

INVITED REVIEW

The rise and fall of Neotropical biodiversity

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The exceptional levels of biodiversity found today in the American tropics are the outcome of tens of millions of years of evolution, shaped by the tumultuous geological history of the region, its heterogeneous habitats, climate change, ecological interactions and, in recent millennia, human influence. Although our understanding of diversity patterns and their underlying processes grows steadily in breadth and depth, Neotropical biodiversity is rapidly breaking down. Here, I contrast the long-term evolution of Neotropical biodiversity with its recent and rapid deterioration due to anthropogenic factors. I consider the impacts of the early arrival of humans to the region and the modern intensification of land-use change (primarily driven by agriculture) and other drivers of biodiversity loss, such as direct exploitation, invasive species and climate change. Together, these threats have led to 33% of all Neotropical species for which sufficient data are available being currently threatened with extinction. I outline emerging opportunities for conservation and restoration under the post-2020 Global Biodiversity Framework and call for urgent action from the biodiversity community, for the benefit of people and nature.

ADDITIONAL KEYWORDS: conservation – evolution – extinction.

INTRODUCTION

There are two key features of Neotropical biodiversity: one is that it is astonishing and the other is that it is disappearing. It is astonishing because of the long-term, complex and intricate ways by which the myriad life forms living today in the region evolved, building complex ecological interactions and resulting in enormous variation at the ecosystem, species, population and molecular levels. Today, Latin America contains more species of vascular plants, butterflies, amphibians and snakes than tropical Africa and Southeast Asia combined, and it has the highest richness among those three tropical regions also for breeding birds, ants, lizards and mammals (Raven *et al.*, 2020). However, the rate at which Neotropical diversity is now breaking down is at an entirely different temporal scale, with

potential large-scale consequences for ecosystem functioning, climate and people.

DEEP-TIME EVOLUTION

The exceptional biodiversity found today in the Neotropics is best explained as a result of the large area, diverse ecosystems, high environmental and climatic heterogeneity and deep evolutionary history of the region that are intrinsically linked with abiotic processes (e.g. geology, climate, catastrophic events) and biotic events (e.g. major phases of diversification including adaptive radiations, extinction, colonizations and range expansions) (Antonelli & Sanmartín, 2011; Rull, 2011; Hughes *et al.*, 2013) (Fig. 1).

Some Neotropical lineages, such as freshwater fish and terrestrial geckos, began to diversify in South America following its separation from Africa some 100 Mya (Lundberg *et al.*, 1998; Antonelli *et al.*, 2010a). However, a broader major biotic turnover

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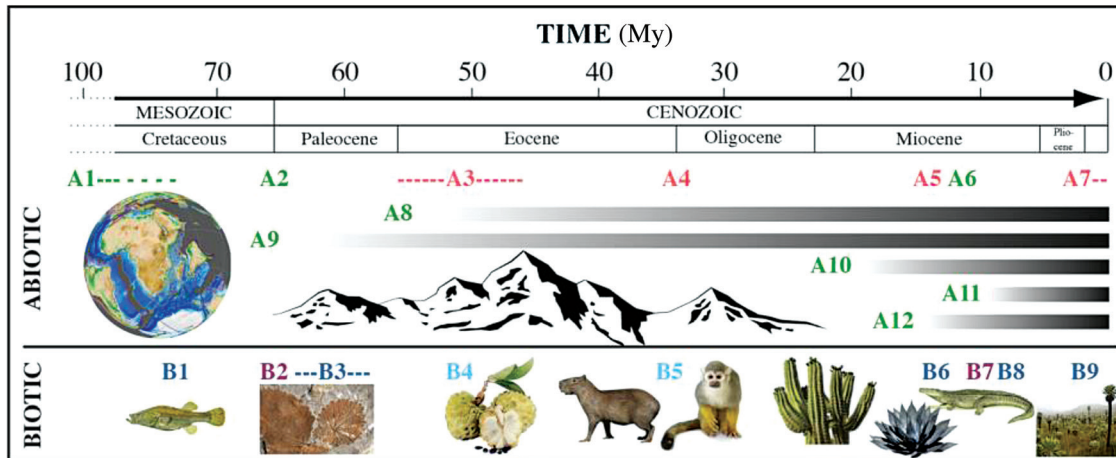


Figure 1. Selected abiotic and biotic events of relevance for the evolution of Neotropical biodiversity. Abiotic (red: climatic; others: green): A1: start of separation of South America and Africa; A2: asteroid impact off the coast of Yucatán in Mexico; A3: thermal maximum followed by sustained high temperatures; A4: rapid global cooling and glaciation of Antarctica; A5: global warming immediately followed by cooling; A6: closure of the Central American Seaway and gradual emergence of Panamanian land bridge; A7: onset of ice ages in the north and global climatic oscillations. The following events describe major uplift phases for the Andes: A8: Western Cordillera; A9: Western Puna; A10: Eastern Puna; A11: Altiplano; A12: Eastern Cordillera. Biotic (blue: speciation; purple: extinction; light blue: colonization): B1: early diversification of Gondwanan-derived freshwater fish; B2: widespread extinction triggered by collision (asteroid) event; B3: taxonomic and vegetational recovery and turnover; B4: arrival of boreotropical plant lineages; B5: trans-Atlantic arrival of the ancestors of New World monkeys and caviomorph rodents from Africa; B6: diversification of succulents and C_4 grasses; B7: extinction event in western Amazonian wetland fauna; B8: diversification of lowland terrestrial taxa; B9: radiation of highland Andean taxa and biotic rearrangements in speciation in the lowlands. See text for references; dates are indicative only. Inset images: public domain.

