Opinion

Climate change and tropical biodiversity: a new focus

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Considerable efforts are focused on the consequences of climate change for tropical rainforests. However, potentially the greatest threats to tropical biodiversity (synergistic interactions between climatic changes and human land use) remain understudied. Key concerns are that aridification could increase the accessibility of previously non-arable or remote lands, elevate fire impacts and exacerbate ecological effects of habitat disturbance. The growing climatic change literature often fails to appreciate that, in coming decades, climate–land use interactions might be at least as important as abiotic changes *per se* for the fate of tropical biodiversity. In this review, we argue that protected area expansion along key ecological gradients, regulation of human-lit fires, strategic forest–carbon financing and re-evaluations of agricultural and biofuel subsidies could ameliorate some of these synergistic threats.

Climate change in the tropics

A large and growing literature has assessed the ecological impacts of climate change, and the bulk of this work focuses on the direct impacts of changing abiotic conditions on specific organisms or habitats [1]. For example, rising temperatures are projected to lead to a decline or loss of approximately 30% of epiphyte species and nearly 80% of ant species in the lowlands of Costa Rica [2]. Temperature increases could be particularly crucial for tropical ectotherms [3] and trees [4], which have narrower thermal-tolerance ranges than do their temperate-zone counterparts. Mirroring the ecological literature, conservation strategies in the tropics are often focused on direct impacts of climate change, such as rising sea levels, increasing temperatures and altered hydrology [5].

Although these research and conservation efforts are unquestionably important, less attention has been devoted to an additional factor: the potentially devastating interactions between human behavior and environmental alteration. Because humans are dominant agents of ecosystem change, their transforming interactions with other species have great potential to shape the impacts of global climate change on biodiversity. Such impacts, we believe, could exceed the direct effects of climate change on the ecophysiology and behavior of individual species [6–8].

Here, we focus on how climate change and human behavior interact synergistically, in that changing land-use patterns could exacerbate climatic impacts, and vice versa. This is distinct from recent studies that have assessed how climate change and land-use change affect biodiversity [9,10] and human livelihoods (e.g. [11]) additively, without considering how climatic and land-use changes could magnify each other's impacts. We emphasize that ongoing and future warming and drying conditions in many tropical forests could elevate the impacts of habitat disruption, overexploitation and anthropogenic fires on biodiversity. We also assert that human land-use changes can increase the vulnerability of tropical forests to climatic changes. Finally, we argue that a focus on human responses to climate change could lead to different priorities for tropical climate-change research and more effective strategies for conservation.

Synergistic impacts of climate change and human land use

Warming temperatures in altered habitats

In a tropical biome unaltered by human activity, the response of biodiversity to long-term warming might be less negative than is sometimes assumed, at least for some components of biodiversity. For instance, floral diversity increased rapidly during the sudden warming of the Paleocene–Eocene Thermal Maximum event (PETM; 56.3 million years ago [12]) and this event corresponded with major radiations in epiphytic orchids [13] and ferns [14].

However, although the PETM is in many ways the best prehistoric analog for current warming in the tropics, the analogy is clearly imperfect. The PETM was probably not associated with drying conditions [12], whereas current climate models predict increased near-future aridity in at least some tropical areas [15]. Rainforest floras were different during the early Eocene compared with those of today, although nearly all extant plant families were represented. The PETM warming, although extremely rapid by geological standards, was evidently one to two orders of magnitude slower than current rates. The rate of contemporary warming could be fast enough to push ecosystems towards thresholds beyond which they destabilize and further changes become difficult to predict [16].

The PETM analogy does, however, illustrate that the response of rainforest biodiversity to rising temperature is

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not simply negative. This is further supported by ecophysiological work suggesting that some tropical trees are relatively robust to rising temperatures [17–19], although certain animal species might have more narrow thermal tolerances [3,20]. Recent predictions that many lowland tropical taxa might be unable to cope with even modest, near-term temperature increases (e.g. [2,4]) highlight important uncertainties about the effects of rising temperatures on biodiversity.

Notably, one of the primary ways in which tropical floras in the PETM adapted to rapid warming was through shifting distributions, both within and between continents [21], whereas such spatial reorganization will be hampered or even precluded today by large-scale forest loss and fragmentation in the tropics [22]. Even in areas where forest reclamation efforts have been ongoing, the original species composition often does not re-establish because disturbance can promote large numbers of exotic species [23]. Thus, the detrimental impacts of habitat destruction and fragmentation in tropical forests could be greatly magnified via synergies between climatic warming and obstructed shifts in the ranges of species.

