (San Sebastian and Hurtig 2004; Vargas-Cuentas and Gonzalez 2019; Cardona 2020; Esterhuyse *et al.* 2022). For example, in the northeastern Ecuadorian Amazon, 464 oil spills occurred between 2001 and 2011, totaling 10,000 metric tons of crude oil released into the environment (Durango-Cordero *et al.* 2018). This corresponds to approximately ¼ of the amount leaked in the Exxon Valdez oil spill. However, the number of oil spills across the Amazon is largely underestimated (Orta-Martínez *et al.* 2007). The impacts of oil spills on terrestrial ecosystems remain poorly understood. Nevertheless, it has been reported that lowland tapirs, pacas, collared peccaries, and red-brocket deer consume soil and water contaminated by oil spilled from oil tanks and abandoned wells (Orta-Martínez *et al.* 2018). It is unclear how this consumption may affect animal populations.

Figure 10. Oil and gas leases across the Amazon. The Amazon biome is outlined in green, while the Amazonian Basin is outlined in blue. Sources: Venticinque *et al*. (2016), RAISG (2020).

Indirect impacts – As is the case of mineral exploitation, indirect effects of oil and gas exploitation on terrestrial ecosystems dwarf direct ones. The construction of a large road network to access oil fields has led to colonization of previously remote areas, especially in Ecuador, resulting in increased deforestation (Bilsborrow *et al.* 2004). Animal populations around these roads are negatively affected (Zapata-Ríos *et al.* 2006), with large and medium-sized mammals and game birds declining by 80% (Suárez *et al.* 2013). Some of these roads penetrate protected areas and Indigenous lands, where they have led to deforestation, habitat fragmentation, logging, overhunting, vehicle-wildlife collision, and soil erosion (Finer *et al.* 2009). Plans for a massive oil and gas project in a 740,000 km^2 area in Brazil's state of Amazonas increase the likelihood of building the AM-366 highway, branching of the controversial BR-319 (Manaus-Porto Velho) highway, thus opening the vast "Trans-Purus" area west of the Purus River to the entry of deforesters (Fearnside 2022a).

DEGRADATION – AN OVERVIEW

Forest degradation is defined as the reduction of the overall capacity of a forest to supply goods and services (Parrotta *et al.* 2012), representing a loss in ecological value of the area affected (Putz and Redford 2010). While deforestation is binary (i.e., either the forest is present or absent), forest degradation is characterized by an impact gradient, ranging from forests with little, although significant, loss of ecological value, to those suffering with severe disruption to ecosystem functions and processes (Berenguer *et al.* 2014; Longo *et al.* 2020; Barreto *et al.* 2021). In total, approximately 1 million km^2 of Amazonian forests were degraded by 2017 (Figure 11), equivalent to 17% of the Amazon forest, mostly in Brazil (Bullock *et al.* 2020a,b). These degraded forests are a persistent part of the landscape, as only 14% of them were later deforested (Bullock *et al.* 2020b).

A variety of anthropogenic disturbances act as direct drivers of forest degradation in the Amazon (Figure 12), such as understory fires, selective logging, edge effects, hunting, and climate change (Barlow *et al.* 2016; Bustamante *et al.* 2016; de Andrade *et al.* 2017; Phillips *et al.* 2017; Lapola *et al*. 2023). A forest can be degraded by the occurrence of a single or multiple disturbances (Nepstad *et al.* 1999; Michalski and Peres 2017). For example, a forest fragment experiencing edge effects may also be logged and/or burned (Figure 13). Between 1995 and 2017, 29% of the degraded forest across the biome experienced multiple disturbances (Bullock *et al.* 2020b). Furthermore, climate change is an omnipresent driver of degradation, affecting all Amazonian forests, whether already degraded or not (Flores *et al*. 2024)

