# The future of hyperdiverse tropical ecosystems

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

## Introduction

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 conservation[1]. Yet, tropical ecosystems are undergoing rapid environmental, socio-economic and demographic change[2], often driven by forces from extra-tropical, developed countries. The scale of these changes is unprecedented, and decisions implemented in the coming decades will define the future diversity and sustainability of the tropics.

Guiding these decisions depends on understanding the diversity and vulnerability of the four major tropical ecosystems: the forests and mesic savannas 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 foster positive change and help overcome the challenges arrayed against a sustainable tropical future.

**The global importance of tropical ecosystems**

Over evolutionary time, the tropics have acted both as a source and refuge for most 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, repeats 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 >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, with almost half of all Nearctic species migrating to the Neotropics[5] and over 2 billion passerine and near-passerines crossing the Sahara each autumn[6]. Moreover, a disproportionate number of the world's species are endemic to the tropics. For example, there are 4.5 times more endemic amphibians in the tropics than in temperate regions (Fig 2a). Tropical zones are less important for marine mammals and birds, taxa that peak in diversity at mid-latitudes[7,8]. Nonetheless, >55% of these species use the tropics (Fig. 2a).

Overall, 78% of species across the ten taxa we assessed occurred within tropical latitudes, but incomplete taxonomic inventories mean that this is almost certainly an underestimate[9]. Between 15,000-19,000 new species are described annually[10], and the majority of recently described terrestrial vertebrates[11] or predicted discoveries of invertebrates[12] are from the tropics. Even terrestrial mammals are still being discovered at a rate of c. 25 species a year, with the highest numbers in the Neo- and Afrotropics[13]. Shortfalls in species descriptions for other taxa are often far greater. For example, only 70,000 of an estimated 830,000 multi-cellular plants and animals have been named on coral reefs[14], and the c. 500 spider species described each year represent a tiny fraction of the estimated 150,000 undescribed tropical species[15].

Tropical taxonomic shortfalls are further compounded by a suite of systematic sampling biases. These include undersampling compared with temperate regions[16], the spatial aggregation of sampling effort around coastal areas[17], roads, rivers, urban settlements and high-profile research stations[18], biases in favour of dry-season sampling when many invertebrate taxa are least abundant[19], and the paucity of samples from ecosystems that are harder to access, such as mesophotic and rariphotic reefs[20].

The biological diversity of the tropics is mirrored by many forms of societal diversity[21]. For example, tropical countries contain 40% of the world's population yet 85% of extant languages are spoken within them[22]. The tropics also provide incalculable benefits to humanity. They house most of the key centres of plant domestication[23] 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: covering just 0.1% of the ocean surface, coral reefs provide fish resources for 275 million people that live within 30 km of them[24] and coastal protection for up to 197 million people[25]; humid tropical forests cover <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 biosphere[26]; while tropical savannas provide a further 30% of net primary productivity and 15% of carbon storage[27]. Tropical ecosystems also help drive vital atmospheric teleconnections. For instance, 70% of the rainfall in the 3.2M km$^2$ *Rio de la Plata* catchment is estimated to come from evaporation in Amazonia[28].

## Vulnerability of tropical biota and ecosystems

For all five vertebrate groups with comprehensive IUCN assessments and spatial occurrence data[29], globally threatened species are more dependent on the tropics than those classed as Least Concern (Fig. 2b). In addition, 85% of species extinctions from these vertebrate groups have been of species that use the tropics[29]. Consequently, although extinctions of other groups are less well understood, we can assume that most of the estimated 130,000 modern invertebrate extinctions[30] will also have been of tropical species. Thus, not only are the tropics vastly more diverse than temperate regions, this diversity is at far greater risk from human impacts[31]. Moreover, given that the tropics have the highest proportion of Data Deficient species and the lowest level of biodiversity-threat assessment[16], information shortfalls mean we are likely 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 rates of land-use change and degradation. While the spatial coverage of temperate forests has increased since 1990, tropical deforestation rates exceed 5M ha/yr[32]. Additional impacts stem from the expansion of large infrastructure projects (e.g. dams) and the growing demand for agricultural commodities, biofuels, timber, fuelwood and other natural resources[33]. These all result in severe biotic responses. Even with mitigation, dams present a near-impassable barrier for river fish[34], while deforestation replaces a species-rich pool of forest-specialists with a smaller pool of common open-area species[35]. The influence of land-use change also extends far into remaining natural areas through isolation and edge effects[36], additional anthropogenic disturbances[37] and altered climatic conditions[38]. Edge effects suppress the abundance of threatened vertebrates up to 200-400 m into tropical forests[36], leaving almost no core forest refugia in the Brazilian Atlantic Forest where >80% is within 500 m of an edge[39]. Even low levels of landscape modification have significant effects on range-restricted species[37], and time lags mean that some of the most deleterious effects are observed decades after landscape modification[40].

