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# The future of hyperdiverse tropical ecosystems

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

## 31 Introduction

32 The tropics hold a disproportionate amount of global biological diversity, and are key to meeting  
33 the international community's aims of socially-just sustainable development and effective  
34 biodiversity conservation<sup>1</sup>. Yet, tropical ecosystems are undergoing rapid environmental, socio-  
35 economic and demographic change<sup>2</sup>, often driven by forces from extra-tropical, developed  
36 countries. The scale of these changes is unprecedented, and decisions implemented in the  
37 coming decades will define the future diversity and sustainability of the tropics.

38 Guiding these decisions depends on understanding the diversity and vulnerability of the four  
39 major tropical ecosystems: the forests and mesic savannas that cover most of the terrestrial  
40 tropics, the extensive freshwater systems that receive half of the world's rainfall, and the  
41 shallow-water coral reefs distributed along 150,000 km of coastline (Fig. 1). Here, we quantify  
42 and review the global importance of tropical biodiversity, evaluate the vulnerability of tropical

43 ecosystems to proximate stressors, and assess whether global and regional socio-economic  
44 changes will exacerbate or ameliorate biodiversity loss. We then examine the effectiveness of  
45 conservation approaches, and highlight the scientific advances required to foster positive  
46 change and help overcome the challenges arrayed against a sustainable tropical future.

#### 47 **The global importance of tropical ecosystems**

48 Over evolutionary time, the tropics have acted both as a source and refuge for most extra-  
49 tropical terrestrial and marine species<sup>3,4</sup>; but just how diverse and irreplaceable are the tropics  
50 today? The increase in species richness from polar to tropical regions, known as the latitudinal  
51 diversity gradient, repeats across a wide range of taxa and biomes. As a result of this gradient,  
52 tropical latitudes, which cover just 40% of the Earth's surface, hold a startling proportion of the  
53 planet's species: our assessment reveals that almost all shallow-water zooxanthellae corals, 91%  
54 of terrestrial birds, and >75% of amphibians, terrestrial mammals, freshwater fish, ants,  
55 flowering plants and marine fish have ranges that intersect tropical latitudes (Fig. 2a). For birds,  
56 the importance of the tropics extends far beyond 23.5 degrees of latitude, with almost half of all  
57 Nearctic species migrating to the Neotropics<sup>5</sup> and over 2 billion passerine and near-passerines  
58 crossing the Sahara each autumn<sup>6</sup>. Moreover, a disproportionate number of the world's species  
59 are endemic to the tropics. For example, there are 4.5 times more endemic amphibians in the  
60 tropics than in temperate regions (Fig 2a). Tropical zones are less important for marine  
61 mammals and birds, taxa that peak in diversity at mid-latitudes<sup>7,8</sup>. Nonetheless, >55% of these  
62 species use the tropics (Fig. 2a).

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

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

78 The biological diversity of the tropics is mirrored by many forms of societal diversity<sup>21</sup>. For  
79 example, tropical countries contain 40% of the world's population yet 85% of extant languages  
80 are spoken within them<sup>22</sup>. The tropics also provide incalculable benefits to humanity. They  
81 house most of the key centres of plant domestication<sup>23</sup> and have been a vital laboratory for the  
82 development of science itself – the disciplines of ecology, biogeography and evolutionary

83 biology are founded on evidence gleaned from tropical ecosystems. Tropical ecosystems also  
84 make vital contributions to globally-important ecosystem services: covering just 0.1% of the  
85 ocean surface, coral reefs provide fish resources for 275 million people that live within 30 km of  
86 them<sup>24</sup> and coastal protection for up to 197 million people<sup>25</sup>; humid tropical forests cover <12%  
87 of the world's ice-free land surface but produce 33% of global net primary productivity and  
88 store 25% of the carbon in the terrestrial biosphere<sup>26</sup>; while tropical savannas provide a further  
89 30% of net primary productivity and 15% of carbon storage<sup>27</sup>. Tropical ecosystems also help  
90 drive vital atmospheric teleconnections. For instance, 70% of the rainfall in the 3.2M km<sup>2</sup> *Rio de*  
91 *la Plata* catchment is estimated to come from evaporation in Amazonia<sup>28</sup>.

## 92 **Vulnerability of tropical biota and ecosystems**

93 For all five vertebrate groups with comprehensive IUCN assessments and spatial occurrence  
94 data<sup>29</sup>, globally threatened species are more dependent on the tropics than those classed as  
95 Least Concern (Fig. 2b). In addition, 85% of species extinctions from these vertebrate groups  
96 have been of species that use the tropics<sup>29</sup>. Consequently, although extinctions of other groups  
97 are less well understood, we can assume that most of the estimated 130,000 modern  
98 invertebrate extinctions<sup>30</sup> will also have been of tropical species. Thus, not only are the tropics  
99 vastly more diverse than temperate regions, this diversity is at far greater risk from human  
100 impacts<sup>31</sup>. Moreover, given that the tropics have the highest proportion of Data Deficient  
101 species and the lowest level of biodiversity-threat assessment<sup>16</sup>, information shortfalls mean we  
102 are likely underestimating the vulnerability of the tropical biome. We assessed this vulnerability  
103 in more depth by examining the effect of local and global stressors, the interactions between  
104 them, and the resulting changes to tropical ecosystems.