A disturbed Amazonian forest can be characterized as degraded due to significant changes in its structure, microclimate, and biodiversity, all of which impact ecosystem functions and processes. For example, understory fires, selective logging, and edge effects can lead to elevated tree mortality, increased liana dominance, greater presence of canopy gaps, decreased forest basal area and carbon stocks, changes in stem density, and a decrease in the presence of large trees, accompanied by an increase in the occurrence of small-diameter individuals (Uhl and Vieira 1989; Pereira *et al.* 2002; Laurance *et al.* 2006, 2011; Schulze and Zweede 2006; Barlow and Peres 2008; Balch *et al.* 2011; Berenguer *et al.* 2014; Brando *et al.* 2014; Alencar *et al.* 2015; da Silva *et al.* 2018). These structural changes can result in significantly higher light intensity, temperature, wind exposure, and vapor pressure deficit, as well as lower air and soil humidity (Kapos 1989; Balch *et al.* 2008; Laurance *et al.* 2011; Mollinari *et al.* 2019). These abiotic and biotic changes affect biodiversity, which is further impacted by hunting. Communities of both fauna and flora will experience compositional and functional shifts, with some species declining severely, leading to local extinctions (Zapata-Ríos *et al.* 2009; de Andrade *et al.* 2014; Barlow *et al.* 2016; Paolucci *et al.* 2016; Miranda *et al.* 2020). The duration of the impacts of anthropogenic disturbances on Amazonian forests vary depending on the nature, frequency, and intensity of the disturbance; while logged forests may return to baseline carbon stocks within a few decades (Rutishauser *et al.* 2015), burned forests may never recover their original stocks (da Silva *et al.* 2018). Recovery of degraded forests is also dependent on their landscape context, *i.e.*, whether there are nearby forests that can act as sources of seeds and animals, thus speeding up recovery.

There is a large gap in our understanding of the regional impacts of forest degradation; a knowledge gap with an urgent need to be filled. Globally, the main impact of forest degradation is an increase in greenhouse gas emissions due to carbon loss (Aguiar *et al.* 2016). It is estimated that CO_2 emissions resulting from forest degradation already surpasses those from deforestation (Baccini *et al.* 2017; Qin *et al.* 2021).

UNDERSTORY FIRES

In most years, and in most undisturbed forests, the high moisture load in the understory of Amazonian primary forests keeps flammability levels close to zero (Nepstad *et al.* 2004; Ray *et al.* 2005, 2010). However, thousands of hectares of forests burn across the basin every year (Aragão *et al.* 2018; Withey *et al.* 2018). These understory fires, also called forest fires or wildfires, spread slowly, have flame heights of 30-50 cm, and release little energy (≤ 250 kW m^{-1}) (Cochrane 2003; Brando *et al.* 2014). However, their impacts can be enormous as Amazonian forests have not co-evolved with fires.

Direct impacts – Understory fires cause important long-term ecological impacts. They cause high levels of stem mortality, negatively affecting carbon stocks (Barlow *et al.* 2003; Berenguer *et al.* 2014; Brando *et al.* 2019), and forests

Figure 11. Forests degraded (red) and deforested (white) between 1995-2017 across the Amazon Basin (Bullock et al. 2020b). The Amazon biome is outlined in green, while the Amazonian limits are outlined in blue. Areas deforested are represented in white (MapBiomas 2020). Sources: Venticinque *et al*. (2016), RAISG (2020).

Figure 12. Direct drivers of forest degradation in Amazonia.

Figure 13. A small forest fragment, surrounded by soy fields, that has been selectively logged and then burned during the 2015 El Niño, in Belterra, Pará, Brazil. Photo: Marizilda Cruppe/Rede Amzônia Sustentável.

take many years to recover. One study estimated that burned forests have carbon stocks that are 25% lower than expected 30 years after fires, with growth and mortality dynamics suggesting recovery had plateaued (da Silva *et al.* 2018). Fire impacts also vary regionally. Mortality rates tend to be lower in forests in the drier regions of the Amazon, potentially reflecting regional variation in bark thickness (Staver *et al.* 2020). Impacts are much higher in flooded forests than in *terra firme* (Supplementary Material, Appendix S4). In the southern part of the basin, in the ecotone between the Amazon and the Cerrado, native and exotic grass species have been observed to invade burned forests (Silvério *et al.* 2013) – a pattern not recorded elsewhere in the region. In the southwestern part of the basin, burned forests have experienced an increase in dominance by native bamboo species (Ziccardi *et al.* 2019; da Silva *et al.* 2021). Both grass and bamboo invasion significantly increase the flammability of these already burned forests (Silvério *et al.* 2013; Dalagnol *et al.* 2018).

High tree mortality caused by understory fires leads to significant taxonomic and functional changes in the plant community, which loses high wood-density climax species and sees a dominance of light-wood pioneer species (Barlow *et al.* 2012; Berenguer *et al.* 2018; Ziccardi *et al.* 2021). It is currently unknown whether burned forests will eventually return to their original plant community composition. Due to changes in forest structure and in the abundance of fruiting trees, fauna is also impacted by understory fires. For example, fires extirpate many forest specialist birds and mammals, while favoring species that occur in forest edges and secondary forests (Barlow and Peres 2004a,b, 2006). Additionally, understory fires negatively affect the abundance of several orders of leaf-litter invertebrates, such as Coleoptera, Collembola, Dermaptera, Diptera, Formicidae, Isoptera, Hemiptera, and Orthoptera (Silveira *et al.* 2010; França *et al.* 2020). These changes are long-lasting even in continuous forests where there should be no barriers to recolonization (Mestre *et al.* 2013). All these direct impacts are much greater in forests that have burned multiple times, which results in structure that resembles that of a young secondary forest, with an open canopy and few large trees (Barlow and Peres 2008).