Pollution presents a diverse set of threats to tropical ecosystems. Inputs of sediments and nutrients from land-use change are well-established drivers of biodiversity loss across freshwater[41] and coastal systems, including coral reefs[42] . Pesticide use is increasing across the tropics, reflecting rapid intensification of farming practices[43] and high pest pressures on tropical crops[44]. Tropical Asian rivers are a major source of the 1.2-2.4 million tonnes of plastic that enters the world's oceans each year[45], with micro-plastics entering into coral diets[46] and larger debris increasing rates of coral disease[47]. These examples of chronic pollution are exacerbated by extreme events, such as of the *Fundão* Dam collapse, which released c. 50M $m^3$ of waste into a 600 km stretch of river in south-east Brazil, causing a 7,000 $km^2$ toxic plume in the Atlantic Ocean[48].

Overexploitation is also pervasive across the tropics. Fishing has reduced fish biomass by over 75% across a third of coral reefs[49] and is shrinking the mean body size of exploited freshwater taxa[50]. Hunting contributed to the loss of charismatic mega-herbivores, extirpating African elephants, rhinos and large predators from most of their original ranges[51,52]. The world's tropical forests are affected by extensive over-harvesting of wildlife[31], with estimates of the annual harvests of highly-trafficked animals such as pangolins reaching into the millions of individuals[53]. Moreover, the growth in non-food uses of wildlife means that even small-bodied songbirds are at risk of global extinction[54]. Overexploitation also extends beyond fauna and is driving economically valuable tropical trees to extinction[55].

Invasive species have been the second most important extinction driver of vertebrates since 1500 CE[56]. Within terrestrial ecosystems, invasive species have exerted the strongest influence on islands and coastal mainlands[57], having driven thousands of species extinctions and altered trophic structures[58]. On continents, they currently have a greater impact on economically developed and extra-tropical regions, but tropical ecosystems are predicted to become increasingly vulnerable to invasion in the 21st century[59]. Despite a deficit of research in the tropics[60], two prominent examples highlight the scope and magnitude of species invasions into terrestrial tropical ecosystems: there has been an 84% increase of alien species detections between 2003 and 2010 in Singapore[61], while invasive African grasses could threaten up to 380,000 $km^2$ of Australia's savannas by promoting landscape flammability[62]. In aquatic ecosystems, invasive predatory fishes, such as the Indo-Pacific lionfish in Caribbean coral reefs[63] and the Nile perch in African lakes[64], have contributed to the loss of native species. Marine invasions are also facilitated by the mass transport of species in ship ballast water, resulting in widespread biotic homogenisation[65].

*Global climatic change*

While many of the "local" stressors described above are promoted by globalised drivers, climate change is truly global. Increases in atmospheric $CO_2$ concentrations to levels >400 ppm has important implications for tropical terrestrial and aquatic ecosystems. Ocean acidification from dissolved $CO_2$ is changing ocean chemistry to the extent that declining coral calcification has already been detected[66]. Conditions for reef accretion and growth may be mostly absent throughout the tropics by 2100 under business-as-usual emission scenarios[67]. Within savannas, elevated $CO_2$ levels favour the growth of woody plants over grasses, contributing to woody encroachment and the potential for a switch in biome state[68,69]. $CO_2$ fertilisation may have also contributed to enhanced tree productivity and mortality rates observed in humid tropical forests[70].

Global warming does not proceed 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 day[72] and will endure climatic conditions without present-day equivalents[71,]. In addition, some of the most important climate oscillations, including El Niño and the Indian Ocean Dipole, take place within, and have their greatest influence on, tropical regions. It is unclear if 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 poleward shifts of species ranges or movement to higher altitudes or deeper depths[73]. For example, corals in southern Japan are extending northwards at c. 14 km/yr[74], and temperate macroalgal communities are being replaced with corals and other tropical species along large stretches of Australian coastline[75]. Latitudinal shifts in terrestrial and freshwater tropical species distributions are less certain because of the many natural and anthropogenic barriers, and the low dispersal capacity of many tropical species[76]. Furthermore, the responses of terrestrial species are defined by changes in rainfall as well as temperature[77].

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 rate of environmental change[78]. 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 1980s[79]. Higher temperatures also affect tropical vertebrates, causing, for example, an extreme female bias in the sex ratio of green turtles in the warmer regions of the Great Barrier Reef[80] and a reduction in the reproductive success of African wild dogs[81]. Altered rainfall is also critical. Droughts are drying up biologically diverse small streams[82], while even modest changes in dry-season length increase tropical tree mortality[70] and modify tropical forest bird community structure[83].

*Stressor interactions and indirect effects*

Stressors affecting tropical species can interact in myriad ways[84]. We demonstrate this by compiling data from six case studies within a co-tolerance framework that allows species responses to two dominant stressors to be examined[85]. 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, indicating a negative response to both stressors. While 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, these co-tolerance analyses simplify the reality facing tropical ecosystems because most are affected by more than two stressors at any given location and time[84].