Regional drying and the accessibility of remote areas

Increasingly severe dry seasons could also exacerbate the impacts of land-use change on tropical forest biodiversity. Roads that are impassable during the rainy season disrupt vehicle movements in many tropical forests [24]. This suggests that if dry seasons become longer, the economic feasibility of forest colonization and logging could increase and many of the last remaining ‘remote’ forests could become accessible to large-scale exploitation. Indeed, dry season severity is already a strong, positive predictor of deforestation pressure in the Amazon [25], implying that drying trends in certain tropical forests could increase their vulnerability. Hunting pressure, which increases with logging and associated road expansion [26], is so pervasive in tropical forests that abundant populations of large vertebrates are increasingly restricted to inaccessible areas [27] and to limited numbers of well-staffed protected areas (PAs) [28]. Hence, increasing physical accessibility could both destroy forests outright [25] and diminish wildlife populations in the habitat remnants that remain. The resulting increases in deforestation, fragmentation and hunting might push some species that are already struggling to cope with direct, negative impacts

Figure 1. Land-use changes, such as large-scale deforestation and fragmentation, can increase the vulnerability of tropical forests to desiccation and destructive fires. **(a)** Deforestation in Sumatra, Indonesia; **(b)** slash-and-burn farming in the central Amazon; and **(c)** massive smoke plume in the Amazon. Reproduced, with permission, from W.F. Laurance **(a,b)** and M. Welling **(c)**.

of climate change, such as several genera of ateline primates [29], past thresholds beyond which they cannot recover.

Increasing threats from fire

Synergies between climate change and human-lit fires represent another severe threat to tropical ecosystems that is likely to increase in importance with future warming. Although many tropical tree species might be reasonably resilient to rising temperature [30] and even moderate water stress [19,31,32], few are adapted to fire [33], and most tropical rainforests are fire sensitive [34]. Over 70% of tropical forests already suffer from ‘degraded’ fire regimes [34]. Substantial expanses of the tropics could become warmer and drier in the future, potentially in conjunction with increasingly intense El Niño events [35,36] and droughts driven by anomalously warm sea-surface temperatures [37]. Such conditions can increase the incidence, magnitude and duration of human-lit fires, including wildfires that escape from control [38]. Flammability can increase both through reduced annual precipitation and via increased rainfall seasonality, which generates more intense dry seasons [22].

Crucially, human land-use changes can dramatically increase forest vulnerability to fire (Figure 1), magnifying the impacts of climatic drying. As human numbers increase, drought cycles in Indonesia become increasingly coupled with fire cycles [39]. Moreover, logged or fragmented forests are far more vulnerable to fire than are intact forests [40–42]. In fragmented landscapes, canopy desiccation [43] and fire [44] can penetrate deeply into forest remnants. Canopy desiccation can infiltrate approximately 1.5 km from the forest edge in moderately fragmented areas (50–65% forest cover) and >2.5 km in heavily fragmented landscapes (20% forest cover) [43]. Such edge effects are among the strongest drivers of changes in tree and animal communities, microclimate and carbon storage in fragmented forests [45]. In the Brazilian Amazon, over 70 000 km of new forest edge was created annually from 2000 to 2002, and the amount of forest within 2 km of an edge rose by 4% per year [46], thereby increasing forest susceptibility to desiccation and fires.

Forest loss also reduces moisture inputs to the atmosphere from evapotranspiration. The synergistic interactions among regional drying, forest disruption and increasing anthropogenic fires could promote a massive replacement of Amazonian forests by savannahs or secondary forest over the next century [38]. This in turn could exacerbate climatic warming both through a decline in low-level clouds, which help to reflect intense solar radiation in the tropics back into space [47], and via the substantial contributions of forest destruction to atmospheric CO_2 emissions [48]. Forest replacement could also further exacerbate drying at local scales, because declining evapotranspiration can decrease local humidity and precipitation [49].