### 105 *Local stressors*

106 The tropics are subject to some of the highest rates of land-use change and degradation. While  
107 the spatial coverage of temperate forests has increased since 1990, tropical deforestation rates  
108 exceed 5M ha/yr<sup>32</sup>. Additional impacts stem from the expansion of large infrastructure projects  
109 (e.g. dams) and the growing demand for agricultural commodities, biofuels, timber, fuelwood  
110 and other natural resources<sup>33</sup>. These all result in severe biotic responses. Even with mitigation,  
111 dams present a near-impassable barrier for river fish<sup>34</sup>, while deforestation replaces a species-  
112 rich pool of forest-specialists with a smaller pool of common open-area species<sup>35</sup>. The influence  
113 of land-use change also extends far into remaining natural areas through isolation and edge  
114 effects<sup>36</sup>, additional anthropogenic disturbances<sup>37</sup> and altered climatic conditions<sup>38</sup>. Edge effects  
115 suppress the abundance of threatened vertebrates up to 200-400 m into tropical forests<sup>36</sup>,  
116 leaving almost no core forest refugia in the Brazilian Atlantic Forest where >80% is within 500 m  
117 of an edge<sup>39</sup>. Even low levels of landscape modification have significant effects on range-  
118 restricted species<sup>37</sup>, and time lags mean that some of the most deleterious effects are observed  
119 decades after landscape modification<sup>40</sup>.

120 Pollution presents a diverse set of threats to tropical ecosystems. Inputs of sediments and  
121 nutrients from land-use change are well-established drivers of biodiversity loss across  
122 freshwater<sup>41</sup> and coastal systems, including coral reefs<sup>42</sup>. Pesticide use is increasing across the  
123 tropics, reflecting rapid intensification of farming practices<sup>43</sup> and high pest pressures on tropical

124 crops<sup>44</sup>. Tropical Asian rivers are a major source of the 1.2-2.4 million tonnes of plastic that  
125 enters the world's oceans each year<sup>45</sup>, with micro-plastics entering into coral diets<sup>46</sup> and larger  
126 debris increasing rates of coral disease<sup>47</sup>. These examples of chronic pollution are exacerbated  
127 by extreme events, such as of the *Fundão* Dam collapse, which released c. 50M m<sup>3</sup> of waste into  
128 a 600 km stretch of river in south-east Brazil, causing a 7,000 km<sup>2</sup> toxic plume in the Atlantic  
129 Ocean<sup>48</sup>.

130 Overexploitation is also pervasive across the tropics. Fishing has reduced fish biomass by over  
131 75% across a third of coral reefs<sup>49</sup> and is shrinking the mean body size of exploited freshwater  
132 taxa<sup>50</sup>. Hunting contributed to the loss of charismatic mega-herbivores, extirpating African  
133 elephants, rhinos and large predators from most of their original ranges<sup>51,52</sup>. The world's tropical  
134 forests are affected by extensive over-harvesting of wildlife<sup>31</sup>, with estimates of the annual  
135 harvests of highly-trafficked animals such as pangolins reaching into the millions of individuals<sup>53</sup>.  
136 Moreover, the growth in non-food uses of wildlife means that even small-bodied songbirds are  
137 at risk of global extinction<sup>54</sup>. Overexploitation also extends beyond fauna and is driving  
138 economically valuable tropical trees to extinction<sup>55</sup>.

139 Invasive species have been the second most important extinction driver of vertebrates since  
140 1500 CE<sup>56</sup>. Within terrestrial ecosystems, invasive species have exerted the strongest influence  
141 on islands and coastal mainlands<sup>57</sup>, having driven thousands of species extinctions and altered  
142 trophic structures<sup>58</sup>. On continents, they currently have a greater impact on economically  
143 developed and extra-tropical regions, but tropical ecosystems are predicted to become  
144 increasingly vulnerable to invasion in the 21<sup>st</sup> century<sup>59</sup>. Despite a deficit of research in the  
145 tropics<sup>60</sup>, two prominent examples highlight the scope and magnitude of species invasions into  
146 terrestrial tropical ecosystems: there has been an 84% increase of alien species detections  
147 between 2003 and 2010 in Singapore<sup>61</sup>, while invasive African grasses could threaten up to  
148 380,000 km<sup>2</sup> of Australia's savannas by promoting landscape flammability<sup>62</sup>. In aquatic  
149 ecosystems, invasive predatory fishes, such as the Indo-Pacific lionfish in Caribbean coral reefs<sup>63</sup>  
150 and the Nile perch in African lakes<sup>64</sup>, have contributed to the loss of native species. Marine  
151 invasions are also facilitated by the mass transport of species in ship ballast water, resulting in  
152 widespread biotic homogenisation<sup>65</sup>.

### 153 *Global climatic change*

154 While many of the "local" stressors described above are promoted by globalised drivers, climate  
155 change is truly global. Increases in atmospheric CO<sub>2</sub> concentrations to levels >400 ppm has  
156 important implications for tropical terrestrial and aquatic ecosystems. Ocean acidification from  
157 dissolved CO<sub>2</sub> is changing ocean chemistry to the extent that declining coral calcification has  
158 already been detected<sup>66</sup>. Conditions for reef accretion and growth may be mostly absent  
159 throughout the tropics by 2100 under business-as-usual emission scenarios<sup>67</sup>. Within savannas,  
160 elevated CO<sub>2</sub> levels favour the growth of woody plants over grasses, contributing to woody  
161 encroachment and the potential for a switch in biome state<sup>68,69</sup>. CO<sub>2</sub> fertilisation may have also  
162 contributed to enhanced tree productivity and mortality rates observed in humid tropical  
163 forests<sup>70</sup>.