Future of fires and their impacts – Interactions between climate and land-use change across the Amazon can create the conditions needed for more widespread and intense fires (Malhi *et al.* 2008; de Faria *et al.* 2017; Brando *et al.* 2019). As the climate changes, we expect to observe increased frequency of extreme weather events and warmer climatic conditions (de Faria *et al.* 2017; Le Page *et al.* 2017; Fonseca *et al.* 2019). At the same time, deforestation continues to promote forest fragmentation and associated edge effects (Alencar *et al.* 2006; Armenteras *et al.* 2017a). In some parts of the Amazon we can already observe how interactions among these factors have contributed to larger and more frequent understory fires that burned close to 85,000 km^2 of primary forests in the southern Amazon during the 2000s (Morton *et al.* 2013; Aragão *et al.* 2018). Continued changes in climate and land use in the near future may trigger fires burning even larger areas (Pueyo *et al*. 2010; Le Page *et al.* 2017; Brando *et al.* 2020a,b). Consequently, fires could become the main source of carbon emissions in the Amazon, surpassing those associated with deforestation (Aragão *et al.* 2018; Brando *et al.* 2020a,b).

A major cause for concern is that the current transformations in forests caused by climate and land-use change will not only burn large areas but will also kill more trees than they currently do. In the southeastern Amazon, an increase of 100 kW/m in fire-line intensity results in tree mortality increasing by 10% (Brando *et al.* 2014). With more edges and drier climatic conditions, we expect fire-line intensity to increase greatly, potentially causing the mortality of many more trees. In addition, some projections point to a potential expansion of fire geography to historically wetter areas, a likely effect of climate and land-use change.

EDGE EFFECTS

Between 2001 and 2015, around 180,000 km^2 of forest edges were created in the Amazon (Silva Junior *et al.* 2020). The resulting proliferation in edge habitat, often with no habitat 'core,' is ubiquitous in farm-frontier landscapes in the Amazonian parts of Brazil (Fearnside 2005; Broadbent *et al.* 2008; Numata *et al.* 2017; Silva Junior *et al.* 2018), Bolivia (Paneque-Gálvez *et al.* 2013), Colombia, Ecuador, and Peru (Armenteras *et al.* 2017b).

Direct impacts – At local scales, increases in light intensity, air temperature, vapor pressure deficit, and wind exposure, accompanied by decreases in air humidity and soil moisture, result in desiccation around edges (Kapos 1989; Broadbent *et al.* 2008; Laurance *et al.* 2018), which may extend hundreds of meters into adjacent forests (Briant *et al.* 2010). This change in microclimate contributes to elevated tree mortality, which in turn leads to biomass collapse, especially within the first 100 m of a forest edge (Laurance *et al.* 1997; Numata *et al.* 2011). Across the Amazon, 947 Tg C were lost between 2001 and 2015 due to edge effects, representing a third of the losses from deforestation in the same period (Silva Junior *et al.* 2020). Some of the carbon in the dead biomass near forest edges is transferred to the soil carbon pool, which increases near edges (Barros and Fearnside 2016), although eventually this carbon can be expected to emitted to the atmosphere as the intact forest soil is losing carbon (Barros and Fearnside 2019). Carbon losses from the vegetation are not offset by tree growth or recruitment; forest edges suffer a drastic change in species composition, becoming dominated by lianas and trees of smaller size and with low wood density, which store less carbon (Laurance *et al.* 2006; Michalski *et al.* 2007). Ultimately, the proliferation of pioneer trees causes the parts of the forest that are close to an edge to have higher tree densities than in the parts further away from an edge (Laurance *et al.* 2011).