Many changes to tropical ecosystems result from indirect consequences of single or multiple stressors. On coral reefs, nutrient inputs from land may increase susceptibility to coral bleaching, disease, and outbreaks of pests[86], while poleward reef expansion is supported by feedbacks from range-shifting tropical herbivorous fish[75]. 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, increasing net primary productivity and respiration[87]. On reefs, overfishing of keystone predators has repercussions for benthic structure[88], while removal of herbivores can limit coral recovery from mass-mortality events[89]. In mesic savannas, changes to herbivore numbers alter ecosystem functions and structure via their interactions with wildfire regimes[90]. Invasive species are also frequently linked to other stressors: the introduction of the Nile perch played a major role in the decline of endemic fish species in Lake Victoria, but its effects were likely catalyzed by a combination of other drivers including soil erosion, eutrophication and overfishing[64].

*Ecosystems in transition*

Interactions between multiple anthropogenic stressors are causing pervasive changes in the tropics, such that alternate states are emerging across all major tropical ecosystems (Box 1). Perhaps counter-intuitively, trees are encroaching on savannas while grasses are invading disturbed tropical forests – but in both cases, changes are from species-rich to species-poor systems[68,91].

These drastic 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 dominance[92]; extirpation of native fish has followed species introductions in lakes[64]; liana biomass has increased in otherwise undisturbed Neotropical forests[93]; 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 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, leaving the system over-reliant on sea urchins for grazing algae. Then Hurricane Allen impacted the system in 1980, creating a substantial amount of dead substrate. Although corals began recovering after the hurricane, the subsequent mass mortality of sea urchins due to disease, combined with the already low abundance of herbivorous fish, led to a phase shift from coral to macroalgal dominance[95,96].

## 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 (Fig. 4a-b), socio-political factors (Fig. 4c-d), markets (Fig. 4e-f) and technology (Fig. 4g-h)[97] 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 (Fig. 4i-j) and research capacity (Fig. 4k-l).

The immense biodiversity of the tropics exists in the context of rapid demographic and economic growth (Fig. 4a-b). Human population is growing at a faster rate in the tropics than elsewhere (Fig. 4a) and by 2050 half of the world's population will live in the tropics[2]. These demographic changes are accompanied by steady GDP growth, linked, in part, to the rapid expansion of agricultural and extractive industries. However, tropical per capita GDP – an important measure of human well-being – remains far lower than the non-tropical average (Fig. 4b), and the rates of change suggest little closing of the inequality gap between global south and north[98]. Although the relationship between development and natural resource conservation does not have to be negative[99,100], measures reflecting higher social performance are almost always associated with higher resource use[100]. 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 impacts to less-developed areas[101]. Indeed, despite high levels of tropical cultural diversity[21,22], external socio-political influences (Fig. 4c-d) suggest that tropical countries have become increasingly susceptible to globalisation. For example, the proportion of imported food crops (Fig. 4c) and foreign-land acquisitions are far higher in the tropics than elsewhere (Fig. 4d) and are associated with extensive road building[102] and agricultural investment[103]. These trends towards increasing tropical globalisation are reinforced by changes in market integration (Fig. 4e-f) and technological development (Fig. 4g-h). For example, agricultural exports (Fig. 4e) 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. 4g) or fertilizers (Fig. 4h), there is enormous risk that the rate of natural resource extraction in many tropical countries will increase further, supplying both domestic and export markets[104,105]. Taken together, these examples highlight the crucial role that external markets will play in determining the fate of tropical ecosystems.

Effective environmental governance (Fig. 4i-j) is a necessary condition for improved sustainability outcomes[106], particularly when domestic (Fig. 4a-d) and global (Fig. 4c-f) distal drivers are expected to exert increasing and unsustainable pressure on tropical ecosystems[2,103]. However, the World Bank's national-level assessments of governance effectiveness from the tropics sit in stark contrast to measures from extra-tropical countries, with no sign of improvement (Fig. 4i). External support for environmental governance may help where local governance is weak (Fig. 4j). Yet, despite greater OECD (Organisation for Economic Cooperation and Development) environmental aid in the tropics than elsewhere (Fig. 4j), these investments are dwarfed by the value of domestic resource extraction (e.g. agricultural exports; Fig. 4e), 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 term[107].

Low governance capacity in the tropics is further exacerbated by insufficient research and development investment (Fig. 4k) and low levels of scientific output (Fig. 4l). Research investment is critical for driving innovation and the development of evidenced-based solutions to environmental degradation[108]. Despite some notable centres of excellence, the vast majority of biodiversity-related data and research is concentrated in wealthy, non-tropical countries[17] and manuscripts submitted by authors from low-income countries are less than half as likely to be published as those from high-income countries[109]. These trends highlight an alarming disconnect between the global scientific process and the people that are most capable of engaging with decision makers, who have the best understanding of local context and, arguably, have the strongest incentive to achieve positive impacts through their research.