took place as a result of the Cretaceous-Palaeogene meteorite impact 66 Mya, which led to a decline in plant morphotype diversity by 45% that took *c.* 6 Mya to recover to previous diversity levels, albeit with angiosperm-dominated and stratified forests (Carvalho *et al.*, 2021). The underlying mechanisms and timings of Andean orogeny remain disputed (Pérez-Escobar *et al.*, *in press*), but it probably progressed at different times for different sections, starting in the Late Cretaceous but intensifying since the Miocene (Boschman, 2021). As the Andean cordilleras were formed, they drastically changed rainfall and drainage patterns, increasing soil heterogeneity and creating novel habitats at high and low elevations where speciation could take place (Hoorn *et al.*, 2010, 2013). The closure of the Central American Seaway *c.* 13 Mya (Montes *et al.*, 2015) and the subsequent terrestrial connection between South and Central America then led to widespread biotic interchange on land, ended gene flow across the warm parts of the Pacific and Atlantic (Bacon *et al.*, 2015) and promoted the diversification of some lineages and the extinction, through competition, of others (Carrillo *et al.*, 2020). The demise of predominantly wetland conditions in western Amazonia *c.* 12 Mya led to the extinction of a typical fauna of crocodylians

and molluscs (Wesselingh *et al.*, 2010; Salas-Gismondi *et al.*, 2015), but it was followed by rapid diversification of rainforest trees in the lowlands from *c.* 10 Mya (Richardson *et al.*, 2001; Erkens *et al.*, 2007) and rapid radiations in high-elevation Andean habitats in the last few million years (Madriñán *et al.*, 2013). Throughout this period, dispersals and range expansions across biomes contributed to the assembly of characteristic and diverse species communities (Antonelli *et al.*, 2018b).

Climatic changes during the Cenozoic (Westerhold *et al.*, 2020) of major biological significance for the Neotropics include the Palaeocene-Eocene Thermal Optimum at 56 Mya, which generated a peak in plant diversity (Jaramillo *et al.*, 2010), and the maintained higher global temperatures (10 °C warmer than today) until the end of the Early Eocene Climate Optimum at 47 Mya; the Eocene-Oligocene cooling event, which led to the glaciation of Antarctica and a major drop in Neotropical plant diversity (Jaramillo *et al.*, 2006); and the Miocene Climatic Optimum *c.* 17–14 Mya, which was followed by a cooling period that triggered the expansion of savannas and diversification of C_4 grasses and several other clades (e.g. Antonelli *et al.*, 2010b; Edwards *et al.*, 2010; Arakaki *et al.*, 2011). The onset of ice ages at *c.* 2.6 Mya, which in the Neotropics may have

led to an initial extinction of warm-adapted lineages (Silva *et al.*, 2018), was followed by oscillatory changes in rainfall patterns, which probably contributed to rearrangements in taxonomic distributions (Rull, 2005) and may have, in connection with further land emergence across the Isthmus of Panama, facilitated terrestrial dispersal (Bacon *et al.*, 2016).

Probably disconnected from any geological event, but potentially linked to climatic changes, the arrival of immigrant lineages from other landmasses contributed to new radiations and interactions with the native South American biota. Notable examples in the Eocene include the arrival of multiple boreotropical plant lineages from North America (Davis *et al.*, 2002; Antonelli *et al.*, 2009; Zhang *et al.*, 2021) and the presumed rafting of New World monkeys and caviomorph rodents (comprising capybaras) from Africa (Defler 2019; Silvestro *et al.*, 2019). A semi-continuous chain of islands (the Greater Antilles and Aves Ridge, often abbreviated to GAARlandia) has been repeatedly evoked to explain plant and animal dispersals between South America and the West Indies around the Eocene-Oligocene boundary (34 ± 1 Mya). However, molecular and geological evidence for an emergent land bridge at that time has been increasingly contested (Ali, 2012; Nieto-Blázquez *et al.*, 2017; Crews & Esposito, 2020), and recently rejected by Ali & Hedges (2021) based on novel geological surveys in the region (e.g. Cornée *et al.*, 2021; Garrocc *et al.*, 2021).

This exceedingly brief snapshot of Neotropical diversification attempts by no means to summarise the comprehensive reviews, comparative analyses and taxon-specific studies published on the topic (see e.g. Antonelli *et al.*, 2009; Rull, 2011; Hughes *et al.*, 2013; Antonelli *et al.*, 2018a). Instead, it is intended to provide the simple message that current Neotropical biodiversity is the outcome of manifold processes played out over long timescales, and to set the scene for the latest in a long series of events that have significantly affected the region's biodiversity: the arrival of humans.

