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The future of hyperdiverse tropical ecosystems

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The tropics contain the overwhelming majority of Earth's biodiversity: their terrestrial, freshwater and marine ecosystems hold more than three-quarters of all species, including almost all shallow-water corals and over 90% of terrestrial birds. However, tropical ecosystems are also subject to pervasive and interacting stressors, such as deforestation, overfishing and climate change, and they are set within a socio-economic context that includes growing pressure from an increasingly globalized world, larger and more affluent tropical populations, and weak governance and response capacities. Concerted local, national and international actions are urgently required to prevent a collapse of tropical biodiversity.

The tropics hold a disproportionate amount of global biological diversity and are key to meeting the international community's aims of socially just sustainable development and effective biodiversity conservation¹. Yet, tropical ecosystems are undergoing rapid environmental, socio-economic and demographic change², often driven by forces originating in extra-tropical developed countries. The scale of these changes is unprecedented, and decisions implemented in the coming decades will define the future sustainability of the tropics.

Guiding these decisions depends on understanding the diversity and vulnerability of the four major tropical ecosystems: the forests and mesic savannahs that cover most of the terrestrial tropics, the extensive freshwater systems that receive half of the world's rainfall and the shallow-water coral reefs distributed along 150,000 km of coastline (Fig. 1). Here we quantify and review the global importance of tropical biodiversity, evaluate the vulnerability of tropical ecosystems to proximate stressors and assess whether global and regional socio-economic changes will exacerbate or ameliorate biodiversity loss. We then examine the effectiveness of conservation approaches and highlight the scientific advances required to support a sustainable tropical future.

The global importance of tropical ecosystems

Over evolutionary time, the tropics have acted as both a source of and a refuge for extra-tropical terrestrial and marine species^{3,4}; but just how diverse and irreplaceable are the tropics today? The increase in species richness from polar to tropical regions, known as the latitudinal diversity gradient, is found across a wide range of taxa and biomes. As a result of this gradient, tropical latitudes – which cover just 40% of the Earth's surface – hold a startling proportion of the planet's species: our assessment reveals that almost all shallow-water zooxanthellae corals, 91% of terrestrial birds, and over 75% of amphibians, terrestrial mammals, freshwater fish, ants, flowering plants and marine fish have ranges

that intersect tropical latitudes (Fig. 2a). For birds, the importance of the tropics extends far beyond 23.5 degrees of latitude, given that almost half of all Nearctic species migrate to the Neotropics⁵ and over 2 billion individual passerines and near-passerines cross the Sahara each autumn⁶. Moreover, a disproportionate number of species are endemic to the tropics. For example, there are more than six times as many endemic terrestrial bird species in the tropics as in temperate regions (Fig. 2a). Tropical zones are less important for marine mammals and birds, which peak in diversity at mid-latitudes^{7,8}. Nonetheless, more than 55% of these species use the tropics (Fig. 2a).

Overall, 78% of species across the ten taxa that we assessed occurred within tropical latitudes, but incomplete taxonomic inventories mean that this is almost certainly an underestimate⁹. Between 15,000 and 19,000 new species are described annually¹⁰, and the majority of recently described terrestrial vertebrates¹¹ or predicted discoveries of invertebrates¹² are from the tropics. Even terrestrial mammals are still being discovered at a rate of about 25 species a year, with the highest numbers in the Neo- and Afrotropics¹³. Shortfalls in species descriptions for other taxa are often far greater. For example, only 70,000 of an estimated 830,000 multicellular plants and animals have been named on coral reefs¹⁴, and although approximately 500 spider species are described each year, this is a tiny fraction of the estimated 150,000 undescribed tropical species¹⁵.

Tropical taxonomic shortfalls are further compounded by a suite of systematic sampling biases. These include undersampling when compared with temperate regions¹⁶, the spatial aggregation of sampling effort around coastal areas¹⁷, roads, rivers, urban settlements and high-profile research stations¹⁸, biases in favour of dry-season sampling when many invertebrate taxa are least abundant¹⁹, and the paucity of samples from ecosystems that are harder to access, such as mesophotic and rariphotic reefs²⁰. The biological diversity of the tropics is

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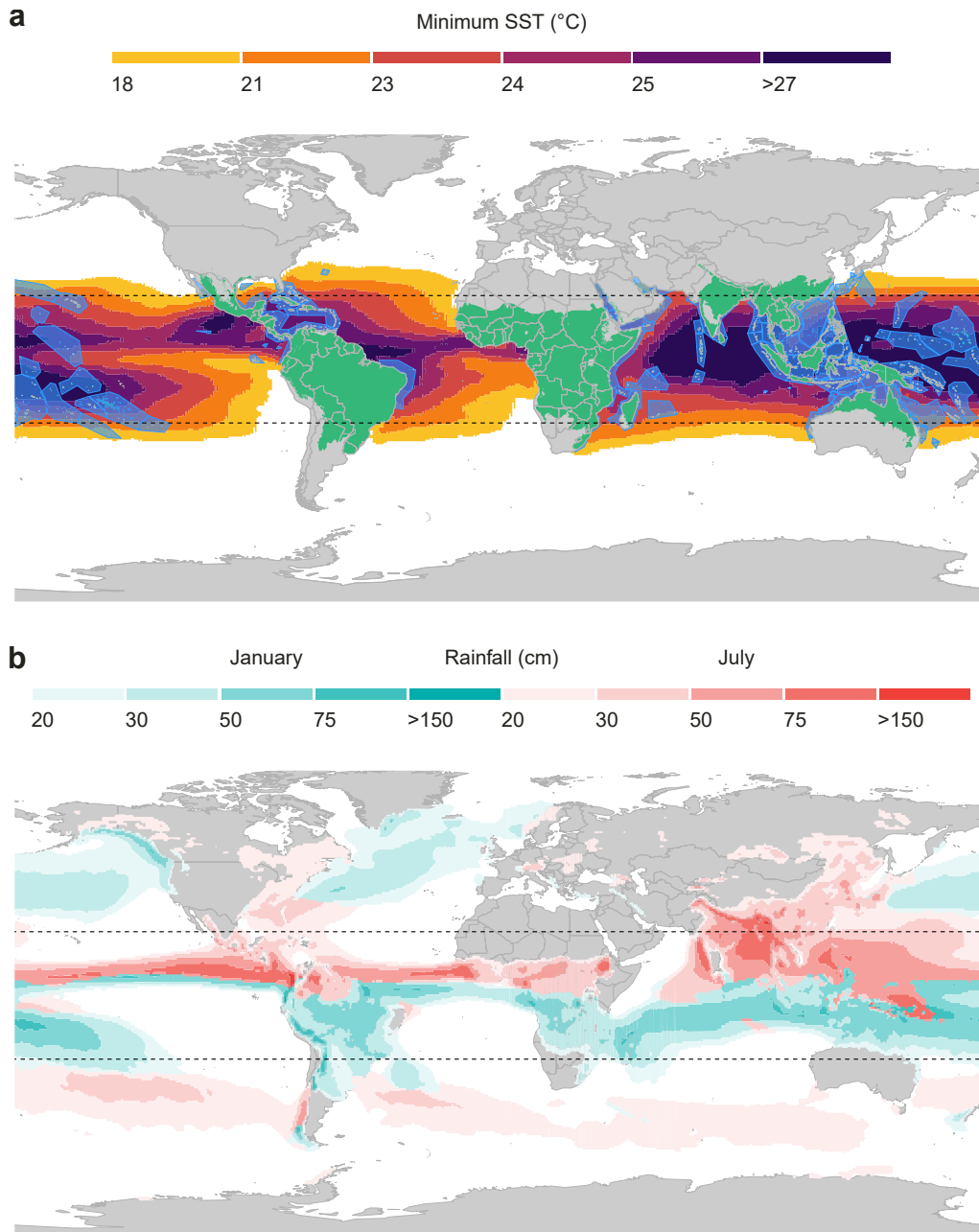