It is not only the flora that is directly impacted by edge effects; both vertebrate and invertebrate fauna also experience considerable compositional and functional shifts, with some species thriving while others decline (Santos-Filho *et al.* 2012; Bitencourt *et al.* 2020). Overall, generalist species are favored by edge habitats, while specialists become restricted to the forest core. This may lead to local extinctions of specialist species unable to adapt to the new disturbed conditions, favoring edge and gap specialist species or even facilitating colonization and range expansion for non-forest species (Mahood *et al.* 2012; Rutt *et al.* 2019; Palmeirim *et al.* 2020). For example, ungulates avoid forest edges, while rodents have similar abundances in forest edges and cores (Norris *et al.* 2008). Among invertebrates, a striking example is that of leaf-cutting ants; within the first 50 m the density of colonies increases almost 20-fold when compared to the interior of the forest (Dohm *et al.* 2011).

Indirect impacts – Forest edges are more susceptible to other types of disturbance (Brando *et al.* 2019), especially understory fires (Armenteras *et al.* 2013b,c; Devisscher *et al.* 2016; Silva Junior *et al.* 2018). This is mediated by changes in the structure and composition of the vegetation, in addition to the microclimatic alterations that occur when an edge is created (Cochrane 2003), which are exacerbated by climate change (Cochrane and Laurance 2008; Cochrane and Barber 2009). Fragmented forest regions in the basin experience a higher frequency of forest fires, including Bolivia (Maillard *et al.* 2020), Brazil (da Silva *et al.* 2018; Silva *et al.* 2018; Silvério *et al.* 2019), and Colombia (Armenteras *et al.* 2013b, 2017b).

LOGGING

Timber production through selective logging is one of the most important activities and land uses in tropical forest areas (Edwards *et al.* 2014) (Figure 14). The Pan-Amazonian countries represent 13% of the tropical sawnwood production, where Brazil alone is responsible for more than half (52%) of the Pan-Amazonian production followed by Ecuador (11%), Peru (10%), and Bolivia (10%). Venezuela, Colombia, Suriname, and Guyana represent the remaining 17% (Silvério *et al.* 2019; Matricardi *et al.* 2020), concentrated mostly along the deforestation frontier and surrounding major logging centers (Hummel *et al.* 2010). Selective logging is the second most common driver of forest degradation in the Brazilian Amazon, behind only edge effects (Matricardi *et al.* 2020).

Direct impacts – The illegality of logging in the countries of the Amazon Basin is commonly associated with conventional logging practices, which differ from reduced-impact logging (RIL). Conventional logging extracts a higher amount of timber per hectare (*e.g.*, volume and number of species) and does not follow a coherent infrastructure extraction plan that allows less impact for future harvest (*e.g.*, more roads and logging decks) (Sist and Ferreira 2007; Lima *et al.* 2020). Conventional logging practices increase soil compaction from unplanned skid trails (DeArmond *et al.* 2019) and have a larger impact on reducing carbon stocks (Sasaki *et al.* 2016), increasing necromass and tree falls (Schulze and Zweede 2006; Palace *et al.* 2007), and enhancing CO_2 emissions