EARLY HUMAN IMPACTS

The timing of the arrival of *Homo sapiens* from Asia across the Bering Strait to North America, followed by colonization across the American continent, are matters of active research and intense debate. The earliest human presence in the Americas has been estimated to date back to *c.* 24 000 years before present (BP) in the region corresponding to Alaska, where humans were confined until after the Last Glacial Maximum when the Canadian ice sheet began to melt and opened a coastal corridor to the south (Goebel *et al.*, 2008; Bourgeon *et al.*, 2017; Moreno-Mayar *et al.*, 2018). Stone artefacts dated to 19 000–18 000

BP or older may represent the earliest presence in the northern Neotropics (Mexico) (Ardelean *et al.*, 2020). Arrival to South America happened later under many scenarios, starting *c.* 14 000 BP, through several (two to four) independent waves and paths, including along the Andes, along eastern South America and perhaps through Amazonia, some reaching the southernmost margins of the continent (Moreno-Mayar *et al.*, 2018; Posth *et al.*, 2018). Puzzling anomalies exist in several colonization scenarios, such as a site dated to > 28 000 BP in north-eastern Brazil that contains potentially human-made stone tools (Fariña *et al.*, 2014).

The impact of early humans on Neotropical vegetation is becoming increasingly understood, thanks to the quantification of changes in pollen composition and charcoal deposits in lake sediments (Bush *et al.*, 2004; Power *et al.*, 2008). Ellis *et al.* (2021) compiled extensive data on historical land use and human populations, which indicate that by 12 000 BP > 87% of Latin America and the Caribbean were already occupied by humans, even if at low human densities (Fig. 2). Of the land occupied by indigenous people, *c.* 50% was in woodlands and *c.* 35% in drylands. Human occupancy at that stage was considerably higher than in North America, which was then inferred to have just > 50% of the land area unoccupied despite the earlier human colonization.

Humans cleared forests for agriculture through the use of fire, leaving rich deposits of charcoal that today enable the reconstruction of land use and, with pollen sediments, provide a window into past vegetation changes (Bush *et al.*, 2021). The per capita use of land in South America was presumably higher than in North America and the Caribbean, with > 1.2 ha per person in Amazonia and slightly more in the Andes (Koch *et al.*, 2019). Besides their effect on vegetation cover, humans

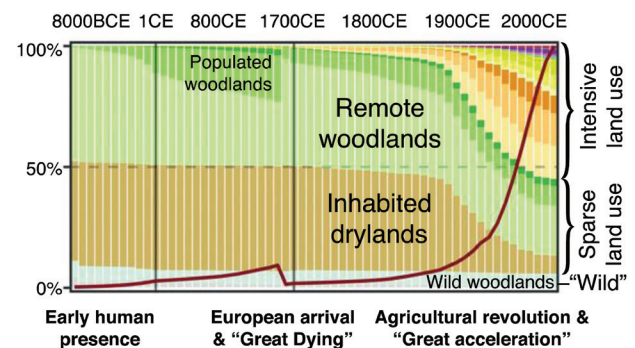


Figure 2. Changes in land occupancy and use over the last 12 000 years in Latin America, in relation to population growth relative to today (red line). BCE = Before Common Era, CE = Common Era. Adapted from Ellis *et al.* (2021); see that reference for a description of all land use categories and the colour codes used, which are grouped here for simplicity.

also actively dispersed useful plant species, such as food sources, leaving an imprint in current species distributions, diversity and abundance (Levis *et al.*, 2017; Maezumi *et al.*, 2018; McMichael, 2021).

Human population sizes increased gradually through time until c. 1200 Common Era (CE), after which they began to decline, possibly as a result of levels reaching carrying capacity and/or changing dynamics between local cultures, diseases and warfare (Arroyo-Kalin & Riris, 2021; Bush *et al.*, 2021). This decline led to the natural reforestation of large parts of Amazonia (Bush *et al.*, 2021). A second and much greater decline happened in connection with the arrival of European colonizers, which over the course of a hundred years led to the ‘Great Dying’ event, the death of an estimated 56 million humans, representing some 90% or more of the indigenous people (Koch *et al.*, 2019), mainly through the spread of diseases such as smallpox, measles and the common cold, but also due to warfare and slavery.

The large-scale and brutal displacement of Native American people by European immigrants and enslaved African peoples was also associated with drastic changes in agricultural practice, which increasingly relied on large plantations and monoculture crops, as compared to a much more varied landscape (Fig. 3).

Despite increasing documentation of how humans influenced Neotropical ecosystems at a large scale, their potential impact on driving species extinctions is poorly understood. Early anthropogenic impacts following the arrival of humans to different land masses were assessed by Andermann *et al.* (2020), who modelled changes in extinction rates and species richness over time based on a comprehensive data set of fossil mammals. For North America, South America and the Caribbean, the study inferred substantial increases in extinction and relatively small (North and South America) to substantial (Caribbean) drops in species richness (Fig. 4). Those changes appear, at least to some extent, to be correlated with human arrival (a timing which remains debated, as previously mentioned). Climate as an alternative driver of those changes was strongly rejected by the model.

MODERN THREATS

The human population in Latin America and the Caribbean grew gradually until the 1900s, after which it increased at an unprecedented rate: from c. 60 million in 1900 to > 652 million today. Although



Figure 3. ‘Heart of the Andes’ (Frederic Edwin Church, 1859). This painting, from Ecuador, shows a landscape already altered by human influence, but much more heterogeneous than the current agricultural practice of predominantly large plantation fields. Species migrations across the landscape and elevation gradients, especially for non-flying animals and plants with low dispersal ability (such as those with large or mammal-dispersed seeds), were certainly far easier than in the current highly fragmented habitats separated by roads and urban environments (public domain).