Fig. 1 | The tropical biosphere. a, Tropical terrestrial and marine biomes. The tropical terrestrial biome (green) was defined as all tropical mesic ecoregions¹⁶³. These ecoregions span 82% of the 50 million km² of land between 23.5° N and 23.5° S, but extend into the subtropics in some areas. The tropical marine biome was defined by the 1988-2018 mean minimum monthly 18 C sea-surface isotherm. This isotherm bounds the latitudinal extent of shallow-water coral-forming ecoregions (blue)¹⁶⁴. **b,** The intertropical convergence zone (ITCZ). The ITCZ was defined as regions that received a mid-summer (January (turquoise colour gradient) or July (red colour gradient)) mean monthly total rainfall of >20 cm, for the period 1979-2017. Where both January and July had rainfall of >20 cm, we show the measurement from the month with the largest total. The ITCZ is a strong predictor of the distribution of the tropical terrestrial ecoregions shown in **b**. Data sources are presented in Supplementary Table 1.

mirrored by many forms of societal diversity²¹. For example, tropical countries contain 40% of the world's population yet 85% of extant languages are spoken within them²². The tropics also provide incalculable benefits to humanity. They housed most of the key centres of plant domestication²³ and have been a vital laboratory for the development of science itself – the disciplines of ecology, biogeography and evolutionary biology are founded on evidence gleaned from tropical ecosystems. Tropical ecosystems also make vital contributions to globally important ecosystem services. Although they cover just 0.1% of the ocean surface, coral reefs provide fish resources for the 275 million people that live within 30 km of them²⁴ and coastal protection for up to 197 million people²⁵. Humid tropical forests cover less than 12% of the world's ice-free land surface but produce 33% of global net primary productivity and store 25% of the carbon in the terrestrial biosphere²⁶, and tropical savannahs provide a further 30% of global net primary productivity and 15% of carbon storage²⁷. Tropical ecosystems also help drive vital

atmospheric teleconnections. For instance, 70% of the rainfall in the 3.2-million-km² Rio de la Plata catchment is estimated to come from evaporation in Amazonia²⁸.

Vulnerability of tropical biodiversity

For each of the five vertebrate groups that have been comprehensively assessed by the International Union for the Conservation of Nature (IUCN) and for which spatial occurrence data are available²⁹, species classified as Vulnerable, Endangered or Critically Endangered are more dependent on the tropics than are those classified as Least Concern (Fig. 2b). In addition, 85% of species extinctions from these vertebrate groups have been of species that use the tropics²⁹. Consequently, although extinctions of other groups are less well understood, we can assume that most of an estimated 130,000 modern invertebrate extinctions³⁰ will also have been of tropical species. Thus, not only are the tropics