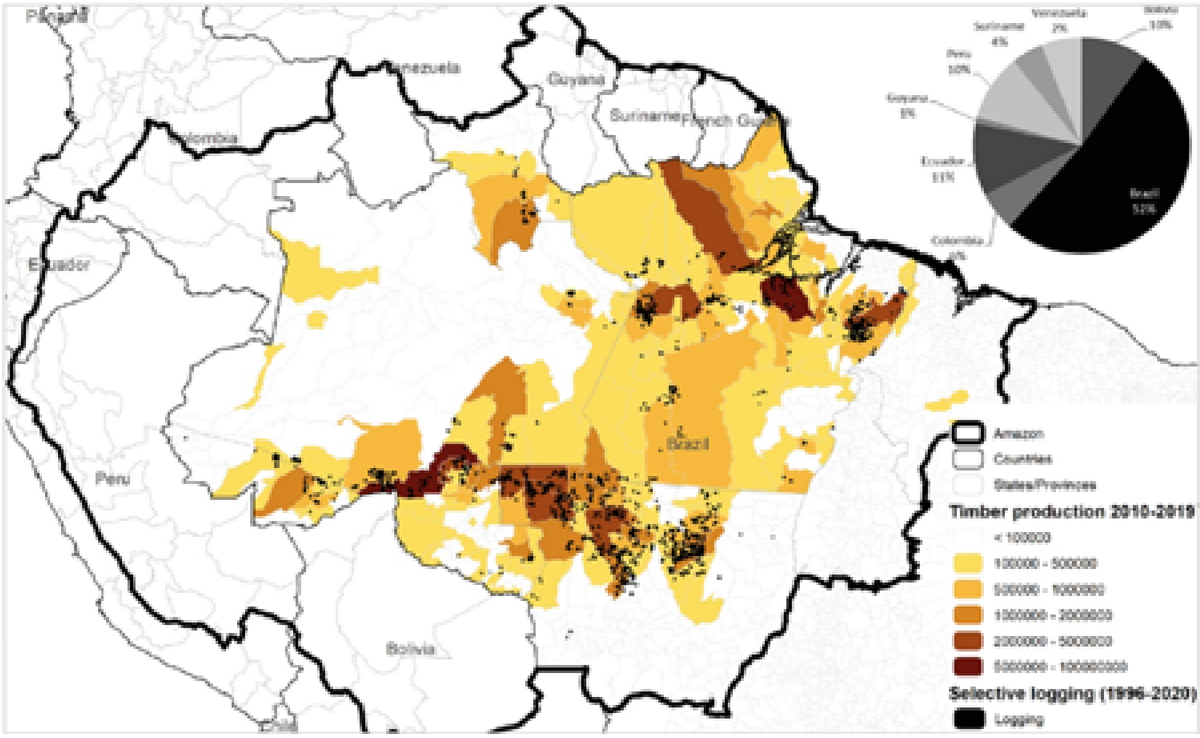

Figure 14. Selective logging across Amazonia. Pie chart – distribution of timber production in Amazonian countries (ITTO 2021). Map - legal timber production by Brazilian municipality from 2010 to 2019 (IBGE 2020).

(up to 30%) when compared with unlogged forest (Blanc *et al.* 2009; Pearson *et al.* 2014). In addition, conventional logging practices have greater impacts on biodiversity when compared to RIL, including reducing species abundance, richness, and phylogenetic and function diversity, mainly during the first years after logging (Azevedo-Ramos *et al.* 2006; Montejo-Kovacevich *et al.* 2018; Mestre *et al.* 2020; Jacob *et al.* 2021). Changes in species richness and abundance may in part be explained by post-logging increases in individuals' physiological stress (França *et al.* 2016). Ultimately, these lead to subsequent impacts on ecosystem processes; for example, in the Brazilian Amazon, selective logging led to the decline of dung beetle richness and significantly changed their community composition, which, in turn, decreased rates of soil bioturbation, a function performed by these animals (França *et al.* 2017). Distinct logging practices also impact ecosystem dynamics and services in logged forests in the Amazon. Logging affects energy and water fluxes due to changes in albedo and surface roughness caused by high levels of canopy openness, mainly in the short-term (1-3 years) (Huang *et al.* 2020). These practices also promote warmer temperatures inside the forest (Mollinari *et al.* 2019), and depending on the intensity of extraction, biomass recovery for further cutting cycles is compromised.

Commercial production cannot be sustained after the first cutting cycle, even assuming reduced-impact logging practices and compliance with Brazil's regulations for supposedly "sustainable" forest management (Sist *et al.* 2021). When a second cut occurs, it is to harvest less-valuable species that were not harvested in the initial cut rather than regenerating individuals of the most valuable species (Richardson and Peres 2016). The slow growth rates of Amazonian hardwoods make a biologically sustainable management system completely unviable in economic terms (Sist *et al.* 2021), and, although subsidies to compensate for this are theoretically possible (Fearnside 1989b), the amounts that would need to be offered and/or the size and timing of an assumed subsequent market for environmental services make this option unreasonable as a conservation priority (Fearnside 2003, 2022b).

Indirect impacts – The road network created by selective logging provides access to new hunting grounds (Robinson *et al.* 1999), which can lead to declines in animal populations. Logging also facilitates the occurrence of understory fires; the intense canopy damage caused by logging activities leads to microclimate changes in the first two years following the logging operations (Mollinari *et al.* 2019). The hotter and drier forest is therefore more likely to sustain understory fires (Uhl and Vieira 1989). The effect of logging greatly increases the probability of forest catching fire and increases fire intensity and tree mortality in the areas that do catch fire; together these effects of logging on fire behavior have more than double the impact on biomass loss as compared to the logging itself (Barni *et al.* 2021).

HUNTING

Overexploitation of Amazonian wildlife has a deep history, starting with the arrival of the first people at the Pleistocene–Holocene transition. The first humans in the region quickly depleted megafaunal populations leading to the regional and global extinction of entire branches of the mammalian tree of life. These historical losses are mirrored by ongoing population declines in many mammal, reptile, and bird species associated with over-harvesting, and like the historical losses are also biased towards remaining large-bodied species. The results of this defaunation can have profound consequences for species composition, population biomass, ecosystem processes, and human well-being in over-hunted Amazonian landscapes.