164 Global warming does not proceed at the same rate across the planet. Although the greatest  
165 absolute temperature increases are occurring at higher latitudes, the tropics are already some  
166 of the hottest places on the planet and have the lowest inter-annual temperature variability<sup>71,72</sup>.  
167 Consequently, they will be the first areas to experience significantly warmer climates than the  
168 present day<sup>72</sup> and will endure climatic conditions without present-day equivalents<sup>71</sup>. In addition,  
169 some of the most important climate oscillations, including El Niño and the Indian Ocean Dipole,  
170 take place within, and have their greatest influence on, tropical regions. It is unclear if these  
171 oscillations will change in a warming world, but extremes of their phases have the potential to  
172 exacerbate or ameliorate the overall warming trend. One outcome of increasing temperatures is  
173 the poleward shifts of species ranges or movement to higher altitudes or deeper depths<sup>73</sup>. For  
174 example, corals in southern Japan are extending northwards at c. 14 km/yr<sup>74</sup>, and temperate  
175 macroalgal communities are being replaced with corals and other tropical species along large  
176 stretches of Australian coastline<sup>75</sup>. Latitudinal shifts in terrestrial and freshwater tropical species  
177 distributions are less certain because of the many natural and anthropogenic barriers, and the  
178 low dispersal capacity of many tropical species<sup>76</sup>. Furthermore, the responses of terrestrial  
179 species are defined by changes in rainfall as well as temperature<sup>77</sup>.

180 If movement is not an option, tropical species must adapt or face extinction. Unfortunately,  
181 there is evidence that some species are either approaching their physiological limits or are  
182 unable to adapt to the rate of environmental change<sup>78</sup>. Increasing ocean temperature extremes  
183 are driving mass bleaching events and mortality of reef-forming corals, with the time between  
184 bleaching events declining by 76-80% since the early 1980s<sup>79</sup>. Higher temperatures also affect  
185 tropical vertebrates, causing, for example, an extreme female bias in the sex ratio of green  
186 turtles in the warmer regions of the Great Barrier Reef<sup>80</sup> and a reduction in the reproductive  
187 success of African wild dogs<sup>81</sup>. Altered rainfall is also critical. Droughts are drying up biologically  
188 diverse small streams<sup>82</sup>, while even modest changes in dry-season length increase tropical tree  
189 mortality<sup>70</sup> and modify tropical forest bird community structure<sup>83</sup>.

#### 190 *Stressor interactions and indirect effects*

191 Stressors affecting tropical species can interact in myriad ways<sup>84</sup>. We demonstrate this by  
192 compiling data from six case studies within a co-tolerance framework that allows species  
193 responses to two dominant stressors to be examined<sup>85</sup>. Only a small subset of species or genera  
194 (8-32%) showed no or positive responses when both stressors were combined (Fig. 3), and up to  
195 55% fell within the “double jeopardy” quadrant, indicating a negative response to both  
196 stressors. While our summary does not quantify the magnitude of effects, it clearly  
197 demonstrates that stressors can act together to reduce the abundance or occupancy of tropical  
198 species. Moreover, these co-tolerance analyses simplify the reality facing tropical ecosystems  
199 because most are affected by more than two stressors at any given location and time<sup>84</sup>.

200 Many changes to tropical ecosystems result from indirect consequences of single or multiple  
201 stressors. On coral reefs, nutrient inputs from land may increase susceptibility to coral  
202 bleaching, disease, and outbreaks of pests<sup>86</sup>, while poleward reef expansion is supported by  
203 feedbacks from range-shifting tropical herbivorous fish<sup>75</sup>. Overexploitation can result in  
204 surprising changes in tropical ecosystem properties through trophic cascades. For instance, the

205 extirpation of a single detritivore fish species in the Orinoco basin reduced downstream organic-  
206 carbon transport, increasing net primary productivity and respiration<sup>87</sup>. On reefs, overfishing of  
207 keystone predators has repercussions for benthic structure<sup>88</sup>, while removal of herbivores can  
208 limit coral recovery from mass-mortality events<sup>89</sup>. In mesic savannas, changes to herbivore  
209 numbers alter ecosystem functions and structure via their interactions with wildfire regimes<sup>90</sup>.  
210 Invasive species are also frequently linked to other stressors: the introduction of the Nile perch  
211 played a major role in the decline of endemic fish species in Lake Victoria, but its effects were  
212 likely catalyzed by a combination of other drivers including soil erosion, eutrophication and  
213 overfishing<sup>64</sup>.

#### 214 *Ecosystems in transition*

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

220 These drastic ecosystem transitions are accompanied by widespread modification of species  
221 composition. For example, the relative abundance of coral species has been altered on reefs  
222 that maintain coral dominance<sup>92</sup>; extirpation of native fish has followed species introductions in  
223 lakes<sup>64</sup>; liana biomass has increased in otherwise undisturbed Neotropical forests<sup>93</sup>; and  
224 patterns of plant regeneration in humid forests have been altered by the overharvesting of  
225 seed-dispersing vertebrates<sup>31,94</sup>. Altered species composition is a cause for concern because it  
226 could signal the onset of more severe modification, especially if dominant species are  
227 vulnerable or if there are cascading implications for ecosystem functioning. The collapse of  
228 Jamaican coral reefs provides one of the starkest examples. First, chronic overfishing depleted  
229 herbivorous fish populations, leaving the system over-reliant on sea urchins for grazing algae.  
230 Then Hurricane Allen impacted the system in 1980, creating a substantial amount of dead  
231 substrate. Although corals began recovering after the hurricane, the subsequent mass mortality  
232 of sea urchins due to disease, combined with the already low abundance of herbivorous fish, led  
233 to a phase shift from coral to macroalgal dominance<sup>95,96</sup>.