## Diverse solutions for diverse systems

Tropical ecosystems – and therefore at least 78% of the world´s 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[92,110] (Box 1) are set within a changing socio-economic context (Fig. 4). This changing context is characterised by growing and more affluent populations, an increasingly globalised world, and weak governance and research capacity – all of which threatens to increase environmental degradation, conflict and inequality[103]. 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 goals[111]. 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 impact of local stressors. These are supported by a wealth of scientific evidence outlining the pervasive impact of local stressors across tropical ecosystems[37,49] (Fig. 3) combined with an eco-centric philosophy that emphasizes the intrinsic rights of nature[112]. Yet, despite significant expansion of protected-area coverage in the marine and forested tropics[113], the current network remains poorly designed, has very limited coverage of tropical freshwaters and grasslands, and is inadequately resourced[114]. Moreover, a strategy focused solely on protected areas will not foster environmental conservation outside of reserves[115] and fails to engage with the distal drivers of biodiversity loss (Fig. 4) that can undermine the effectiveness of protected areas themselves[116].

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 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 epitomised by the growth in market-based conservation payment mechanisms, such as REDD+[117], investments in the "blue economy"[118] and a step change in the number of companies making sustainability commitments[119]. These approaches have strengthened the conservation toolkit, especially where strict regulatory approaches have failed. Encouraging examples range from the positive effects of commodity certification (e.g. palm oil[120]) to payment for ecosystem service schemes (e.g. watershed protection[121]). However, such approaches also attract significant criticism with implementation often lagging commitments[119], persistent concerns around the social legitimacy of compensation schemes[122], and the misalignment of market-based mechanisms with local needs and perceptions of environmental values[123].

A third and more diverse set of approaches is based on recognition of the interdependencies between people and nature, the coevolution of ecological and socio-economic systems at local, regional and global scales[124], and perspectives about the co-existence of people and nature. This set of more "systems-based" approaches includes: (1) an appreciation of the importance of bottom-up, community-based conservation approaches in human-dominated land- and seascapes (e.g. small-scale fisheries[125] and community-managed forests[126]); (2) recognition of the role of indigenous people as environmental stewards, and shifts towards an appreciation of more collective relationships with nature (e.g. the Ecuadorian constitution[127]); (3) landscape- and ecosystem-wide approaches that attempt to bridge the role of actors working at different scales and in different sectors (e.g. jurisdictional approaches to curb deforestation[128]); and (4) a more explicit accounting of multi-scale feedbacks, including the role of distant market actors and distal drivers[124]. 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 ways[129].

*Acting together and acting now*

The three broad approaches to the conservation and governance of tropical ecosystems outlined above are often associated with alternative researcher and practitioner worldviews[130,131]. But the inherent ecological diversity (Fig. 2a), vulnerability (Figs. 2b & 3) and socio-economic complexity (Fig. 4) of the tropics highlights the importance of pluralism[132] and the need to adopt a variety of what are often complementary and synergistic approaches[131]. For all their limitations, protected areas are indispensable to limit the impact of local stressors, and it will be impossible to avoid further biodiversity loss unless they are strengthened and expanded[133]. However, conservation strategies must also address the underlying drivers of environmental change (Fig. 4) and avoid exacerbating deeply rooted inequalities[115]. 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 playing vital roles[134].

Another clear message is that conservation efforts need to operate at local, regional and global scales to be effective. Many distal drivers are disconnected from sites of impact in both space and time, 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 goals[135], the need for multinational environmental governance approaches, especially for aquatic systems[82], and recognition of the importance of tackling demand for unsustainable products from downstream buyers and investors[119]. 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 reefs[92] or tropical forests[110].

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 last 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 corals[136]; ecological engineering to recover lost trophic interactions by species re-introductions, ecological replacements and rewilding[137]; to radical new legal frameworks such as France's "Loi de vigilance" (2017-399) that places an unprecedented due diligence obligation on major companies to assess social and environmental risks in their supply chains beyond French borders. While 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 legitimate 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. Whilst these challenges are common to all conservation and sustainability science, they are magnified in the tropics due to their unique diversity, high vulnerability and the low research capacity of most tropical countries. Here, we examine four areas where 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 significant knowledge shortfalls in taxonomy and species distributions[138]. Overcoming these shortfalls will require targeting resources towards the information "black holes" that cover large regions of the tropics[18]. At the ecosystem level, there is a need for increased study of structurally and functionally distinct systems, particularly tropical grassy biomes[68], dry forests[139] and low-order stream systems[140]. Progress in these areas will likely be aided by significant advances in DNA sequencing and informatics, which have the potential to invigorate taxonomic discovery, and reaching across cultural divides to incorporate national, regional and local knowledge that often remains ignored because it is not in English[141], included in standard databases[142], or recognised by conventional science[143].