Commercial exploitation of animal hides in the 20th century was intense; between 1904 and 1969, it is estimated that 23.3 million wild mammals and reptiles of at least 20 species were commercially hunted for their hides (Antunes *et al.* 2016). This commercial exploitation is now much reduced, although approximately 41,000 peccary skins (mostly collared peccary, *Pecari tajacu*) are exported for the fashion industry annually (Sinovas *et al.* 2017). Exploitation is now predominantly for food, with Peres *et al.* (2016) estimating that hunting affects 32% of remaining forests in the Brazilian Amazon (~1M km^2), with a strong depletion of large vertebrate populations in the vicinity of settlements, roads, and rivers (Peres and Lake 2003).

Direct impacts – Impacts vary across species depending on their life-history characteristics; taxa that are typically long-lived, with low rates of increase, and long generation times, are more vulnerable to local extinction (Bodmer *et al.* 1997). For example, in southeastern Peru hunting resulted in the local extirpation of large primate species and reduced populations of medium-sized primates by 80% (Nuñez-Iturri and Howe 2007). Vulnerability to hunting may also be exacerbated by biogeographic quirks, with hunting representing a major threat to micro-endemic species like the black-winged trumpeter (*Psophia obscura*) or terrestrial species restricted to specific habitats which are more accessible like the wattled curassow (*Crax globulosa*), which is found only along more accessible river-edge forests. Habitat loss, fragmentation, and degradation interact synergistically with hunting in reducing and isolating populations that do not use the non-forest habitat matrix, inhibiting 'rescue effects' from neighboring forests and hence source-sink dynamics (Peres 2001). Additionally, there is evidence of sublethal impacts from hunting on Amazonian vertebrates, with lead being found in the livers of Amazonian game species (Cartró-Sabaté *et al.* 2019).

Although hunting represents the major driver of direct defaunation, other drivers of loss include human-wildlife conflicts arising from livestock depredations by jaguar (*Panthera onca*) (Michalski *et al.* 2006) and harpy eagles (*Harpia harpyja*) (Trinca *et al.* 2008). The wildlife trade also impacts a diverse set of taxa; for example, live parrot exports average 12,000 birds annually, mostly wild-caught individuals from Guyana, Peru, and Suriname (Sinovas *et al.* 2017), and ~4000 night monkeys (*Aotus* sp.) were estimated to have been sold to a biomedical laboratory on the Colombian side of the tri-border region of the north-western Amazon (Maldonado *et al.* 2009). Direct depletion for the pet trade has a long history and likely drove regional extinction of species such as the golden parakeet (*Guaruba guarouba*) from as long ago as the mid-19th century (Moura *et al.* 2014). Although trade has been reduced by effective command-and-control strategies, it remains the main threat to regionally critically endangered species like the great-billed seed finch (*Sporophila maximiliani*) (Ubaid *et al.* 2018).

Indirect impacts – Over-hunting may have pervasive impacts on Amazonian forests by disrupting or entirely removing 'top-down' control on ecosystems that are mediated by large-bodied predators and herbivores, leading to widespread and potentially irreversible ecosystem alteration and to loss of resilience and function (Ripple *et al.* 2016). Historical megafaunal extinctions have triggered declines in large-seeded tree species dispersed by the large-bodied frugivores (Doughty *et al.* 2016), and this trend continues with overhunting disrupting the ecological interactions between plants and their seed dispersers, with some large mammals performing non-redundant seed dispersal services (Ripple *et al.* 2016). Consequently, there is a shift in recruiting patterns of saplings in heavily hunted areas (Bagchi *et al.* 2018), with an increase in wind-dispersed and small-seeded species (Terborgh *et al.* 2008). This, in turn, could lead to a decrease in forests' future carbon stocks, as the species favored in hunted forests tend to have lower carbon storage capacity (Peres *et al.* 2016).

CONCLUSIONS

As of 2018, approximately 14% of the Amazon forest had been deforested, mainly due to the replacement of forests by pastures. Forest loss affects local temperature and precipitation, with increases in land surface temperatures and reductions in precipitation of up to 1.8% across the Amazon. Local extinctions are also a direct result of deforestation. The fact that there is no official record of a regional or global species extinction in the Amazon should bring no comfort, as a vast number of species remain to be described by science; it is possible, and even likely, that species are disappearing before they become known. Forest fires, selective logging, edge effects, and hunting put additional pressure on biodiversity, contributing to severe compositional shifts in remaining forests. The interactions between the multiple drivers of deforestation and forest degradation amplify their individual effects. An immediate halt to the drivers of deforestation and forest degradation is necessary to avoid further greenhouse gas emissions and biodiversity loss.