#### 234 **Socio-economic context and response capacity**

235 The interacting proximate stressors causing tropical environmental change are underpinned by  
236 broader changes in socio-economic and political factors. We examined the trajectories of four  
237 types of underlying distal drivers, including demography (Fig. 4a-b), socio-political factors (Fig.  
238 4c-d), markets (Fig. 4e-f) and technology (Fig. 4g-h)<sup>97</sup> to explore how tropical countries are  
239 changing relative to the rest of the world and to evaluate the relative influence of local and  
240 global drivers. We also examined how the capacity of tropical countries to reduce or cope with  
241 proximate stressors compares to non-tropical countries based on underlying governance (Fig.  
242 4i-j) and research capacity (Fig. 4k-l).

243 The immense biodiversity of the tropics exists in the context of rapid demographic and  
244 economic growth (Fig. 4a-b). Human population is growing at a faster rate in the tropics than

245 elsewhere (Fig. 4a) and by 2050 half of the world's population will live in the tropics<sup>2</sup>. These  
246 demographic changes are accompanied by steady GDP growth, linked, in part, to the rapid  
247 expansion of agricultural and extractive industries. However, tropical per capita GDP – an  
248 important measure of human well-being – remains far lower than the non-tropical average (Fig.  
249 4b), and the rates of change suggest little closing of the inequality gap between global south  
250 and north<sup>98</sup>. Although the relationship between development and natural resource conservation  
251 does not have to be negative<sup>99,100</sup>, measures reflecting higher social performance are almost  
252 always associated with higher resource use<sup>100</sup>. A larger and more affluent tropical population  
253 will increase demands for timber, water, food, energy, and land, all of which are strongly linked  
254 with environmental degradation.

255 These internal changes will be exacerbated by economic growth in non-tropical countries, and  
256 the continued displacement of environmental impacts to less-developed areas<sup>101</sup>. Indeed,  
257 despite high levels of tropical cultural diversity<sup>21,22</sup>, external socio-political influences (Fig. 4c-d)  
258 suggest that tropical countries have become increasingly susceptible to globalisation. For  
259 example, the proportion of imported food crops (Fig. 4c) and foreign-land acquisitions are far  
260 higher in the tropics than elsewhere (Fig. 4d) and are associated with extensive road building<sup>102</sup>  
261 and agricultural investment<sup>103</sup>. These trends towards increasing tropical globalisation are  
262 reinforced by changes in market integration (Fig. 4e-f) and technological development (Fig. 4g-  
263 h). For example, agricultural exports (Fig. 4e) are steadily increasing, albeit from a far lower  
264 baseline than the rest of the world. Moreover, given comparatively low levels of adoption of  
265 technological developments, such as industrial fishing techniques (Fig. 4g) or fertilizers (Fig. 4h),  
266 there is enormous risk that the rate of natural resource extraction in many tropical countries  
267 will increase further, supplying both domestic and export markets<sup>104,105</sup>. Taken together, these  
268 examples highlight the crucial role that external markets will play in determining the fate of  
269 tropical ecosystems.

270 Effective environmental governance (Fig. 4i-j) is a necessary condition for improved  
271 sustainability outcomes<sup>106</sup>, particularly when domestic (Fig. 4a-d) and global (Fig. 4c-f) distal  
272 drivers are expected to exert increasing and unsustainable pressure on tropical ecosystems<sup>2,103</sup>.  
273 However, the World Bank's national-level assessments of governance effectiveness from the  
274 tropics sit in stark contrast to measures from extra-tropical countries, with no sign of  
275 improvement (Fig. 4i). External support for environmental governance may help where local  
276 governance is weak (Fig. 4j). Yet, despite greater OECD (Organisation for Economic Cooperation  
277 and Development) environmental aid in the tropics than elsewhere (Fig. 4j), these investments  
278 are dwarfed by the value of domestic resource extraction (e.g. agricultural exports; Fig. 4e), the  
279 value of which is two orders of magnitude greater than overseas environmental aid.  
280 Furthermore, OECD environmental aid has been declining in recent years and seems unlikely to  
281 increase in the short term<sup>107</sup>.

282 Low governance capacity in the tropics is further exacerbated by insufficient research and  
283 development investment (Fig. 4k) and low levels of scientific output (Fig. 4l). Research  
284 investment is critical for driving innovation and the development of evidenced-based solutions  
285 to environmental degradation<sup>108</sup>. Despite some notable centres of excellence, the vast majority  
286 of biodiversity-related data and research is concentrated in wealthy, non-tropical countries<sup>17</sup>

287 and manuscripts submitted by authors from low-income countries are less than half as likely to  
288 be published as those from high-income countries<sup>109</sup>. These trends highlight an alarming  
289 disconnect between the global scientific process and the people that are most capable of  
290 engaging with decision makers, who have the best understanding of local context and, arguably,  
291 have the strongest incentive to achieve positive impacts through their research.