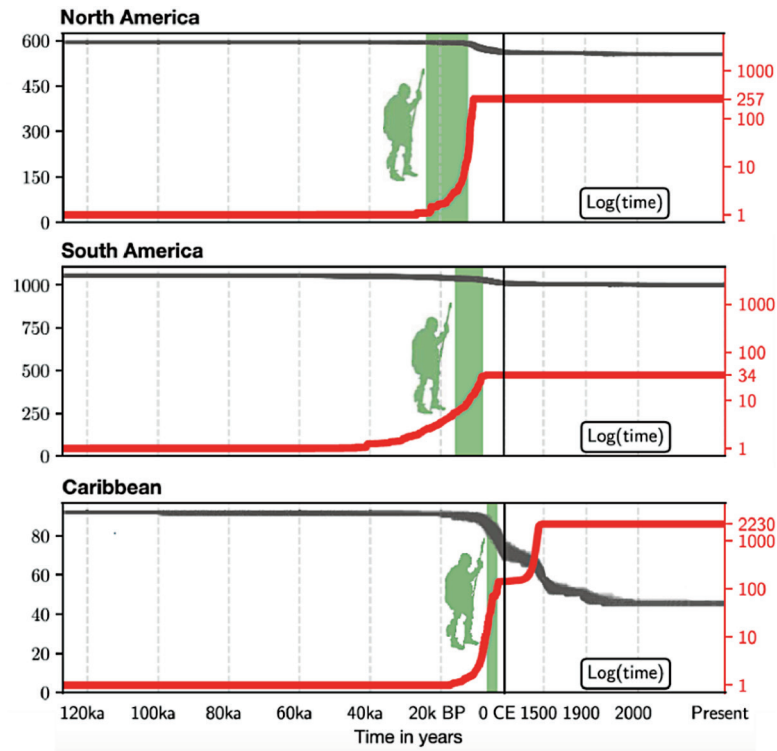


Figure 4. Changes in extinction rate (red) and species richness (grey) for mammals over the last 120 000 years across the Americas. For all regions, the early arrival of humans (approximated here by the green bars, but see text for discussion on uncertainties) appears to be associated with a first significant increase of extinction rates over the period surveyed. From [Andermann *et al.* \(2020\)](#) (Creative Commons).

the yearly growth has slowly but steadily declined since the early 1960s (1960: 2.7%; 2020: 0.9%), the demographics and mortality rates under this period mean that the total population has increased linearly over the same period (<https://www.worldometers.info>; accessed August 2021). The massive changes in population growth and human activities, including agricultural intensification and other recent land-use changes, beg the question: what is the modern human impact on Neotropical biodiversity?

As for the early influence of humans, there is again limited direct evidence of biodiversity losses but, in contrast, abundant circumstantial considerations. Let us take Amazonia as an example. Out of the 16 000 native tree species estimated to occur in the region in [ter Steege *et al.* \(2013\)](#) (later revised to *c.* 15 000; [ter Steege *et al.*, 2020](#)), 6000 were estimated to be represented by < 1000 individuals, reflecting the globally documented commonness of rarity for plants ([Enquist *et al.*, 2019](#)). Even some seemingly abundant and widespread species may in fact represent multiple narrowly distributed species when densely sampled phylogenetically ([Damasco *et al.*, 2021](#)). Rather than being concentrated in particular areas of Amazonia, such as its core or most humid segments, [Zizka *et al.*,](#)

(2018) found that these rare species have unpredictable distributions, in many cases far apart from each other. Plants seem no exception: fungi, for instance, are highly diverse in Amazonia and in many cases only known from single localities, as revealed by environmental DNA studies of soil and litter ([Ritter *et al.*, 2018, 2019](#)). Taken together, these lines of evidence suggest that *any* changes in Amazonian land use that leads to substantial habitat loss, e.g. agricultural expansion in southern Amazonia ([Maeda *et al.*, 2021](#)), illegal mining ([Sonter *et al.*, 2017](#)) or the flooding of large areas for hydroelectric dams ([Fearnside 2006](#)), are *certain* to be reducing genetic diversity, and *very likely* to be driving a large number of species to extinction, often unnoticeably.

Biodiversity loss in the Neotropics is exacerbated by the high degree of habitat fragmentation already inflicted. Even if deforestation were to stop immediately, many species in the remaining forest fragments of the Atlantic rainforest may still be doomed to disappear. This is mainly due to the ‘extinction debt’ effect, which can be calculated in different ways ([Ridding *et al.*, 2021](#)) but relies primarily on the strong and well-studied species-area relationship (SAR) that can serve as a proxy for estimating species losses worldwide

(Ellis *et al.*, 2012). As compared to documented extinctions, they can be at least an order of magnitude higher (Wearn *et al.*, 2012; Halley *et al.*, 2014). Additional factors, such as edge effects (Murcia, 1995), are likely to further impact on the biodiversity of fragmented ecosystems. The negative effect of habitat fragmentation on biodiversity is now well established for the Atlantic rainforest (de Lima *et al.*, 2020), and is likely to also be the case for most other Neotropical biomes.

CONSERVATION STATUS AND THREATS

To date, the global conservation statuses of 37 214 Neotropical species across all taxonomic groups and environments have been assessed for the International Union for Conservation of Nature's Red List of Threatened Species (hereafter Red List) and their partners (<https://www.iucn.org>; v.2021-1, accessed August 2021; filtered by Biogeographic Realm) (Table 1).