RECOMMENDATIONS

- Governments, the private sector, and civil society need to take urgent action to avoid further deforestation in the Amazon, particularly of primary forests. Avoiding loss of primary forest is by far the highest priority to avoid carbon emissions, biodiversity loss, and regional hydrological changes.
- Governments must enforce existing laws and control land speculation in the region.
- Governments must close down markets for illegal products (*e.g.*, timber, gold, and bush meat).
- Implement an integrated monitoring system for deforestation and forest degradation across the basin with comparable, transparent, and accessible datasets. Datasets can be generated through partnerships between governments and the scientific community. It is no longer acceptable for deforestation to be the sole focus of forest monitoring.
- Develop basin-wide environmental impact assessments for infrastructure, such as roads, waterways, and dams, as their impacts are not only local. Planning must account for the indirect impacts of infrastructure on surrounding ecosystems, as these can outweigh direct impacts.
- Licensing, concessions and permits for land-use activity and infrastructure development must be accessible across the Amazon Basin to support integration with ground and satellite-based monitoring systems, enabling supply-chain traceability and risk assessment of investments.
- Urbanization needs planning to replace the current, organic encroachment mode.
- Develop large-scale emergency mechanisms, a fire-risk monitoring system, and an early warning system to prevent and combat forest fires, especially in years of extreme drought when fires are more likely to escape from non-forest land uses. These should be accompanied by programs stimulating alternative land-management techniques that do not use fire.

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SUPPLEMENTARY MATERIAL

Berenguer *et al*. Drivers and ecological impacts of deforestation and forest degradation in the Amazon

Appendix S1. Why current tallies of threatened species in the Amazon are gross underestimates

To understand how many Amazonian species are threatened we first need to know how many species there are in the basin. It is estimated that 86% of existing species on Earth and 91% of species in the ocean still await formal scientific description; just 1.7 million species have been cataloged to date (Mora *et al.* 2011). The bulk of this undiscovered diversity is expected to be found in tropical forests like the Amazon. Undertaking the first step and putting names to life on Earth is the greatest impediment to understanding how much of that life is threatened with extinction. Global estimates of over one million threatened species (*e.g.*, IPBES 2019) are derived from estimates of the total number of species that may exist combined with ratios of how many described species are threatened. For example, around 10% of described insects are known to be threatened with extinction.

The number of species officially listed as threatened in the Amazon is low for a variety of reasons. Firstly, we are unlikely to have described more than 10% of all the species in the basin. Secondly, even for those species that have been named, the Red Listing process disproportionately covers vertebrate species and not other species on the evolutionary tree of life. Even many vertebrate species that have been officially assessed have been classified as 'Data Deficient,' meaning there is insufficient information available to apply the criteria and evaluate their conservation status. The vast majority of described species have not been assessed, either because of a lack of information about their geographic distribution, responses to global change, or population trends, compounded by a lack of human resources to carry out the task of assessment and verification (IPBES 2019). Thirdly, taxonomy is an iterative process, and genetic data increasingly point towards a mismeasure of Amazonian taxonomic diversity by uncovering multiple lineages within described species that have not shared genes for very long period of time (as much as millions of years) and that might be better treated at the species level. This taxonomic inflation (Isaac *et al.* 2004) tends to produce more 'new' restricted range species, which are thus more likely to meet Red List criteria if their ranges have suffered intensive habitat loss.

The current low level of 'officially' threatened species is thus primarily a product of a dearth of knowledge about how many species inhabit the basin and what proportion of this 'unknown' biodiversity is therefore threatened. Secondarily, it also reflects shortcomings in our knowledge of the response of 'known' species to habitat loss, fragmentation, and disturbance, and how their geographical ranges overlap with regions exposed to stressors. In summary, we currently do not yet know how many Amazonian species are threatened.