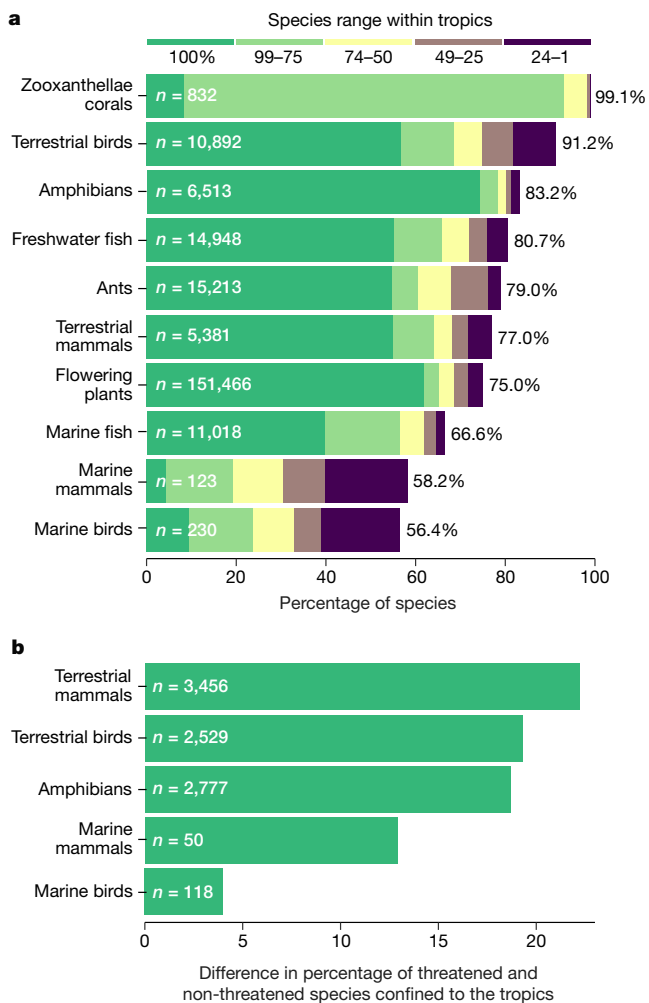


Fig. 2 | Tropical hyperdiversity. a, The proportion of species found within tropical latitudes for ten taxonomic groups. Bars are colour-coded to show the percentage of species ranges within the tropics. *n* gives the total number of species analysed in each group. Only birds, amphibians and mammals have been comprehensively sampled. Numbers at the end of the bars give the precise percentage of species whose ranges overlap tropical latitudes, as shown in the bars. **b**, The difference in the proportion of threatened (IUCN Critically Endangered, Endangered and Vulnerable categories) and non-threatened (IUCN Least Concern category) species found exclusively within tropical latitudes for the five comprehensively sampled groups. For example, 66% of threatened and 44% of nonthreatened terrestrial mammals are confined to the tropics. The bars show the difference between these figures, which is 22% in the case of terrestrial mammals. Data are from Birdlife International¹⁶⁵ (for birds), the IUCN²⁹ (for amphibians and mammals), the Ocean Biogeographic Information System (for marine fish), C. Veron (personal communication) (for shallow-water zooxanthellate corals), the Global Biodiversity Information Facility (for flowering plants) and a previous publication¹⁶⁶ (for freshwater fish). Data sources are presented in Supplementary Table 1.

vastly more diverse than temperate regions, but this diversity is also at far greater risk from human actions³¹. Moreover, given that the tropics have the highest proportion of species classified by the IUCN as Data Deficient and the lowest level of biodiversity-threat assessment¹⁶, information shortfalls mean we are probably underestimating the vulnerability of the tropical biome. We assessed this vulnerability in more depth by examining the effect of local and global stressors, the interactions between them and the resulting changes to tropical ecosystems.

Local stressors

The tropics are subject to some of the highest global rates of land-use change and degradation. Since 1990, while the spatial coverage of temperate forests has increased, tropical deforestation rates have

exceeded five million hectares per year³². Additional effects stem from the expansion of large infrastructure projects, such as dams, and the growing demand for agricultural commodities, biofuels, timber, wood for fuel, and other natural resources³³. All of these result in severe biotic responses. Even with mitigation, dams present a near-impassable barrier for river fish³⁴, and deforestation replaces a species-rich pool of forest specialists with a smaller pool of common open-area species³⁵. The influence of land-use change also extends far into remaining natural areas through isolation and edge effects³⁶, additional anthropogenic disturbances³⁷ and altered climatic conditions³⁸. Edge effects suppress the abundance of threatened vertebrates up to 200-400 m into tropical forests³⁶; this has left almost no core forest refugia in the Brazilian Atlantic forest, of which over 80% is within 500 m of an edge³⁹. Even low levels of landscape modification have marked effects on range-restricted species³⁷, and time lags mean that some of the most deleterious effects are only observed decades after landscape modification⁴⁰.

Pollution presents a diverse set of threats to tropical ecosystems. Inputs of sediment and nutrients from land-use change are well-established drivers of biodiversity loss across freshwater⁴¹ and coastal systems, including coral reefs⁴². Pesticide use is increasing across the tropics, reflecting rapid intensification of farming practices⁴³ and high pressures from pests on tropical crops⁴⁴. Tropical Asian rivers are a major source of the 1.2-2.4 million tonnes of plastic that enters the world's oceans each year⁴⁵, with micro-plastics entering coral diets⁴⁶ and larger debris increasing rates of coral disease⁴⁷. These examples of chronic pollution are exacerbated by extreme events such as the collapse of the Fundão Dam, which released about 50 million cubic metres of waste into a 600-km stretch of river in south-east Brazil and caused a 7,000-km² toxic plume in the Atlantic Ocean⁴⁸.

Overexploitation is also pervasive across the tropics. Fishing has reduced fish biomass by over 75% across a third of coral reefs⁴⁹ and is shrinking the mean body size of exploited freshwater taxa⁵⁰. Hunting has contributed to the loss of charismatic megafauna, extirpating African elephants, rhinoceroses and large predators from most of their original ranges^{51,52}. Tropical forests are affected by extensive over-harvesting of wildlife³¹, with estimates of the annual harvests of highly trafficked animals such as pangolins reaching into the millions of individuals⁵³. Moreover, the growth in non-food uses of wildlife means that even small-bodied songbirds are at risk of global extinction⁵⁴. Overexploitation also extends beyond fauna and is driving economically valuable tropical tree species to extinction⁵⁵.

Invasive species have been the second most important driver of vertebrate extinctions since AD 1500⁵⁶. Within terrestrial ecosystems, invasive species have exerted the strongest influence on islands and coastal mainlands⁵⁷, causing thousands of species extinctions and altering trophic structures⁵⁸. On continents, invasive species currently have a greater effect on biodiversity in economically developed and extra-tropical regions, but tropical ecosystems are predicted to become increasingly vulnerable to invasion as the 21st century continues⁵⁰. Despite a deficit of research in the tropics⁶⁰, two prominent examples highlight the scope and magnitude of species invasions into terrestrial tropical ecosystems: there was an 84% increase in detections of alien species between 2003 and 2010 in Singapore⁶¹, and invasive African grasses could threaten up to 380,000 km² of Australia's savannahs by promoting landscape flammability⁶². In aquatic ecosystems, invasive predatory fish – such as the Indo-Pacific lionfish in Caribbean coral reefs⁶³ or the Nile perch in African lakes⁶⁴ – have contributed to the loss of native species. Marine invasions are also facilitated by the mass transport of species in the ballast water of ships, which results in widespread biotic homogenization⁶⁵.