## 292 **Diverse solutions for diverse systems**

293 Tropical ecosystems – and therefore at least 78% of the world’s biodiversity (Fig. 2a) – are at a  
294 critical juncture. Multiple interacting local and global stressors (Fig. 3) that are driving species  
295 extinctions and potentially irreversible ecosystem transitions<sup>92,110</sup> (Box 1) are set within a  
296 changing socio-economic context (Fig. 4). This changing context is characterised by growing and  
297 more affluent populations, an increasingly globalised world, and weak governance and research  
298 capacity – all of which threatens to increase environmental degradation, conflict and  
299 inequality<sup>103</sup>. Countering these threats requires major improvements in local and global  
300 governance capacity and a step-change in how environmental objectives are integrated into  
301 broader development goals<sup>111</sup>. We review the opportunities and limitations presented by three  
302 well-established and non-mutually exclusive approaches to conservation, before highlighting  
303 priorities for research.

### 304 *Conservation approaches*

305 A fundamental element of tropical conservation relies on protected areas to limit demographic  
306 pressures and the impact of local stressors. These are supported by a wealth of scientific evidence  
307 outlining the pervasive impact of local stressors across tropical ecosystems<sup>37,49</sup> (Fig. 3) combined  
308 with an eco-centric philosophy that emphasizes the intrinsic rights of nature<sup>112</sup>. Yet, despite  
309 significant expansion of protected-area coverage in the marine and forested tropics<sup>113</sup>, the  
310 current network remains poorly designed, has very limited coverage of tropical freshwaters and  
311 grasslands, and is inadequately resourced<sup>114</sup>. Moreover, a strategy focused solely on protected  
312 areas will not foster environmental conservation outside of reserves<sup>115</sup> and fails to engage with  
313 the distal drivers of biodiversity loss (Fig. 4) that can undermine the effectiveness of protected  
314 areas themselves<sup>116</sup>.

315 A second set of approaches for tropical conservation is based on the notion that people need to  
316 perceive the benefits of nature to justify conservation. These emphasize the need to pursue  
317 conservation objectives in human-dominated landscapes, the provision of ecosystem services,  
318 and the involvement of private-sector actors. In the tropics, they are epitomised by the growth  
319 in market-based conservation payment mechanisms, such as REDD+<sup>117</sup>, investments in the “blue  
320 economy”<sup>118</sup> and a step change in the number of companies making sustainability  
321 commitments<sup>119</sup>. These approaches have strengthened the conservation toolkit, especially  
322 where strict regulatory approaches have failed. Encouraging examples range from the positive  
323 effects of commodity certification (e.g. palm oil<sup>120</sup>) to payment for ecosystem service schemes  
324 (e.g. watershed protection<sup>121</sup>). However, such approaches also attract significant criticism with  
325 implementation often lagging commitments<sup>119</sup>, persistent concerns around the social legitimacy  
326 of compensation schemes<sup>122</sup>, and the misalignment of market-based mechanisms with local  
327 needs and perceptions of environmental values<sup>123</sup>.



328 A third and more diverse set of approaches is based on recognition of the interdependencies  
329 between people and nature, the coevolution of ecological and socio-economic systems at local,  
330 regional and global scales<sup>124</sup>, and perspectives about the co-existence of people and nature. This  
331 set of more “systems-based” approaches includes: (1) an appreciation of the importance of  
332 bottom-up, community-based conservation approaches in human-dominated land- and  
333 seascapes (e.g. small-scale fisheries<sup>125</sup> and community-managed forests<sup>126</sup>); (2) recognition of  
334 the role of indigenous people as environmental stewards, and shifts towards an appreciation of  
335 more collective relationships with nature (e.g. the Ecuadorian constitution<sup>127</sup>); (3) landscape-  
336 and ecosystem-wide approaches that attempt to bridge the role of actors working at different  
337 scales and in different sectors (e.g. jurisdictional approaches to curb deforestation<sup>128</sup>); and (4) a  
338 more explicit accounting of multi-scale feedbacks, including the role of distant market actors  
339 and distal drivers<sup>124</sup>. These broad, multi-layered “people and nature” approaches hold  
340 considerable appeal, but the inherent complexity of local contexts can make them challenging  
341 to conceptualize, implement and measure in joined-up and consistent ways<sup>129</sup>.

#### 342 *Acting together and acting now*

343 The three broad approaches to the conservation and governance of tropical ecosystems  
344 outlined above are often associated with alternative researcher and practitioner  
345 worldviews<sup>130,131</sup>. But the inherent ecological diversity (Fig. 2a), vulnerability (Figs. 2b & 3) and  
346 socio-economic complexity (Fig. 4) of the tropics highlights the importance of pluralism<sup>132</sup> and  
347 the need to adopt a variety of what are often complementary and synergistic approaches<sup>131</sup>. For  
348 all their limitations, protected areas are indispensable to limit the impact of local stressors, and  
349 it will be impossible to avoid further biodiversity loss unless they are strengthened and  
350 expanded<sup>133</sup>. However, conservation strategies must also address the underlying drivers of  
351 environmental change (Fig. 4) and avoid exacerbating deeply rooted inequalities<sup>115</sup>. Practice is  
352 always messier than theory, and the adoption of more sustainable management systems is  
353 usually only possible with the support of a range of actors, as can be seen in the recent  
354 successes of some hybrid governance approaches, with government, the private sector, and civil  
355 society organizations all playing vital roles<sup>134</sup>.