Appendix S2. Fine-scale endemism in Amazonian birds reveals threats of deforestation

Amazonian biodiversity is non-randomly distributed across the basin, with geographic discontinuities like large, wide rivers acting alongside topo-edaphic heterogeneity, climatic variation, and biological interactions to delimit species ranges. Many vertebrates have long been recognized as being restricted to Amazonian 'areas of endemism' delimited by major rivers, with different 'replacement species' present on either side of these fluvial barriers. These areas of endemism are often viewed as planning units for conservation, including protected area designation (da Silva *et al.* 2005). Understanding patterns of endemism is, however, dependent on both the completeness of biodiversity inventories and the refinement of the taxonomy of different groups. For example, there has been a revolution in avian taxonomy driven by the use of molecular toolkits coupled with vocal characteristics, and new data have revealed previously unrecognized fine-scale cryptic diversity. This points towards a mismeasure of Amazonian avian diversity because of a reliance on morphological characteristics to define species, which, for example, may be highly conserved in some lineages of rainforest birds (Fernandes 2013; Pulido-Santacruz *et al.* 2018). For example, molecular data (Tobias *et al.* 2008) led to the description of a new bird species, *Hypocnemis rondoni,* with a tiny range in the Aripuanã-Machado interfluve within the Rondônia area of endemism (Whitney *et al.* 2007). These discoveries and taxonomic rearrangements mean that various species in this complex have restricted ranges that overlap the 'arc of deforestation' and are thus threatened with global extinction (*e.g.*, *Hypocnemis ochrogyna*). Such fine-scale endemism is likely to be a common Amazonian biogeographic feature.

Appendix S3. Fires, deforestation, and drought lead to forest degradation

Fire is an intrinsic part of the deforestation process in the Amazon (Barlow *et al.* 2020). First the land is cleared, and trees can be felled using a variety of methods, from chainsaws to bulldozers. The felled vegetation is then left to dry for a period of a few weeks to a few months in the dry season. When the felled vegetation is dry, it is set on fire, transforming part of the biomass to ash. The land is then ready to be planted. Fires are also used in slash-and-burn agriculture in which Indigenous peoples and small landholders burn a small patch of recently deforested land. After a few years of agricultural use this area will be left as fallow while the farmer rotates agricultural production to another fallow. Finally, fires are also used as a common management tool in pastures to remove weeds and small trees and increase productivity. However, fires from deforestation, subsistence agriculture, or pastures can escape into surrounding agricultural areas, leading to economic losses when crops, fences, and buildings are burned (Cammelli *et al.* 2019). They can also escape to surrounding forests if it is a dry year, as leaf litter with <23% moisture can sustain a fire (Ray *et al.* 2005). Fires in Amazonian forests, or understory fires, tend to be of low intensity, with flame heights ranging from 10 to 50 cm, and slow moving, burning 300 m per day (Cochrane *et al*. 1999; Ray *et al.* 2005). Understory fires can be blocked by the canopy and are hard to detect by remote sensing (Pessôa *et al.* 2020). However, recent technological developments, such as the Visible Infrared Imaging Radiometer Suite (VIIRS) and the Continuous Degradation Detection (CODED) have been fundamental in mapping understory fires across the Amazon, thus helping to reveal the true extent of fires and degradation (Schroeder *et al*. 2014; Oliva and Schroeder 2015; Bullock *et al.* 2020a,b; Dutra *et al.* 2023).

Appendix S4. Wildfire impacts on floodplain forests

Although Amazonian floodplain forests are inundated for several months every year, they are remarkably flammable when compared to upland forests, particularly in black-water rivers (Flores *et al.* 2014, 2017; Resende *et al*. 2014; Nogueira *et al*. 2019). Because of flooding, the forest litter takes longer to decompose and accumulates, forming a root mat (fine roots and humus) on the topsoil that can spread smoldering fires during extreme drought events (dos Santos and Nelson 2013, Flores *et al*. 2014). Compared to uplands, the understory of floodplain forests is also slightly more open, allowing fuel to dry faster (Almeida *et al*. 2016). As a result, when wildfires spread, they can be intense, killing up to 90% of all trees by damaging their root systems (Flores *et al*. 2014; Resende *et al*. 2014). After a single fire, forests can still recover slowly, but remain vulnerable to recurrent fires for decades. Along the middle Rio Negro, for instance, half of all burned forests were affected by another fire, which caused them to become trapped in an open vegetation state (Flores *et al*. 2016). Recent evidence reveals that after a first fire, the topsoil of floodplain forests begins to lose nutrients and fine sediments and gain sand. At the same time, tree composition shifts, with species typical of white-sand savannas becoming dominant, together with native herbaceous plants. In only 40 years, forests on clay soil are replaced by white-sand savannas due to repeated wildfires (Flores *et al.* 2021). Floodplain forests are therefore fragile and flammable ecosystems, and because they are widespread throughout the Amazon, they may potentially spread fires across remote regions (Flores *et al*. 2017), an effect that could accelerate crossing large-scale tipping points. Plans to manage fire in the Amazon must take into account the existence of these flammable floodplain ecosystems to prevent fires from spreading when the next major drought occurs.