Global climate change

Many of these local stressors are promoted by globalized drivers, but climate change is truly global. Increases in atmospheric CO₂ concentrations to levels higher than 400 p.p.m. have important implications for tropical terrestrial and aquatic ecosystems. Ocean acidification from dissolved CO₂ is changing ocean chemistry to the extent that declining coral calcification has already been detected⁶⁶. Conditions for reef accretion and growth may be mostly absent throughout the tropics by the year 2100 under 'business-as-usual' emission scenarios⁶⁷. Within

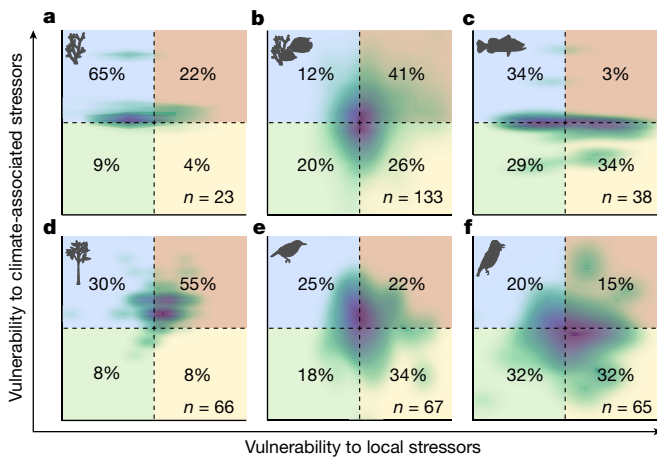


Fig. 3 | Vulnerability of tropical biota to local and climatic stressors. Species co-tolerance to a local and climate-associated stressor⁸⁵. The x axis shows responses to fishing for corals (a), reef fish (b) and freshwater fish (c); changes in landscape configuration for small-stemmed trees (diameter at breast height between 2 and 10 cm (d)) and forest birds (e); and fire suppression for savannah birds (f). The y axis represents longitudinal responses to climate-associated events: the 2015-2016 and 1997-1998 coral bleaching events in the Seychelles for corals (a) and reef fish (b), respectively; the 1997-1998 El Niño-induced drought for lower Amazonian freshwater fish (c); Amazonian fires during the 2015-2016 El Niño event for small-stemmed trees (d) and forest birds (e); and shrub encroachment between 1998-2008 in South Africa for savannah birds (f). Species relative density is represented from low (light green) to high (dark blue). The four quadrants represent the location of ‘survivor’ species tolerant to both stressors (green), species only susceptible to local stressors (yellow), species only vulnerable to climate-associated stressors (blue) and ‘double jeopardy’ species susceptible to both stressors (red). Numbers show the percentage of species that fall into the quadrant. *n* gives the total number of species (genera for corals). Data sources are presented in Supplementary Table 1.

savannahs, elevated CO₂ levels favour the growth of woody plants over grasses, contributing to woody encroachment and the potential for a switch in biome state^{68,69}. CO₂ fertilization may also have contributed to enhanced tree productivity and mortality rates observed in humid tropical forests⁷⁰.

Global warming is not proceeding at the same rate across the planet. Although the greatest absolute temperature increases are occurring at higher latitudes, the tropics are already some of the hottest places on the planet and have the lowest inter-annual temperature variability^{71,72}. Consequently, they will be the first areas to experience significantly warmer climates than the present day⁷² and will endure climatic conditions without present-day equivalents⁷¹. In addition, some of the most important climate oscillations – including El Niño and the Indian Ocean Dipole – take place within and exert their greatest influence on, tropical regions. It is unclear whether these oscillations will change in a warming world, but extremes of their phases have the potential to exacerbate or ameliorate the overall warming trend. One outcome of increasing temperatures is the pole-ward shift of species ranges or movement to higher altitudes or deeper depths⁷³. For example, corals in southern Japan are extending northwards at about 14 kilometres per year⁷⁴, and temperate macroalgal communities are being replaced with corals and other tropical species along large stretches of Australian coastline⁷⁵. Latitudinal shifts in terrestrial and freshwater tropical species distributions are less certain, because of the many natural and anthropogenic barriers to species movement and the low dispersal capacity of many tropical species⁷⁶. Furthermore, the responses of terrestrial species are defined by changes in rainfall as well as temperature⁷⁷.

If movement is not an option, tropical species must adapt or face extinction. Unfortunately, there is evidence that some species are either approaching their physiological limits or are unable to adapt to the current rate of environmental change⁷⁸. Increasing ocean temperature extremes are driving mass-bleaching events and mortality of reef-

-forming corals, with the time between bleaching events declining by 76-80% since the early 1980s⁷⁹. Higher temperatures also affect tropical vertebrates – for example, by causing an extreme female bias in the sex ratio of green turtles in the warmer regions of the Great Barrier Reef⁸⁰ and a reduction in the reproductive success of African wild dogs⁸¹. Altered rainfall is also critical. Droughts are drying up biologically diverse small streams⁸², and even modest changes in dry-season length increase tropical tree mortality⁷⁰ and modify tropical forest bird community structure⁸³.

Interacting stressors and indirect effects

Stressors affecting tropical species can interact in myriad ways⁸⁴. We demonstrate this by compiling data from six case studies within a co-tolerance framework that enables the examination of species responses to two dominant stressors⁸⁵. Only a small subset of species or genera (8-32%) showed no or positive responses when both stressors were combined (Fig. 3), and up to 55% fell within the ‘double jeopardy’ quadrant that indicates a negative response to both stressors. Although our summary does not quantify the magnitude of effects, it clearly demonstrates that stressors can act together to reduce the abundance or occupancy of tropical species. Moreover, most tropical ecosystems are affected by more than two stressors at any given location and time⁸⁴, and co-tolerance analyses of this type are likely to underestimate the reality of human impacts.

Many changes to tropical ecosystems result from the indirect consequences of single or multiple stressors. On coral reefs, nutrient inputs from the land may increase susceptibility to coral bleaching, disease and outbreaks of pests⁸⁶, and pole-ward reef expansion is supported by feedbacks from range-shifts in tropical herbivorous fish⁷⁵. Overexploitation can result in surprising changes in tropical ecosystem properties through trophic cascades. For instance, the extirpation of a single detritivore fish species in the Orinoco basin reduced downstream organic-carbon transport, which in turn increased net primary productivity and respiration⁸⁷. On reefs, the overfishing of keystone predators has repercussions for benthic structure⁸⁸, and the removal of herbivores can limit coral recovery from mass-mortality events⁸⁹. In mesic savannahs, changes to herbivore numbers alter ecosystem functions and structure through their interactions with wildfire regimes⁹⁰. Invasive species are also frequently linked to other stressors: the introduction of the Nile perch had a major role in the decline of endemic fish species in Lake Victoria, but these declines were also catalysed by a combination of other drivers including soil erosion, eutrophication and overfishing⁶⁴.