356 Another clear message is that conservation efforts need to operate at local, regional and global  
357 scales to be effective. Many distal drivers are disconnected from sites of impact in both space  
358 and time, and the engagement of external actors, including in distant markets and governance  
359 processes, is often essential to ensure that local efforts are effective. These include more  
360 strategic integration of environmental policy with development goals<sup>135</sup>, the need for  
361 multinational environmental governance approaches, especially for aquatic systems<sup>82</sup>, and  
362 recognition of the importance of tackling demand for unsustainable products from downstream  
363 buyers and investors<sup>119</sup>. The capstone of such efforts lies in the urgent need to deliver on the  
364 Paris Agreement, without which climate change will undercut or even negate hard-won local  
365 conservation successes, whether in coral reefs<sup>92</sup> or tropical forests<sup>110</sup>.

366 Finally, we need to act now to address the pressing environmental challenges facing the tropics.  
367 This means being adaptive, learning by doing and embracing innovation. The last decades have  
368 seen a boom in proposals, innovations, and insights about the governance and management of

369 tropical ecosystems, ranging from more technocentric proposals to facilitate the evolution of  
370 climate-tolerant corals<sup>136</sup>; ecological engineering to recover lost trophic interactions by species  
371 re-introductions, ecological replacements and rewilding<sup>137</sup>; to radical new legal frameworks such  
372 as France's "Loi de vigilance" (2017-399) that places an unprecedented due diligence obligation  
373 on major companies to assess social and environmental risks in their supply chains beyond  
374 French borders. While these innovations serve different purposes and are varyingly scalable,  
375 they illustrate the potential of solutions-based science and conservation. Of course, acting now  
376 does not mean ignoring the existing evidence base or making uninformed decisions. Rather, it is  
377 vital that researchers and decision makers are vigilant to opportunities and risks and are willing  
378 to learn lessons.

### 379 **Keeping pace with the Anthropocene**

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

#### 389 *Addressing key knowledge shortfalls*

390 Our understanding of tropical biodiversity is limited by significant knowledge shortfalls in  
391 taxonomy and species distributions<sup>138</sup>. Overcoming these shortfalls will require targeting  
392 resources towards the information "black holes" that cover large regions of the tropics<sup>18</sup>. At the  
393 ecosystem level, there is a need for increased study of structurally and functionally distinct  
394 systems, particularly tropical grassy biomes<sup>68</sup>, dry forests<sup>139</sup> and low-order stream systems<sup>140</sup>.  
395 Progress in these areas will likely be aided by significant advances in DNA sequencing and  
396 informatics, which have the potential to invigorate taxonomic discovery, and reaching across  
397 cultural divides to incorporate national, regional and local knowledge that often remains  
398 ignored because it is not in English<sup>141</sup>, included in standard databases<sup>142</sup>, or recognised by  
399 conventional science<sup>143</sup>.

#### 400 *Understanding vulnerability*

401 Our growing knowledge of the role of individual stressors, such as landscape configuration or  
402 overexploitation, needs to be complemented by research on the impact of multiple stressors<sup>84</sup>,  
403 which could help predict and mitigate complex biotic responses when climate and local  
404 stressors act in concert (Fig. 3). Other harder-to-study but important phenomena include the  
405 role of time lags or extinction debts<sup>40</sup>, trophic cascades<sup>31</sup>, or trajectories of ecosystem  
406 degradation and recovery in the face of unprecedented environmental change<sup>144</sup>. Revealing  
407 these more complex forms of vulnerability will often demand longer-term and larger multi-scale  
408 sampling and monitoring programs. New approaches are also needed to overcome one of the

409 more intractable challenges of tropical ecology: we often know least about the rarest and most  
410 vulnerable species or taxonomic groups.

#### 411 *Understanding distal drivers*

412 Conservation does not occur in a vacuum, and localised interventions are likely to be much  
413 more effective if they are guided by a closer understanding of underlying distal drivers of  
414 biodiversity loss and environmental change – including identifying the actors behind such  
415 drivers, helping to determine potential trigger points and identifying more effective policy  
416 responses<sup>97</sup>. Unpicking the role of distal drivers is essential to understand how distant  
417 interactions between social and environmental systems shape local environmental outcomes<sup>145</sup>.  
418 Careful study has revealed many surprising interactions, such as links between the  
419 intensification of commercial fishing and increased bushmeat exploitation in west Africa<sup>146</sup>, the  
420 role of warfare in driving African mammal declines<sup>147</sup>, or the role of exchange rates in driving  
421 deforestation<sup>148</sup>. Achieving this deeper understanding requires greater integration of the natural  
422 and social sciences, with interdisciplinarity included as a core element of tropical-conservation  
423 research<sup>149</sup>.

#### 424 *From research to impact*

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

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

443 Achieving these changes requires building on trends in the technological, disciplinary and  
444 cultural dimensions of research practice. In the technological domain, opportunities for data  
445 collection have been revolutionised by developments in remote sensing and drones<sup>158</sup>, the  
446 plummeting costs of DNA technologies<sup>159</sup>, and the step changes in bioinformatics that have  
447 allowed big data to be stored and retrieved in open-access platforms<sup>160</sup>. In the disciplinary  
448 domain, the last decade has seen a marked uptick in inter- and transdisciplinary research, with a

449 greater – though still insufficient – integration of natural and social sciences. This has resulted in  
450 an increasing openness of researchers towards methodological pluralism and mixed-method  
451 approaches<sup>150</sup> and growing recognition of the contribution that can be made by local people,  
452 citizen- and para-scientists in biodiversity research<sup>161</sup>. Changes in research culture include the  
453 greater internationalisation of ecological science and closer approximation with society<sup>150</sup>, both  
454 of which can help foster a more fertile ground for knowledge exchange and capacity building.  
455 Notable advances include the development of multi-disciplinary and multinational learning  
456 networks<sup>162</sup>, exponential growth in author teams<sup>163</sup>, and major syntheses such as the  
457 Intergovernmental Platform for Biodiversity and Ecosystem Services (IPBES).