### *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 impact of multiple stressors[84], which could help predict and mitigate complex biotic responses when climate and local stressors act in concert (Fig. 3). Other harder-to-study but important phenomena include the role of time lags or extinction debts[40], trophic cascades[31], or trajectories of ecosystem degradation and recovery in the face of unprecedented environmental change[144]. 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: 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 localised 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, helping to determine potential trigger points and identifying more effective policy responses[97]. Unpicking the role of distal drivers is essential to understand how distant interactions between social and environmental systems shape local environmental outcomes[145]. Careful study has revealed many surprising interactions, such as links between the intensification of commercial fishing and increased bushmeat exploitation in west Africa[146], the role of warfare in driving African mammal declines[147], or the role of exchange rates in driving deforestation[148]. Achieving this deeper understanding requires greater integration of the natural and social sciences, with interdisciplinarity included as a core element of tropical-conservation research[149].

*From research to impact*

Achieving positive impacts from conservation research relies on building a stronger science-society interface that challenges the oversimplified assumption of a linear flow from knowledge to action[150]. Engendering positive changes will require closer participation of practitioners in the research process and investments in outreach activities and professional capacity building[150]. These will be supported by studying the knowledge exchange process itself, including the critical role played by knowledge brokers and boundary organizations[151–153]. Part of this process will involve a focus on success stories, or ”bright spots”, enabling the social, institutional, and environmental conditions that create positive outcomes to be identified and replicated[152]. The positive social and ecological outcomes from innovative restoration and rewilding programmes in Costa Rica and Mozambique demonstrate the potential for positive action[154].

Local managers and scientists have a vital role to play in designing and implementing research that can inform regionally-appropriate conservation actions[155] – at present, our knowledge of hyperdiverse ecosystems is over reliant on inferences gleaned from distant research stations or inappropriate temperate theoretical constructs[18,156]. Research is also more likely to have an impact if the spatial scale of studies is more closely matched to the administrative scale at which resource decisions are taken[157]. Sustaining research programmes and learning networks in study landscapes can also help build the vital relationships between researchers, local knowledge holders and decision makers[155].

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 revolutionised by developments in remote sensing and drones[158], the plummeting costs of DNA technologies[159], and the step changes in bioinformatics that have allowed big data to be stored and retrieved in open-access platforms[160]. In the disciplinary domain, the last decade has seen a marked uptick in inter- and transdisciplinary research, with a greater – though still insufficient – integration of natural and social sciences. This has resulted in an increasing openness of researchers towards methodological pluralism and mixed-method approaches[150] and growing recognition of the contribution that can be made by local people, citizen- and para-scientists in biodiversity research[161]. Changes in research culture include the greater internationalisation of ecological science and closer approximation with society[150], both of which can help foster a more fertile ground for knowledge exchange and capacity building. Notable advances include the development of multi-disciplinary and multinational learning networks[162], exponential growth in author teams[163], and major syntheses such as the Intergovernmental Platform for Biodiversity and Ecosystem Services (IPBES).

Recent years have seen a new awakening of environmental consciousness and calls for decisive action, manifest, for example, in the Paris Agreement, the Sustainable Development Goals, and voluntary Zero Deforestation Commitments. Tropical and non-tropical scientists 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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**Author contributions**

JB developed the review with input from NAJG, TAG, CH, ACL and JF. FF and GDL analysed the data, supported by JB, TAG, CH, EB, LC, EPE, BG, CGL, VI, ACL, CLP, SW, PJY and NAJG. JB, TAG, CH, NAJG, LC, ACL, CLP, FF and GDL wrote the manuscript with input from all authors.

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**Figure legends**

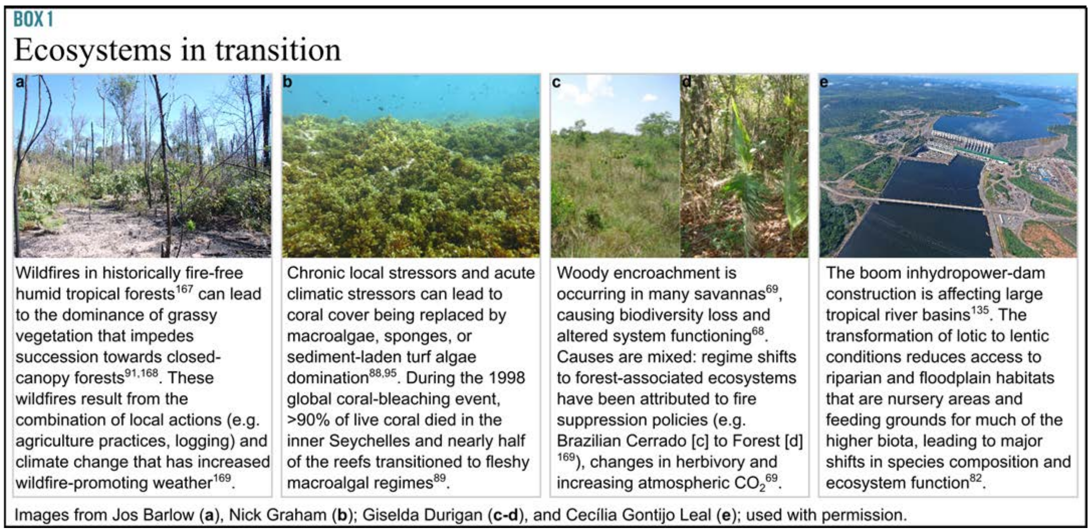
**Figure 1 | The tropical biosphere**. **a,** Tropical terrestrial and marine biomes. The tropical terrestrial biome (green) was defined as all tropical mesic ecoregions[164]. These ecoregions span 82% of the 50 million km$^2$ of land between 23.5° N and 23.5° S, but extend into the subtropics in some 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)[165]. **b,** The Intertropical Convergence Zone (ITCZ). The ITCZ was defined by 1979-2017 mid-summer (January – turquoise colour gradient – and July – red colour gradient) mean monthly total rainfall >20 cm (where both January and July had rainfall >20 cm, we show that with the largest total). The ITCZ is a strong predictor of the distribution of tropical ecoregions (**a**). Data sources are presented in Extended Data Table 1.