Ecosystems in transition

Interactions between multiple anthropogenic stressors are causing pervasive changes in the tropics, such that alternative states are emerging across all major tropical ecosystems (Fig. 4). Perhaps counterintuitively, trees are encroaching on savannahs and grasses are invading disturbed tropical forests – however, in both cases the changes are from species-rich to species-poor systems^{68,91}.

These marked ecosystem transitions are accompanied by widespread modification of species composition. For example, the relative abundance of coral species has been altered on reefs that maintain coral dominance⁹²; the extirpation of native fish has followed species introductions in lakes⁶⁴; liana biomass has increased in otherwise undisturbed Neotropical forests⁹³; and patterns of plant regeneration in humid forests have been altered by the overharvesting of seed-dispersing vertebrates^{31,94}. Altered species composition is a cause for concern because it could signal the onset of more severe modification, especially if dominant species are vulnerable to other stressors or if there are cascading implications for ecosystem functioning. The collapse of Jamaican coral reefs provides one of the starkest examples. First, chronic overfishing depleted herbivorous fish populations, which left the system over-reliant on sea urchins for grazing algae. Then, in 1980, Hurricane Allen affected the system, creating a substantial amount of dead substrate. Although corals began to recover after the hurricane, the subsequent mass mortality of sea urchins owing to disease – combined with the fact that herbivorous fish were already at low levels of abundance – led to a phase shift from coral to macroalgal dominance^{95,96}.

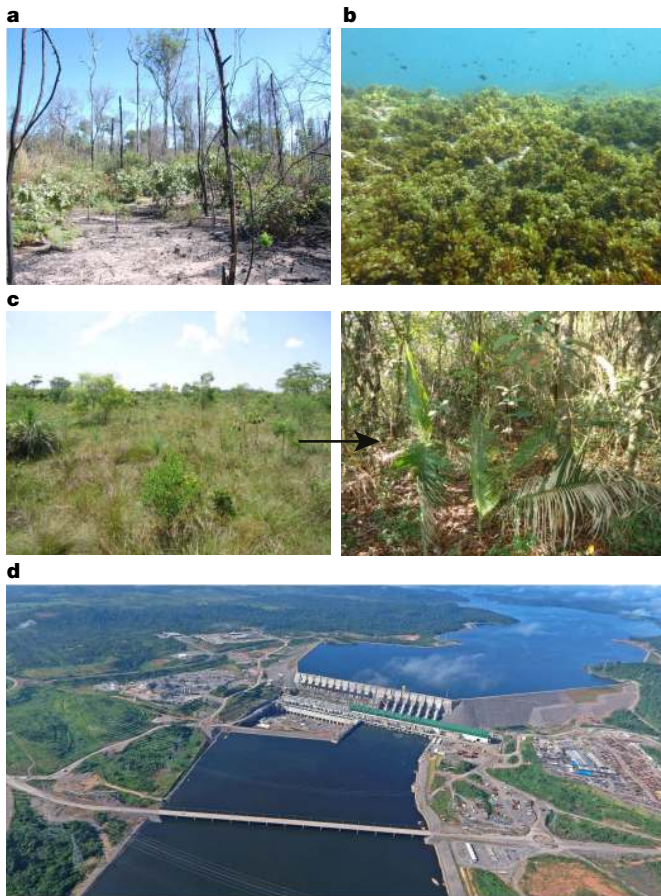


Fig. 4 | Tropical ecosystems in transition. **a**, Recurrent wildfires in historically fire-free humid tropical forests¹⁶⁷ can lead to the dominance of grassy vegetation that impedes succession towards closed-canopy forests^{91,168}. These wildfires result from the combination of local actions (for example, agricultural practices and logging) and climate change that has increased the prevalence of weather that promotes wildfires¹⁶⁹. **b**, Chronic local pressures and acute climatic stressors can lead to coral cover being replaced by macroalgae, sponges or sediment-laden turf algae^{89,95}. During the 1998 global coral-bleaching event, >90% of live coral died in the inner Seychelles and nearly half of the reefs transitioned to fleshy macroalgal regimes⁸⁹. **c**, Woody encroachment is occurring in many savannas⁶⁹, causing biodiversity loss and altered system functioning⁶⁸. Causes are mixed: regime shifts to forest-associated ecosystems have been attributed to fire suppression policies (for example, Brazilian cerrado (left) to forest (right)¹⁷⁰), or changes in herbivory and increasing atmospheric CO₂⁶⁹. **d**, The boom in hydropower dam construction is affecting large tropical river basins¹³⁴. The transformation from lotic to lentic conditions reduces access to riparian and floodplain habitats that are nursery areas and feeding grounds for many of the species occupying higher trophic levels, leading to major shifts in species composition and ecosystem function⁸². Images from J.B. (a), N.A.J.G. (b), G. Durigan (c) and C.G.L. (d), used with permission.

Socio-economic context and response capacity

The interacting proximate stressors causing tropical environmental change are underpinned by broader changes in socio-economic and political factors. We examined the trajectories of four types of underlying distal drivers, including demography and the economy (Fig. 5a, b), socio-political factors (Fig. 5c, d), markets (Fig. 5e, f) and technology⁹⁷ (Fig. 5g, h) to explore how tropical countries are changing relative to the rest of the world and to evaluate the relative influence of local and global drivers. We also examined how the capacity of tropical countries to reduce or cope with proximate stressors compares to non-tropical countries based on underlying governance systems (Fig. 5i, j) and research capacity (Fig. 5k, l).