458 Recent years have seen a new awakening of environmental consciousness and calls for decisive  
459 action, manifest, for example, in the Paris Agreement, the Sustainable Development Goals, and  
460 voluntary Zero Deforestation Commitments. Tropical and non-tropical scientists can inform  
461 these endeavours by developing a reliable knowledge base and innovative management  
462 interventions. Overcoming the remaining research challenges is far from trivial and will require  
463 a massive investment of resources to develop scientific infrastructure and capacity within  
464 tropical nations, as well as profound changes to ways of working and the relationship between  
465 the research process and society at large. But a failure to act decisively and to act now will  
466 greatly increase the risk of unprecedented and irrevocable biodiversity loss in the hyperdiverse  
467 tropics.

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489 **Figure legends**

490 **Figure 1 | The tropical biosphere. a**, Tropical terrestrial and marine biomes. The tropical  
491 terrestrial biome (green) was defined as all tropical mesic ecoregions<sup>164</sup>. These ecoregions span  
492 82% of the 50 million km<sup>2</sup> of land between 23.5° N and 23.5° S, but extend into the subtropics in  
493 some areas. The tropical marine biome was defined by the 1988-2018 mean minimum monthly  
494 18 °C sea-surface isotherm. This isotherm bounds the latitudinal extent of shallow-water coral-  
495 forming ecoregions (blue)<sup>165</sup>. **b**, The Intertropical Convergence Zone (ITCZ). The ITCZ was defined  
496 by 1979-2017 mid-summer (January – turquoise colour gradient – and July – red colour  
497 gradient) mean monthly total rainfall >20 cm (where both January and July had rainfall >20 cm,  
498 we show that with the largest total). The ITCZ is a strong predictor of the distribution of tropical  
499 ecoregions (**a**). Data sources are presented in Extended Data Table 1.

500 **Figure 2 | Tropical hyperdiversity. a**, The proportion of species found within tropical latitudes  
501 for ten taxonomic groups. Bars are colour-coded to show the percentage of species ranges that  
502 overlap the tropics. *n* gives the total number of species analysed in each group. Black boxes  
503 around each bar show the proportion of all species that are endemic to the tropics. Only birds,  
504 amphibians and mammals have been comprehensively sampled. Numbers at the end of the bars  
505 give the precise percentage of species whose ranges overlap tropical latitudes, as shown in the  
506 bars. **b**, The difference in the proportion of threatened (Critically Endangered, Endangered, and  
507 Vulnerable) and non-threatened (Least Concern) species found exclusively within tropical  
508 latitudes for the five comprehensively sampled groups. Data from: Birdlife International for  
509 birds, the IUCN<sup>29</sup> for amphibians and mammals, the Ocean Biogeographic Information System  
510 for marine fish, Charlie Veron for shallow-water zooxanthellate corals, Tedesco et al.<sup>166</sup> for  
511 freshwater fish, and the Global Biodiversity Information Facility for angiosperms. Data sources  
512 are presented in Extended Data Table 1.

513 **Figure 3 | Vulnerability of tropical biota to local and climatic stressors.** Species co-tolerance to  
514 a local and climate-associated stressor<sup>85</sup>. The x-axis shows responses to fishing for corals (**a**) and  
515 reef (**b**) and freshwater fish (**c**); land-use change/deforestation for small-stemmed trees ( $2 \leq$   
516 DBH <10 cm; (**d**)) and forest birds (**e**); and fire suppression for savanna birds (**f**). The y-axis  
517 represents longitudinal responses to climate-associated events: the 2015-16 and 1997-98 coral  
518 bleaching events in the Seychelles for, respectively, corals (**a**) and reef fish (**b**); the 1997-98 El  
519 Niño-induced drought for lower Amazonian freshwater fish (**c**); Amazonian fires during the  
520 2015-16 El Niño for small-stemmed trees (**d**) and forest birds (**e**); and shrub encroachment  
521 between 1998-2008 in South Africa for savanna birds (**f**). Species relative density is represented  
522 from low (dark blue) to high (light green). The four quadrants represent the location of  
523 “Survivor” species tolerant to both stressors (green), species only susceptible to local stressors  
524 (yellow), species only vulnerable to climate-associated stressors (blue) and “double-jeopardy”  
525 species susceptible to both stressors (red). Numbers show the percentage of species that fall  
526 into the quadrant. *n* gives the total number of species – or genera for corals. Data sources are  
527 presented in Extended Data Table 1.