To estimate the proportion of Neotropical species that can be considered threatened, I applied the formulae in the reporting guidelines (IUCN, 2016) to calculate lower, middle and upper boundaries, depending on the assumption applied. The recommended statistic in those guidelines (the mid-point bound) indicates that as many as 33% of all Neotropical species are currently threatened (Table 2).

The statistics reported above could be potentially driven by one or a few species-rich groups and not be representative of other taxa. I explored this possibility by computing the proportion of threatened species in the 15 largest orders of the most species-rich organism group assessed to date: plants (Table 1). I found no systematic bias across those orders (Fig. 5). The average proportion of threatened species, at 37% (standard deviation 9%), is similar to a recent estimate

for all vascular plants in the world (39%) which takes into account several quantitative biases such as the non-random nature with which groups and species are chosen for assessments (Nic Lughadha *et al.*, 2020).

Red List assessments also contain important information on the documented or likely drivers of threat across different categories. Examination of assessment data for all Neotropical species shows that agriculture tops the list of threats, posing risks to 30% of all the species assessed (11 226 out of 37 214; Fig. 6) and 56% of the species currently classified as Critically Endangered, Endangered or Vulnerable (6009 out of 10 801 species). This is followed by unsustainable exploitation of species (including activities such as timber extraction, hunting, fishing and harvesting for illegal trade of species). Climate change, despite its massive global impact on societies, only comes in 7th position on the list of threats, although this needs to be considered in light of the relatively short time span against which threats are assessed (the coming 10 years or three generations, whichever is longer) and challenges in documenting the direct impact of climate change on individual species (Trull *et al.*, 2018).

The threats to Neotropical biodiversity imposed by land use change (orange boxes, Fig. 6) in general and to agriculture in particular also present the greatest risks for global biodiversity (Díaz *et al.*, 2019). However, these threats are assessed on a very immediate time frame [present conditions and next decade(s)], meaning that they do not inform on whether the risks identified are increasing with time or reflect a legacy of the changes that had already taken place in the last century. They also lack details on the geographical location of those changes.

To tackle this shortcoming and identify which Neotropical regions are most affected, I first estimated forest cover loss through time following

Table 1. Number of Neotropical species for which the conservation status has been assessed to date by the IUCN and its partners, broken down by Red List category and major taxonomic group

IUCN category	Plants	Animals	Fungi	Brown algae	Sum
EX - Extinct	26	88	0	0	114
EW - Extinct in the Wild	15	9	0	0	24
CR - Critically Endangered	1309	951	9	4	2273
EN - Endangered	2807	1399	15	1	4222
VU - Vulnerable	2937	1327	41	1	4306
LR/cd - Lower Risk: Conservation Dependent	33	10	0	0	43
NT or LR/nt - Near Threatened	990	974	16	0	1980
LC or LR/lc - Least Concern	9214	10 678	42	0	19 934
DD - Data Deficient	1497	2795	17	9	4318
Total assessed	18 828	18 231	140	15	37 214

Table 2. Proportion and approximate numbers of Neotropical species that can be considered threatened, depending on the assumption applied (IUCN, 2016). The mid-point estimate, which is deemed closest to the true number, is highlighted in bold

Type of estimate	Assumption	Formula	Percentage threatened (%)	Number of species
Lower bound	No Data Deficient species is in fact threatened	$(CR+EN+VU)/(assessed-EX)$	29	10 834
Mid-point	Data Deficient species are threatened in the same proportion as others	$(CR+EN+VU)/(assessed-EX-DD)$	33	12 261
Upper bound	All Data Deficient species are in fact threatened	$(CR+EN+VU+DD)/(assessed-EX)$	41	15 165