The immense biodiversity of the tropics exists in the context of rapid demographic and economic growth (Fig. 5a, b). The human population

is growing at a faster rate in the tropics than elsewhere (Fig. 5a), and by 2050 half of the world's population will live in the tropics². These demographic changes are accompanied by a steady growth in gross domestic product (GDP) that is linked in part to the rapid expansion of agricultural and extractive industries. However, in the tropics, per capita GDP – which is an important measure of human well-being – remains far lower than the non-tropical average (Fig. 5b) and the rates of change suggest that there has been little closing of the global inequality gap. Although the relationship between development and natural resource conservation does not have to be negative^{98,99}, measures that reflect higher social performance are almost always associated with higher resource use⁹⁹. A larger and more affluent tropical population will increase demands for timber, water, food, energy and land, all of which are strongly linked with environmental degradation.

These internal changes will be exacerbated by economic growth in non-tropical countries and the continued displacement of environmental effects to less-developed areas¹⁰⁰. Indeed, despite high levels of tropical cultural diversity^{21,22}, external socio-political influences (Fig. 5c, d) suggest that tropical countries have become increasingly susceptible to globalization. For example, the proportion of imported food crops (Fig. 5c) and foreign land acquisitions are far higher in the tropics than elsewhere (Fig. 5d) and are associated with extensive road building¹⁰¹ and agricultural investment¹⁰². These trends towards increasing tropical globalization are reinforced by changes in market integration (Fig. 5e, f) and technological development (Fig. 5g, h). For example, agricultural exports (Fig. 5f) are steadily increasing, albeit from a far lower baseline than the rest of the world. Moreover, given comparatively low levels of adoption of technological developments, such as industrial fishing techniques (Fig. 5g) or fertilizers (Fig. 5h), there is an enormous risk that the rate of natural resource extraction in many tropical countries will increase further, to supply both domestic and export markets^{103,104}. Taken together, these examples highlight the crucial role that external markets will have in determining the fate of tropical ecosystems.

Effective environmental governance (Fig. 5i, j) is a necessary condition for improved sustainability outcomes¹⁰⁵, particularly when domestic (Fig. 5a, b) and global (Fig. 5c-f) distal drivers are expected to exert increasing and unsustainable pressure on tropical ecosystems^{2,102}. However, national-level assessments of governance effectiveness place the tropics far below extra-tropical countries, with no sign of improvement (Fig. 5i). External support for environmental governance may help where local governance is weak. Yet, despite the biological importance of the tropics, levels of environmental aid from the Organisation for Economic Cooperation and Development (OECD) are only marginally greater in the tropics than elsewhere (Fig. 5j), and these investments are dwarfed by the value of domestic resource extraction (for example, agricultural exports; Fig. 5f), the value of which is two orders of magnitude greater than overseas environmental aid. Furthermore, OECD environmental aid has been declining in recent years and seems unlikely to increase in the short term¹⁰⁶.

Low governance capacity in the tropics is further exacerbated by insufficient research and development investment (Fig. 5k) and low levels of scientific output (Fig. 5l). Research investment is critical for driving innovation and the development of evidence-based solutions to environmental degradation¹⁰⁷. Despite some notable centres of excellence, the vast majority of biodiversity-related data and research is concentrated in wealthy, non-tropical countries¹⁰⁷, and manuscripts submitted by authors from low-income countries are less than half as likely to be published as those from high-income countries¹⁰⁸. These trends highlight an alarming disconnect between the global scientific process and the people that are most capable of engaging with decision makers in tropical countries, who have the best understanding of local context and, arguably, have the strongest incentive to achieve positive outcomes for tropical conservation through their research.

Diverse solutions for diverse systems

Tropical ecosystems – and therefore at least 78% of global biodiversity (Fig. 2a) – are at a critical juncture. Multiple interacting local and global stressors (Fig. 3) that are driving species extinctions and potentially irreversible ecosystem transitions^{92,109} (Fig. 4) are set within

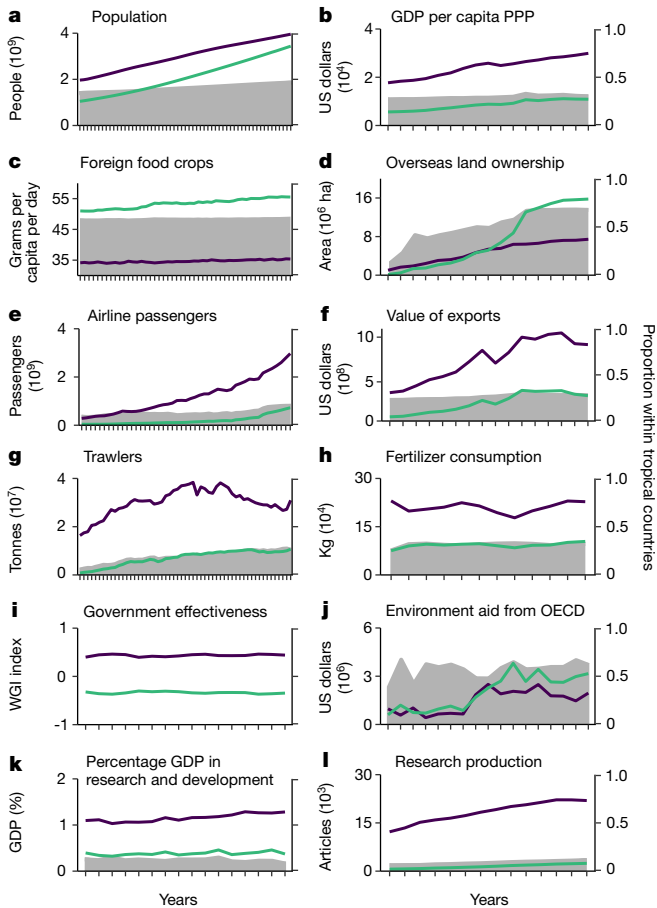


Fig. 5 | Socio-economic drivers of biodiversity loss and societal response capacities. Green lines represent countries with >50% of their area within tropical latitudes; purple lines represent all other countries; grey-shaded areas represent the proportion of the global total within tropical countries. **a.** Population (1960-2016). **b.** GDP per capita (2011 US dollars, based on purchasing power parity; 2000-2016). **c.** Foreign food crops (1961-2009). **d.** Cumulative overseas land ownership (2001-2017). **e.** Domestic and international airline passengers (1970-2016). **f.** Agricultural and forestry commodities export value (2001-2016). **g.** Bottom and pelagic trawler catch tonnages (1960-2014). **h.** Total fertilizer (nitrogen, potash and phosphate) consumption relative to crop area (2002-2013). **i.** Government effectiveness index (2000-2016). WGI, World Governance Indicators. **j.** Environmental aid (2000-2016). **k.** Public and private sector research and development expenditure as a percentage of GDP (2000-2015). **l.** Scientific and technical journal articles per million people in the fields of physics, biology, chemistry, mathematics, clinical medicine, biomedical research, engineering and technology, and Earth and space sciences (2003-2016). Data sources are presented in Supplementary Table 1.