**Figure 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 that overlap the tropics. *n* gives the total number of species analysed in each group. Black boxes around each bar show the proportion of all species that are endemic to the tropics. 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 (Critically Endangered, Endangered, and Vulnerable) and non-threatened (Least Concern) species found exclusively within tropical latitudes for the five comprehensively sampled groups. Data from: Birdlife International for birds, the IUCN[29] for amphibians and mammals, the Ocean Biogeographic Information System for marine fish, Charlie Veron for shallow-water zooxanthellate corals, Tedesco et al.[166] for freshwater fish, and the Global Biodiversity Information Facility for angiosperms. Data sources are presented in Extended Data Table 1.

**Figure 3 | Vulnerability of tropical biota to local and climatic stressors.** Species co-tolerance to a local and climate-associated stressor[85]. The x-axis shows responses to fishing for corals (**a**) and reef (**b**) and freshwater fish (**c**); land-use change/deforestation for small-stemmed trees (2 ≤ DBH <10 cm; (**d**)) and forest birds (**e**); and fire suppression for savanna birds (**f**). The y-axis represents longitudinal responses to climate-associated events: the 2015-16 and 1997-98 coral bleaching events in the Seychelles for, respectively, corals (**a**) and reef fish (**b**); the 1997-98 El Niño-induced drought for lower Amazonian freshwater fish (**c**); Amazonian fires during the 2015-16 El Niño for small-stemmed trees (**d**) and forest birds (**e**); and shrub encroachment between 1998-2008 in South Africa for savanna birds (**f**). Species relative density is represented from low (dark blue) to high (light green). 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 – or genera for corals. Data sources are presented in Extended Data Table 1.

**Figure 4 | Socio-economic drivers of biodiversity loss and societal response capacities.** Green lines represent countries with >50% of their area within tropical latitudes; purple dashed-lines represent all other countries; grey-shaded areas represent the proportion of the global total within tropical countries. **a**, Global population (1960-2016). **b,** Gross domestic product (GDP) per capita (2011 $US 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). **j**, Environmental protection aid (2000-2016). **k**, Public and private sector research and development expenditure (% 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 Extended Data Table 1.

**Box**




**Box text**

Box 1. Tropical ecosystems in transition.

<u>*Forests (a):*</u> Wildfires in historically fire-free humid tropical forests[167] 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 (e.g. agricultural practices, logging) and climate change that has increased wildfire-promoting weather[169].

<u>Corals (b):</u> Chronic local stressors 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 regimes[89].

<u>Savannas (c-d):</u> Woody encroachment is occurring in many savannas[69], causing biodiversity loss and altered system functioning[68]. Causes are mixed: regime shifts to forest-associated ecosystems have been attributed to fire suppression policies (e.g. Brazilian Cerrado [C] to Forest [D][170]), changes in herbivory and increasing atmospheric $CO_2$ [69].

Freshwater (e): The boom in hydropower-dam construction is affecting large tropical river basins[135]. The transformation from lotic to lentic conditions reduces access to riparian and floodplain habitats that are nursery areas and feeding grounds for much of the higher biota, leading to major shifts in species composition and ecosystem function[82].

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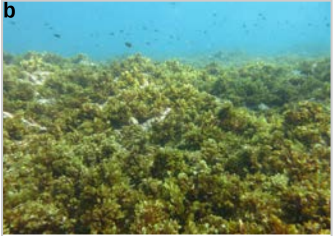
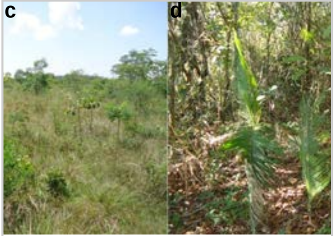
BOX 1

# Ecosystems in transition


Wildfires in historically fire-free humid tropical forests[167] 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 (e.g. agriculture practices, logging) and climate change that has increased wildfire-promoting weather[169].