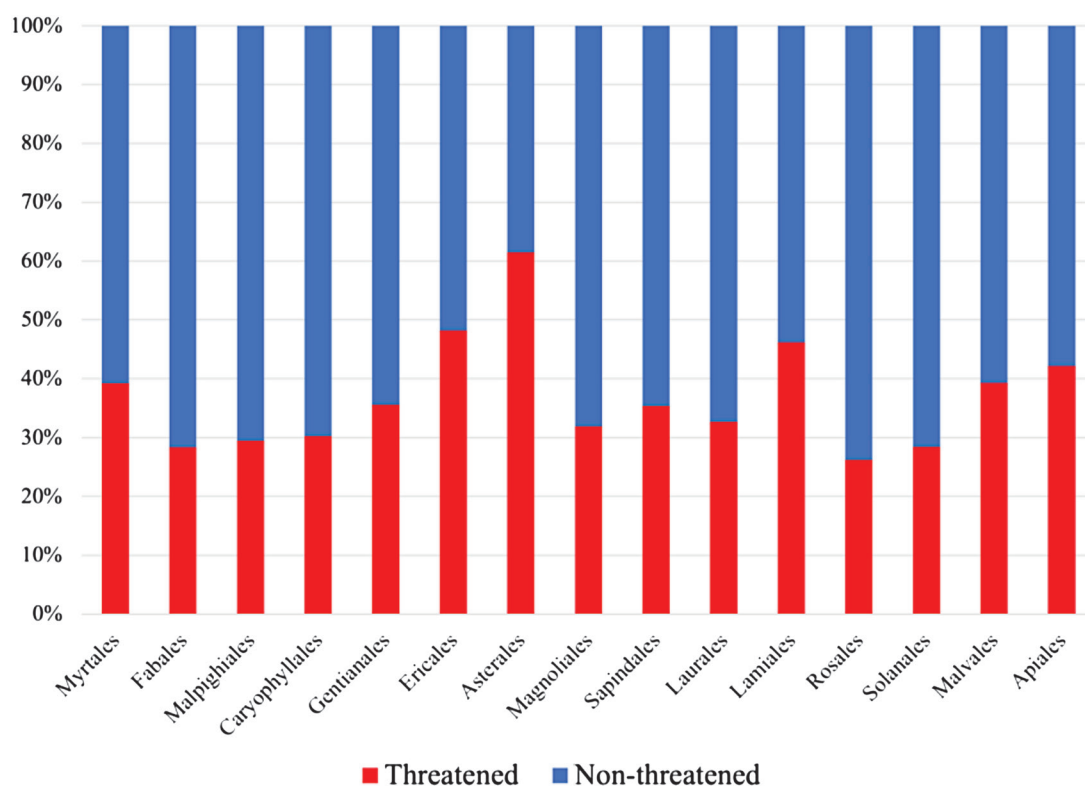


Figure 5. Proportion of threatened species (mid-point estimates; see Table 2 for the formula used) in the 15 plant orders with the greatest number of species that could be assessed. The plot shows relative consistency in the proportion of threatened species for each order surveyed, except for two orders outside the standard deviation of this data: Asterales with 61% and Ericales with 48% of threatened species. See Table S1 in the online Supporting Information for a full breakdown of these orders per Red List category. Data compiled from IUCN (v.2021-1, accessed August 2021).

the methodology available through <https://www.globalforestwatch.org/> powered by the Google Earth Engine, based on high accuracy remote sensing data (Hansen *et al.*, 2013) from Curtis *et al.* (2018) and subsequent updates (accessed May 2021). Between 2001 and 2020, a polygon comprising the Neotropical

region (Morrone, 2014) lost *c.* 10 million hectares of tree cover, equivalent to a 10% decrease. The regions with highest rates of loss were the Amazonian deforestation arc (i.e. the eastern and southern borders of Amazonia), extending south into Paraguay and Argentina, and parts of eastern Central America (Fig. 7A). These

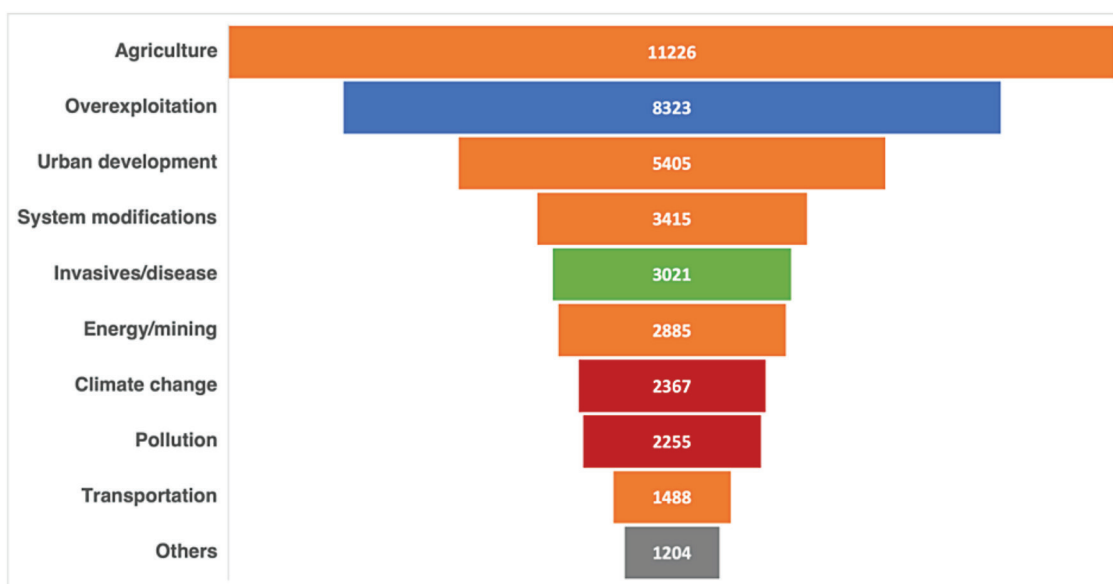


Figure 6. The ten major threats to the 37 214 Neotropical species assessed to date. Numbers within boxes indicate species considered to be affected by each threat. Colours indicate broad classes of threats: orange: activities primarily linked to land use change; blue: exploitation; green: pests and pathogens; red: environmental. One species can be threatened by more than one factor, leading the sum of individual threats to exceed the number of species assessed. Threat labels are simplified. Data compiled from IUCN (v.2021-1, accessed May 2021).

results show that deforestation rates, which are documented to have been high since satellite images came into widespread use in the 1970s, continue at alarming levels even today.

I then used the same platform described above to estimate the location of these changes and their main drivers, classified through the methodology described in Curtis *et al.* (2018) (Fig. 7B). Commodity production is the primary cause of deforestation across the South American Dry Diagonal, comprising most of the Cerrado and Chaco vegetation but also parts of Amazonia, the Caatinga and the Atlantic rainforest; most of this is currently for either cattle ranging or large-scale soy cultivation, a protein-rich crop mainly exported to China and the European Union for the industrial production of beef, poultry and pork (Godfray *et al.*, 2018). As databases on global supply chains improve, it is now becoming increasingly possible to connect habitat degradation in one region to the countries driving it through consumption (Moran & Kanemoto, 2017). In contrast, shifting agricultural practices of small- and medium-scale agriculture characterize most changes related to forest loss in Central America, the tropical Andes and north-eastern Brazil. The relative impact of commodity production appears to be much larger than that of shifting agriculture: Ecuador, for instance, lost 4.6% of its territory in tree cover over the last two decades, whereas Paraguay shows a tree cover loss amounting to nearly six times more (26% of its territory) over the same period. Finally, forestry

activities (primarily the logging of commercial tree plantations but also of some primary forests) is the primary driver in south-eastern Brazil. Urbanization has had only a minor direct impact over the period analysed, reflecting the fact that population growth is mainly happening in already crowded urban developments.