a changing socio-economic context (Fig. 5). This changing context is characterized by growing and more affluent populations, an increasingly globalized world, and weak governance and research capacity – all of which threaten to increase environmental degradation, conflict and inequality¹⁰². Countering these threats requires major improvements in local and global governance capacity and a step-change in how environmental objectives are integrated into broader development goals¹¹⁰. We review the opportunities and limitations presented by three well-established and non-mutually exclusive approaches to conservation, before highlighting priorities for research.

Conservation approaches

A fundamental element of tropical conservation relies on protected areas to limit demographic pressures and the effect of local stressors. These are supported by a wealth of scientific evidence outlining the pervasive effect of local stressors across tropical ecosystems^{37,49} (Fig. 3) combined with an eco-centric philosophy that emphasizes the intrinsic rights of nature¹¹¹. Despite a substantial expansion of protected area

coverage in the marine and forested tropics¹¹², the current network remains poorly designed, has very limited coverage of tropical freshwaters and grasslands, and is inadequately resourced¹¹³. Moreover, a strategy focused solely on protected areas may not foster environmental conservation outside of reserves¹¹⁴ and fails to engage with the distal drivers of biodiversity loss (Fig. 5) that can undermine the effectiveness of protected areas themselves¹¹⁵.

A second set of approaches for tropical conservation is based on the notion that people need to perceive the benefits of nature to justify conservation. These approaches emphasize the need to pursue conservation objectives in human-dominated landscapes, the provision of ecosystem services and the involvement of private-sector actors. In the tropics, they are epitomized by the growth in market-based conservation payment mechanisms, such as REDD+¹¹⁶, investments in the ‘blue economy’¹¹⁷ and a step-change in the number of companies making sustainability commitments¹¹⁸. These approaches have strengthened the conservation toolkit, especially where strict regulatory approaches have failed. Encouraging examples range from the positive effects of commodity certification (for example, palm oil¹¹⁹) to payment for ecosystem service schemes (for example, watershed protection¹²⁰). However, such approaches also attract considerable criticism, with implementation often lagging behind commitments¹¹⁸, persistent concerns around the social legitimacy of compensation schemes¹²¹ and the misalignment of market-based mechanisms with local needs and perceptions of environmental values¹²².

A third and more diverse set of approaches is based on the recognition of the interdependencies between people and nature, the coevolution of ecological and socio-economic systems at local, regional and global scales¹²³, and perspectives about the co-existence of people and nature. This set of ‘systems-based’ approaches includes: (1) an appreciation of the importance of bottom-up, community-based conservation approaches in human-dominated land- and seascapes (for example, small-scale fisheries¹²⁴ and community-managed forests¹²⁵); (2) recognition of the role of indigenous people as environmental stewards and shifts towards an appreciation of more collective relationships with nature (for example, the Ecuadorian constitution¹²⁶); (3) landscape- and ecosystem-wide approaches that attempt to bridge the role of actors working at different scales and in different sectors (for example, jurisdictional approaches to curb deforestation¹²⁷); and (4) a more explicit accounting of multi-scale feedbacks, including the role of distant market actors and distal drivers¹²³. These broad, multi-layered ‘people and nature’ approaches hold considerable appeal but the inherent complexity of local contexts can make them challenging to conceptualize, implement and measure in joined-up and consistent ways¹²⁸.

Acting together and acting now

The three approaches to the conservation and governance of tropical ecosystems outlined above are often associated with alternative researcher and practitioner worldviews^{129,130}. However, the ecological diversity (Fig. 2a), vulnerability (Figs. 2b, 3) and socio-economic complexity (Fig. 5) of the tropics highlights the importance of pluralism¹³¹ and the need to adopt a variety of what are often complementary and synergistic approaches¹³⁰. For all their deficiencies, protected areas are indispensable to limit the effect of local stressors, and it will be impossible to avoid further biodiversity loss unless they are strengthened and expanded¹³². However, conservation strategies must also address the underlying drivers of environmental change (Fig. 5) and avoid exacerbating deeply rooted inequalities¹¹⁴. Practice is always messier than theory, and the adoption of more sustainable management systems is usually only possible with the support of a range of actors, as can be seen in the recent successes of some hybrid governance approaches, with government, the private sector and civil society organizations all having vital roles¹³³.

Another clear message is that conservation efforts need to operate at local, regional and global scales to be effective. Many distal drivers are disconnected in both space and time from the sites they affect, and the engagement of external actors – including in distant markets and governance processes – is often essential to ensure that local efforts are effective. These include more strategic integration of environmental policy with development goals¹³⁴, the need for multi-

national environmental governance approaches, especially for aquatic systems⁸², and recognition of the importance of tackling demand for unsustainable products from downstream buyers and investors¹¹⁸. The capstone of such efforts lies in the urgent need to deliver on the Paris Agreement, without which climate change will undercut or even negate hard-won local conservation successes, whether in coral reefs⁹² or tropical forests¹⁰⁹.

Finally, we need to act now to address the pressing environmental challenges facing the tropics. This means being adaptive, learning by doing and embracing innovation. The past decades have seen a boom in proposals, innovations and insights about the governance and management of tropical ecosystems, ranging from more technocentric proposals to facilitate the evolution of climate-tolerant corals¹³⁵; ecological engineering to recover lost trophic interactions by species re-introductions, ecological replacements and rewinding¹³⁶; to radical new legal frameworks such as France's 'Loi de vigilance' (2017-399; <https://www.legifrance.gouv.fr/eli/loi/2017/3/27/2017-399/loi/texte>) that places an unprecedented due diligence obligation on major companies to assess social and environmental risks in their supply chains that extend beyond French borders. Though these innovations serve different purposes and are varyingly scalable, they illustrate the potential of solutions-based science and conservation. Of course, acting now does not mean ignoring the existing evidence base or making uninformed decisions. Rather, it is vital that researchers and decision makers are vigilant to opportunities and risks and are willing to learn lessons.