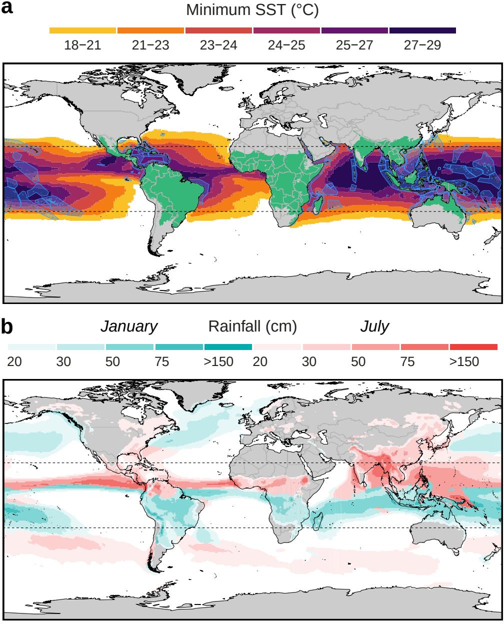

Chronic local stressors and acute climatic stressors can lead to coral cover being replaced by macroalgae, sponges, or sediment-laden turf algae[88,95]. During the 1998 global coral-bleaching event, >90% of live coral died in the inner Seychelles and nearly half of the reefs transitioned to fleshy macroalgal regimes[89].

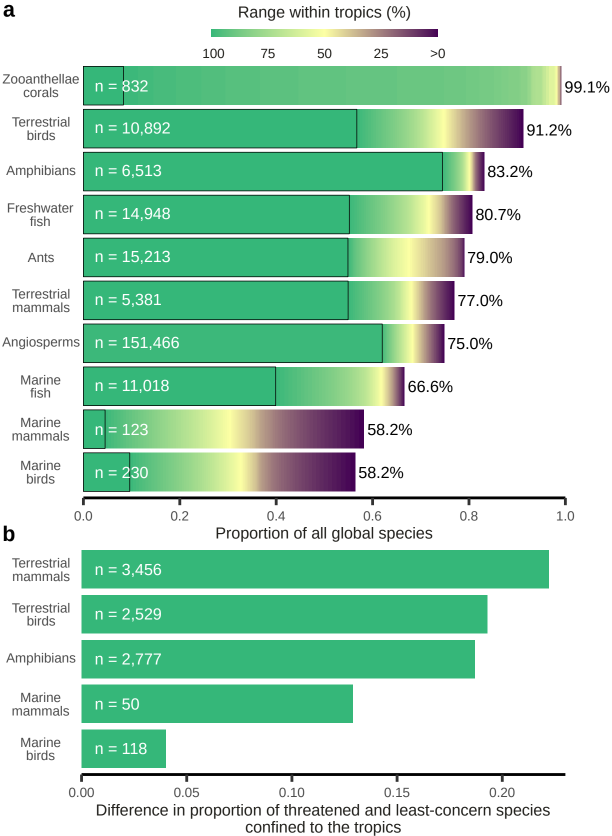


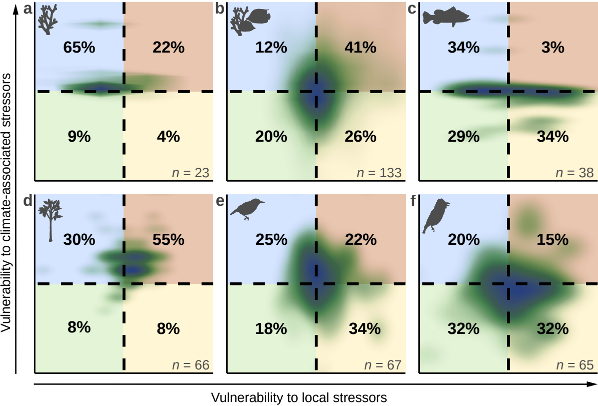

Woody encroachment is occurring in many savannas[69], causing biodiversity loss and altered system functioning[68]. Causes are mixed: regime shifts to forest-associated ecosystems have been attributed to fire suppression policies (e.g. Brazilian Cerrado [c] to Forest [d] [169]), changes in herbivory and increasing atmospheric $CO_2$[69].


The boom inhydropower-dam construction is affecting large tropical river basins[135]. The transformation of lotic to lentic conditions reduces access to riparian and floodplain habitats that are nursery areas and feeding grounds for much of the higher biota, leading to major shifts in species composition and ecosystem function[82].