Current evidence is thus unequivocal in testifying to the massive impacts of human activities on Neotropical ecosystems, both historically and ongoing. Whether negative effects will be allowed to continue depends on our ability to identify and embrace the closing window of opportunities towards a more responsible stewardship of nature (Steffen *et al.*, 2015).

EMERGING OPPORTUNITIES: 'KEEPING' AND 'FIXING'

The post-2020 Global Biodiversity Framework under the Convention on Biological Diversity (<https://www.cbd.int/>) may become the most decisive environmental agreement in human history, past and future. This is because if we are unable to halt biodiversity loss in the next few decades, it is likely that the damage incurred to many natural ecosystems would be so severe as to become irreversible (Leclère *et al.*, 2020). At the time of writing, current drafts of the post-2020 Framework (to be concluded during the 15th Conference of the Parties in 2022) aim to halt biodiversity loss by 2030

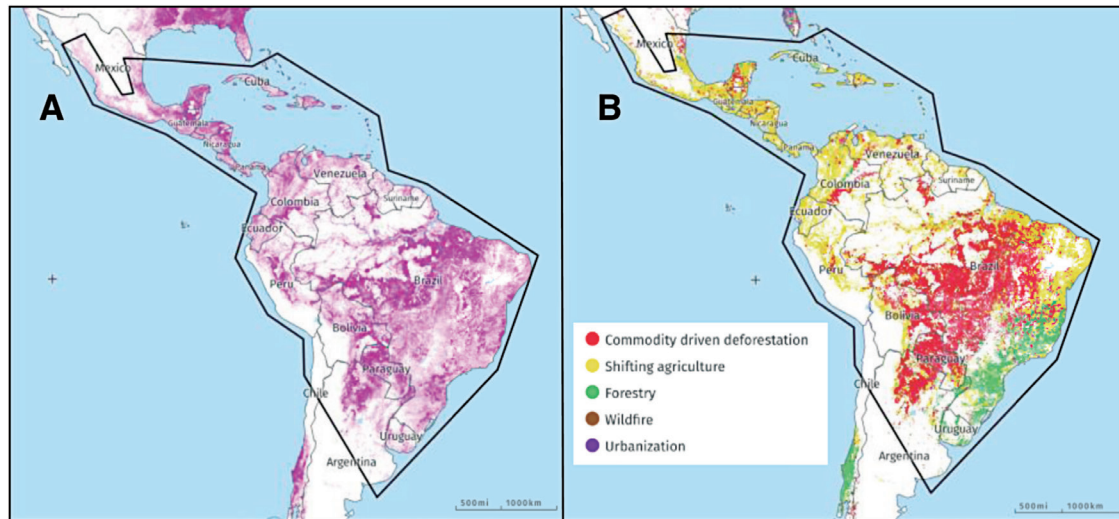


Figure 7. Forest cover loss and its drivers from 2001–2020. A, c. 10% of forest cover was lost within the region outlined. B, drivers of forest loss. Data and analyses from <https://www.globalforestwatch.org/>. The maps show that forest loss is still happening at an alarming pace across the entire Neotropical region but is being driven by different regional pressures.

and to achieve recovery by 2050. There are two key opportunities for the Neotropics: protecting and restoring.

PROTECTING WHAT IS LEFT

It may feel dire that a great but unquantified number of species have probably already been lost in the Neotropics, both during its early colonization and modern agricultural and population expansions; however, we now need to focus primarily on the third of all Neotropical species that are threatened *today*, as well as the other facets of biodiversity at risk, from genes to functions and whole ecosystems. Extinction risks mean that species still have a chance: the conservation status for individual species *can* be improved, and extinction debts for whole ecosystems *can* be reverted (Mair *et al.*, 2021).

Although terms such as ‘wild’ or ‘pristine’ may no longer be appropriate to describe ecosystems that have been impacted by human activities through centuries (Fernández-Llamazares *et al.*, 2020; see also Fig. 2), the value of largely intact forests remains crucial for a large proportion of Neotropical species and in order to sustain their ecological processes and interactions (Watson *et al.*, 2018). The advocacy of a ‘shared Earth’ between humans and other species is socially appealing, and there is ample evidence of sustainable use of natural resources by traditional communities (Obura *et al.*, 2021). There are also calls for increasing the sustainable use of biodiversity through the development of bio-economies (Nobre & Nobre, 2018) and equitable exploration of species properties to develop nature-based solutions to global and regional

challenges, as sources of food, carbon storage, medicines and much more (Seddon *et al.*, 2019; Antonelli *et al.*, 2020; Ulian *et al.*, 2020). However, given current levels of human pressure, and the sensitivity of many species to even low levels of disturbance, more research is needed to identify the right balance between full protection and shared space, with potentially large variations across the various Neotropical regions and ecosystems.