Keeping pace with the Anthropocene

All approaches to governing tropical ecosystems will be more effective if they have local support and are based on strong scientific evidence that ensures, for example, that protected areas are located where they are most needed, ecosystem services are accurately quantified, extractive activities such as fishing and logging are managed sustainably, and underlying drivers of environmental degradation are identified and understood. Although these challenges are common to all conservation and sustainability science, they are magnified in the tropics owing to the unique diversity and high vulnerability of tropical ecosystems and the low research capacity of most tropical countries. Here we examine four areas in which research effort can be more closely aligned with some of the priorities highlighted by this review.

Addressing key knowledge shortfalls

Our understanding of tropical biodiversity is limited by substantial shortfalls in knowledge regarding taxonomy and species distributions¹³⁷. Overcoming these shortfalls will require targeting resources towards the data-scarce regions that cover so much of the tropics¹⁸. At the ecosystem level, there is a need for increased study of structurally and functionally distinct systems, particularly tropical grassy biomes⁶⁸, dry forests¹³⁸ and low-order stream systems¹³⁹. Progress in these areas is likely to be aided by advances in DNA sequencing and informatics, which have the potential to invigorate taxonomic discovery, and by reaching across cultural divides to incorporate national, regional and local knowledge that often remains ignored because it is not available in English¹⁴⁰, included in standard databases¹⁴¹ or recognized by conventional science¹⁴².

Understanding vulnerability

Our growing knowledge of the role of individual stressors, such as landscape configuration or overexploitation, needs to be complemented by research on the effect of multiple stressors⁸⁴, which could help predict and mitigate complex biotic responses when climate and local stressors act in concert (Fig. 3). Other phenomena that are important but harder to study include the role of time lags or extinction debts⁴⁰, trophic cascades³¹ and trajectories of ecosystem degradation and recovery in the face of unprecedented environmental change¹⁴³. Revealing these more-complex forms of vulnerability will often demand longer-term and larger multi-scale sampling and monitoring programs. New approaches are also needed to overcome one of the more intractable challenges of tropical ecology: the fact that we often know least about the rarest and most vulnerable species or taxonomic groups.

Understanding distal drivers

Conservation does not occur in a vacuum, and local interventions are likely to be much more effective if they are guided by a closer understanding of underlying distal drivers of biodiversity loss and environmental change, including identifying the actors behind such drivers, which will help to determine potential trigger points and identify more effective policy responses⁹⁷. Unpicking the role of distal drivers is essential to understand how distant interactions between social and environmental systems shape local environmental outcomes¹⁴⁴. Careful study has revealed many surprising interactions, such as links between the intensification of commercial fishing and increased bushmeat exploitation in west Africa¹⁴⁵, the role of warfare in driving African mammal declines¹⁴⁶ or the role of currency exchange rates in driving deforestation¹⁴⁷. Achieving this deeper understanding requires greater integration of the natural and social sciences, with interdisciplinarity included as a core element of tropical conservation research¹⁴⁸.

From research to impact

Achieving positive effects from conservation research relies on building a stronger interface between science and society that challenges the oversimplified assumption of a linear flow from knowledge to action¹⁴⁹. Engendering positive changes will require closer participation of practitioners in the research process and investments in outreach activities and professional capacity building¹⁴⁹. These will be supported by studying the knowledge exchange process itself, including the critical part that is played by knowledge brokers and boundary organizations¹⁵⁰⁻¹⁵². Part of this process will require a focus on success stories or 'bright spots', which will enable the social, institutional and environmental conditions that create positive outcomes to be identified and replicated¹⁵¹. The positive social and ecological outcomes from innovative restoration and rewinding programmes in Costa Rica and Mozambique demonstrate the potential for positive action¹⁵³.

Local managers and scientists have a vital role in designing and implementing research that can inform regionally appropriate conservation actions¹⁵⁴. At present, our knowledge of hyperdiverse ecosystems is over-reliant on inferences gleaned from distant research stations or inappropriate theoretical constructs developed for temperate contexts^{18,155}. Research is also more likely to have an effect if the spatial scale of studies is closely matched to the administrative scale at which resource decisions are taken¹⁵⁶. Sustaining research programmes and learning networks in study landscapes can help build vital relationships between researchers, local knowledge holders and decision makers¹⁵⁴.

Achieving these changes requires building on trends in the technological, disciplinary and cultural dimensions of research practice. In the technological domain, opportunities for data collection have been revolutionized by developments in remote sensing and drones¹⁵⁷, the plummeting costs of DNA technologies¹⁵⁸ and the step-changes in bioinformatics that have enabled 'big data' to be stored and retrieved in open-access platforms¹⁵⁹. In the disciplinary domain, the past decade has seen a marked upward trend in interdisciplinary and transdisciplinary research and a greater – albeit still insufficient – integration of natural and social sciences. This has resulted in an increasing openness of researchers towards methodological pluralism and mixed-method approaches¹⁴⁹ and a growing recognition of the contribution that can be made by local people and citizen- and para-scientists in biodiversity research¹⁶⁰. Changes in research culture include the greater internationalization of ecological science and closer approximation with society¹⁴⁹, both of which can help foster more fertile ground for knowledge exchange and capacity building. Notable advances include the development of multi-disciplinary and multinational learning networks¹⁶¹, exponential growth in author teams¹⁶² and major syntheses such as the Intergovernmental Platform for Biodiversity and Ecosystem Services.

Recent years have seen an awakening of environmental consciousness and calls for decisive action that are manifest, for example, in the Paris Agreement, the Sustainable Development Goals and voluntary Zero Deforestation Commitments. Scientists from tropical and non-tropical regions can inform these endeavours by developing a reliable knowledge base and innovative management interventions. Overcoming the remaining research challenges is far from trivial and will require a massive investment of resources to develop scientific infrastructure

and capacity within tropical nations, as well as profound changes to ways of working and the relationship between the research process and society at large. But a failure to act decisively and to act now will greatly increase the risk of unprecedented and irrevocable biodiversity loss in the hyperdiverse tropics.

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