528 **Figure 4 | Socio-economic drivers of biodiversity loss and societal response capacities.** Green  
529 lines represent countries with >50% of their area within tropical latitudes; purple dashed-lines

530 represent all other countries; grey-shaded areas represent the proportion of the global total  
 531 within tropical countries. **a**, Global population (1960-2016). **b**, Gross domestic product (GDP) per  
 532 capita (2011 \$US based on purchasing power parity; 2000-2016). **c**, Foreign food crops (1961-  
 533 2009). **d**, Cumulative overseas land ownership (2001-2017). **e**, Domestic and international  
 534 airline passengers (1970-2016). **f**, Agricultural and forestry commodities export value (2001-  
 535 2016). **g**, Bottom and pelagic trawler catch tonnages (1960-2014). **h**, Total fertilizer (nitrogen,  
 536 potash, and phosphate) consumption relative to crop area (2002-2013). **i**, Government  
 537 effectiveness index (2000-2016). **j**, Environmental protection aid (2000-2016). **k**, Public and  
 538 private sector research and development expenditure (% GDP) (2000-2015). **l**, Scientific and  
 539 technical journal articles per million people in the fields of physics, biology, chemistry,  
 540 mathematics, clinical medicine, biomedical research, engineering and technology, and Earth and  
 541 space sciences (2003-2016). Data sources are presented in Extended Data Table 1.

542 **Box**

**BOX 1**  
**Ecosystems in transition**

**a** Wildfires in historically fire-free humid tropical forests<sup>167</sup> can lead to the dominance of grassy vegetation that impedes succession towards closed-canopy forests<sup>91,168</sup>. These wildfires result from the combination of local actions (e.g. agriculture practices, logging) and climate change that has increased wildfire-promoting weather<sup>169</sup>.

**b** Chronic local stressors and acute climatic stressors can lead to coral cover being replaced by macroalgae, sponges, or sediment-laden turf algae domination<sup>88,95</sup>. 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<sup>89</sup>.

**c-d** Woody encroachment is occurring in many savannas<sup>69</sup>, causing biodiversity loss and altered system functioning<sup>68</sup>. Causes are mixed: regime shifts to forest-associated ecosystems have been attributed to fire suppression policies (e.g. Brazilian Cerrado [c] to Forest [d]<sup>169</sup>), changes in herbivory and increasing atmospheric CO<sub>2</sub><sup>69</sup>.

**e** The boom in hydropower-dam construction is affecting large tropical river basins<sup>135</sup>. 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<sup>82</sup>.

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

543 **Box text**

544 Box 1. Tropical ecosystems in transition.

545 Forests (a): Wildfires in historically fire-free humid tropical forests<sup>167</sup> can lead to the dominance  
 546 of grassy vegetation that impedes succession towards closed-canopy forests<sup>91,168</sup>. These  
 547 wildfires result from the combination of local actions (e.g. agricultural practices, logging) and  
 548 climate change that has increased wildfire-promoting weather<sup>169</sup>.

549 Corals (b): Chronic local stressors and acute climatic stressors can lead to coral cover being  
 550 replaced by macroalgae, sponges, or sediment-laden turf algae<sup>89,95</sup>. During the 1998 global  
 551 coral-bleaching event, >90% of live coral died in the inner Seychelles and nearly half of the reefs  
 552 transitioned to fleshy macroalgal regimes<sup>89</sup>.

553 Savannas (c-d): Woody encroachment is occurring in many savannas<sup>69</sup>, causing biodiversity loss  
 554 and altered system functioning<sup>68</sup>. Causes are mixed: regime shifts to forest-associated  
 555 ecosystems have been attributed to fire suppression policies (e.g. Brazilian Cerrado [C] to Forest  
 556 [D]<sup>170</sup>), changes in herbivory and increasing atmospheric CO<sub>2</sub><sup>69</sup>.

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



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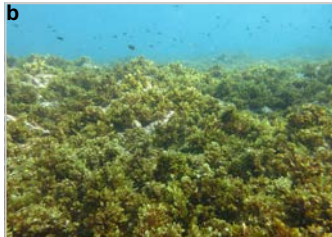
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## Ecosystems in transition



Wildfires in historically fire-free humid tropical forests<sup>167</sup> can lead to the dominance of grassy vegetation that impedes succession towards closed-canopy forests<sup>91,168</sup>. These wildfires result from the combination of local actions (e.g. agriculture practices, logging) and climate change that has increased wildfire-promoting weather<sup>169</sup>.



Chronic local stressors and acute climatic stressors can lead to coral cover being replaced by macroalgae, sponges, or sediment-laden turf algae<sup>88,95</sup>. 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<sup>89</sup>.



Woody encroachment is occurring in many savannas<sup>69</sup>, causing biodiversity loss and altered system functioning<sup>68</sup>. Causes are mixed: regime shifts to forest-associated ecosystems have been attributed to fire suppression policies (e.g. Brazilian Cerrado [c] to Forest [d]<sup>169</sup>), changes in herbivory and increasing atmospheric CO<sub>2</sub><sup>69</sup>.



The boom in hydropower-dam construction is affecting large tropical river basins<sup>135</sup>. 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<sup>82</sup>.

**a**Minimum SST ( $^{\circ}\text{C}$ )

18-21

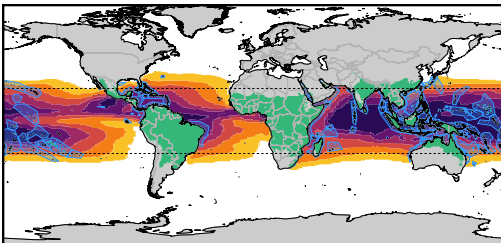
21-23

23-24

24-25

25-27

27-29

**b**

January

Rainfall (cm)

July

20

30

50

75

&gt;150

20

30

50

75

&gt;150