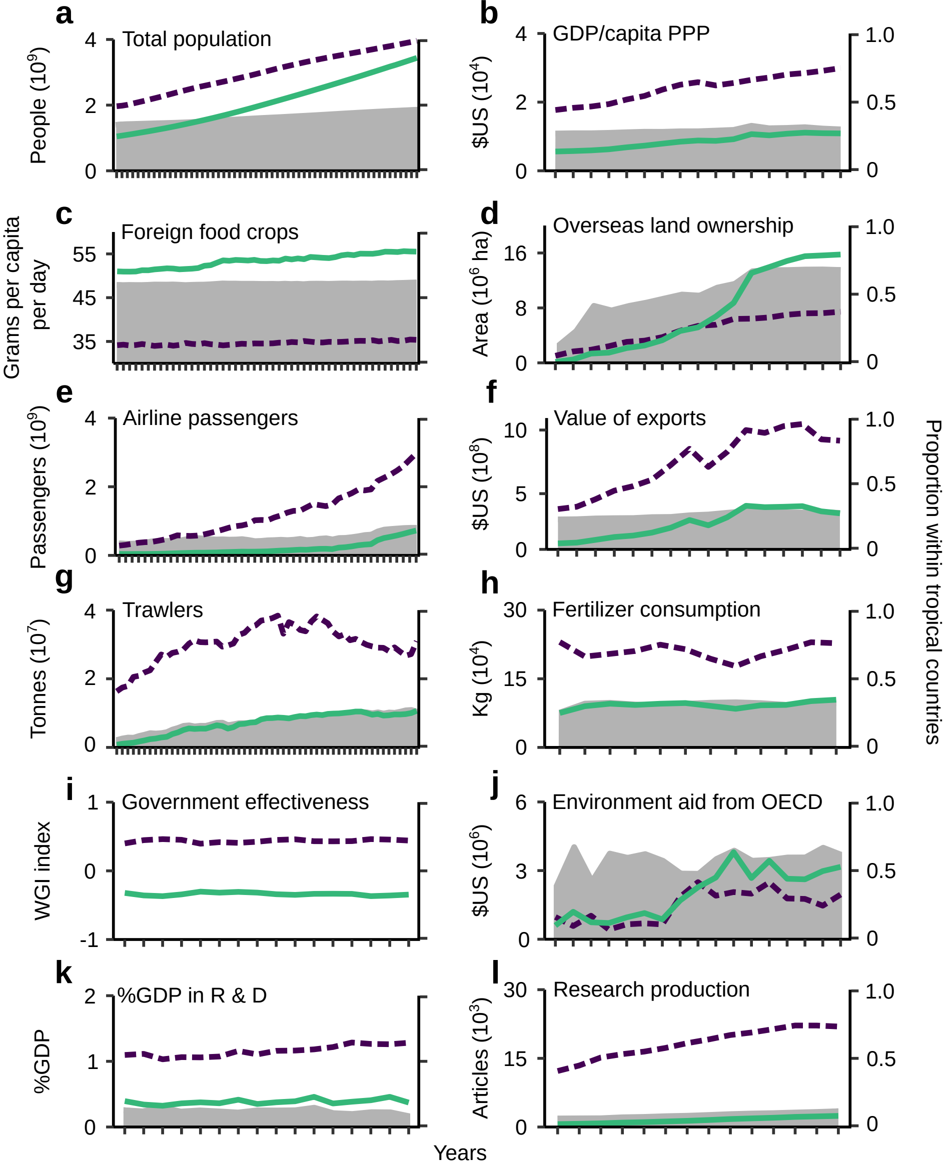
Images from Jos Barlow (**a**), Nick Graham (**b**); Giselda Durigan (**c-d**), and Cecília Gontijo Leal (**e**); used with permission.


a
Minimum SST (°C)
18−21
21−23
23−24
24−25
25−27
27−29
b
January
Rainfall (cm)
July
20
30
50
75
>150
20
30
50
75
>150


a
Range within tropics (%)
100
75
50
25
>0
Zooanthellae corals
n = 832
99.1%
Terrestrial birds
n = 10,892
91.2%
Amphibians
n = 6,513
83.2%
Freshwater fish
n = 14,948
80.7%
Ants
n = 15,213
79.0%
Terrestrial mammals
n = 5,381
77.0%
Angiosperms
n = 151,466
75.0%
Marine fish
n = 11,018
66.6%
Marine mammals
n = 123
58.2%
Marine birds
n = 230
58.2%
0.0
0.2
0.4
0.6
0.8
1.0
Proportion of all global species
b
Terrestrial mammals
n = 3,456
Terrestrial birds
n = 2,529
Amphibians
n = 2,777
Marine mammals
n = 50
Marine birds
n = 118
0.00
0.05
0.10
0.15
0.20
Difference in proportion of threatened and least-concern species confined to the tropics



a
65%
22%
9%
4%
n = 23
b
12%
41%
20%
26%
n = 133
c
34%
3%
29%
34%
n = 38
d
30%
55%
8%
8%
n = 66
e
25%
22%
18%
34%
n = 67
f
20%
15%
32%
32%
n = 65
Vulnerability to climate-associated stressors
Vulnerability to local stressors


a
Total population
People ($10^9$)
b
GDP/capita PPP
$US ($10^4$)
c
Foreign food crops
Grams per capita per day
d
Overseas land ownership
Area ($10^6$ ha)
e
Airline passengers
Passengers ($10^9$)
f
Value of exports
$US ($10^8$)
g
Trawlers
Tonnes ($10^7$)
h
Fertilizer consumption
Kg ($10^4$)
i
Government effectiveness
WGI index
j
Environment aid from OECD
$US ($10^6$)
k
%GDP in R & D
%GDP
l
Research production
Articles ($10^3$)
Years
Proportion within tropical countries