A crucial step in identifying priority areas for new or enhanced protection is to apply data-driven, objective methods (Margules & Pressey, 2000; Sacre *et al.*, 2020). Otherwise, there is a substantial risk of setting aside the cheapest areas for protection (often termed ‘residual’ reserves) when pursuing specific area-based metrics, rather than protecting the optimal (and potentially more expensive) areas from a biodiversity perspective (Devillers *et al.*, 2015; Vieira *et al.*, 2019). Analyses using tools in the field of systematic conservation planning (also termed spatial conservation prioritization) have been applied to the Neotropics (e.g. Vieira *et al.*, 2019), offering evidence-based information on expected protection effectiveness for threatened species. New advances in artificial intelligence, remote sensing, citizen science and environmental DNA analysis now offer powerful tools to scale up such work while considering the complexities of socio-biological systems and climate change (Silvestro *et al.*, 2021).

RESTORING WHAT IS GONE

Besides preventing further loss and fragmentation of ecosystems, global efforts are now focusing on the importance of ecosystem restoration as an equally

critical step towards bending the curve on biodiversity loss (Leclère *et al.*, 2020). This is why the United Nations have declared 2021–2030 the Decade on Ecosystem Restoration (www.decadeonrestoration.org), with ambitious pledges being made by governments, corporations and other organizations around the world.

Fortunately, there are multiple co-benefits to be gained by carefully choosing the right places and habitats to restore, which could create corridors for wildlife, strengthen the long-term survival of currently threatened species and reduce a substantial proportion of imminent extinctions (Strassburg *et al.*, 2020; Mair *et al.*, 2021). Habitat restoration is also likely to diminish the impact of climate change and other synergetic threats on species, in particular where those combined risks are projected to be highest over the course of this century, as in the Cerrado and eastern South America (Segan *et al.*, 2016). Ecosystem restoration, including rewilding (Svenning, 2020) and reforestation, holds great promise to help tackling both the biodiversity and climate crises (Girardin *et al.*, 2021), as long as it is properly designed and implemented (Di Sacco *et al.*, 2021).

The Atlantic rainforest is one region which, after massive degradation and fragmentation triggered during colonial times, is now shifting from being a ‘shrinking biodiversity hotspot’ to becoming a ‘hope spot’ (Rezende *et al.*, 2018). Through community engagement and co-planning (de Siqueira *et al.*, 2021), payments for ecosystem services and legislation that enforce landowners to restore riparian forests (Scarano & Ceotto, 2015), and voluntary protection of land Reservas Particulares de Patrimônio Natural (RPPNs) (Private Natural Heritage Reserves), forest cover could increase substantially in the coming decades, with manifold benefits for biodiversity, local communities (through clean water provision, cultural services and food production) and climate mitigation (through carbon storage, increased shade and local cooling effects). In many places, natural regeneration remains a viable and cost-effective option (de Rezende *et al.*, 2015). Restoration thus offers a powerful way to help protect the vanishing biodiversity of the Neotropics, but it should never be considered a replacement to protecting remaining, old-growth habitats.

CONCLUSIONS

Neotropical biodiversity has been in the making for at least 100 My, accumulating since the separation of South America from Africa. If that was our 24-hour watch to measure events against, the arrival of humans to the Neotropics took place only in the last 15 seconds before midnight. Despite this, the events of

those seconds have resulted in a massive change to all Neotropical ecosystems, most drastically in connection with the nearly exponential growth in the human population since the early 1900s, equivalent to 0.1 seconds before midnight.

Despite all odds, there is still time to make peace with nature (Baste *et al.*, 2021), both for the intrinsic values of nature and the manifold services and benefits we derive from it (Díaz *et al.*, 2018). Protecting and restoring Neotropical biodiversity will require collective action by all sectors of society, a challenge that cannot be understated (Jagers *et al.*, 2020), particularly for tackling seemingly unsurmountable problems such as Amazon deforestation (Bastos Lima *et al.*, 2021).

As scientists, we have a special role to play. However, the knowledge we produce remains too often confined to the limits of academic journals and meetings. I therefore reiterate previous calls (Hendry *et al.*, 2010) for our community to engage more widely in public debate, providing knowledge and advice on the conservation of Neotropical groups or regions we know well. We also need to engage more broadly with non-scientists (local groups, NGOs and local communities) learning from the rich but underappreciated wealth of traditional knowledge they hold (Albuquerque *et al.*, 2021) in order to jointly identify sustainable ways to protect nature while safeguarding the well-being of people. The Brazilian Platform on Biodiversity and Ecosystem Services (BPBES) is one Neotropical example that has successfully built bridges across various stakeholders independently from, but in dialogue with, governmental authorities (Scarano *et al.*, 2019). Finally, we must lead by example: our families, friends and societies look upon us as individuals to live our lives responsibly and sustainably. As long as biodiversity remains and we choose to act, there is hope.

DATA AVAILABILITY STATEMENT

The data used in this study are publicly available.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Fraction of globally threatened species in the 15 largest orders of Neotropical plants. The fraction reported represented a mid-point between the lower and upper bound of threatened species for which sufficient data were available, and it was calculated following the formula $\text{Fraction threatened} = (\text{CR} + \text{EN} + \text{VU}) / (\text{assessed} - [\text{EX} - \text{DD}])^1$. Data compiled from the International Union for Conservation of Nature (IUCN; accessed August 2021). This is

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