Variability in responses to climate change across tropical ecosystems

The ways in which climate change affects biodiversity will surely vary across different tropical ecosystems. Lowland forests might be particularly susceptible to the types of climate–land-use interaction we have outlined above. For example, habitat destruction and fragmentation could cause species extinctions when they preclude organisms from shifting their distributions to avoid temperature increases or heat waves. Such extinctions could be particularly severe in the vast lowlands of the Congo and Amazon drainages, where species would have to move thousands of kilometers to reach higher-elevation thermal refuges [2,4]. Vulnerability might be acute in many canopy trees, such as those in the Fagaceae and Dipterocarpaceae of Southeast Asia, whose potential migration rates are low owing to short seed dispersal distances [50]. Upslope shifts in the ranges of lowland species [2] could place added pressure on higher-elevation species. Yet, in some montane tropical forests, changing climatic conditions themselves could be more important than synergies between climate change and land use. Many species in these systems, such as numerous amphibians and epiphytic plants, are cool-adapted, range-restricted endemics that appear especially vulnerable to further warming, brief but intense heat waves, a rising cloud base, increasing insolation and potentially reduced moisture-stripping from clouds [20,51]. Rising temperatures at higher elevations might also increase the prevalence of virulent pathogens in these systems, such as the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) [52,53].

Global responses to climate change and local tropical land-use

At a global scale, societal and economic responses to climate change can magnify human pressures on tropical forests. Spurred by rising petroleum prices and the need to mitigate greenhouse gas emissions, crop-based biofuel production has increased rapidly in recent years [54,55]. Along with rising demands for food, this has led to a substantial expansion of agricultural lands in the tropics to create new areas for biofuel production or to provide replacement sites for food production when existing croplands are switched to biofuel production [54]. Little of the potential agricultural land in the temperate zone is unused, so most agricultural expansion to meet near-term global food and biofuel demands will occur in the tropics [56]. Most agricultural expansion in the tropics comes at the expense of intact forests [57], and most tropical deforestation is driven by agricultural expansion [58]. Rising demands for land to grow crops and biofuel feedstocks will also increase opportunity costs for conservation, reducing the competitiveness of carbon offsets and other payments for ecosystem services designed to slow forest destruction [59].

Thus, the rapid expansion of biofuel production in the tropics, driven in part by efforts to reduce greenhouse gas emissions, could have severe impacts on tropical ecosystems and biodiversity. For instance, a recent decline in US soybean production in response to generous corn subsidies from the Federal Government to promote ethanol production appeared to prompt Brazilian farmers to increase burning of forests and savanna-woodlands to expand soy production [55]. Perversely, this could also increase net carbon emissions as a result of the loss of forest carbon storage [54,60]. Such complex and often insidious impacts are probably the tip of the proverbial iceberg; numerous interactions between climatic change and land-use alterations could be driven by changing economic and human demographic forces, even from afar.

Conservation strategies in the warming tropics

Many well-known conservation tactics, such as fire regulation, protected areas, community involvement and education, agricultural policy instruments and payments for ecosystem services, could be used in novel ways to ameliorate synergistic climate–land-use interactions. It is vital, for instance, to halt perverse agricultural subsidies for biofuel production that directly or indirectly promote tropical forest destruction. For example, US ethanol subsidies may be indirectly contributing to rising soy prices, thereby increasing deforestation and human-lit fire incidence in soy-producing regions of the tropics [55]. Another key goal is to divert agricultural expansion wherever possible from intact forests to areas that have already been cleared or seriously degraded [56] so as to retain the climate-change resilience of unfragmented forests, while recognizing that selectively logged forests can also retain substantial value for biodiversity conservation [61].

Some evidence suggests that the growing threat of climate-exacerbated fires can be partially ameliorated. For instance, the Wildlife Conservation Society and Rainforest Alliance are working with the Guatemala National Council for Protected Areas to control human-lit fires in the Maya Biosphere Reserve, the largest PA in Central America. These efforts have reduced the number of fires by an order of magnitude in some areas. The Large-scale Atmosphere–Biosphere Experiment in Amazonia is helping to identify 'tipping points' of fire frequency beyond which forests are transformed into artificial savanna-dominated systems [62]. In parts of the Amazon, landowners and certain land-holding corporations are helping to reduce fire use, and if plantations and orchards become more common in the region, landowners are likely to use fires with more discretion [38].

A new focus for protected areas

Although networks of interconnected PAs have been a backbone of conservation strategies for decades, synergisms between climate change and land use require a renewed focus on ecological connectivity, one with a particular emphasis on protecting latitudinal and elevational gradients. PAs in tropical nations range from strict nature reserves to those allocated in part for various forms of resource extraction, and include many 'paper parks' with limited actual protection. These PAs are, on average, only approximately 1000 km^2 each in area and span $<0.4^\circ$ of latitude (World Database on Protected Areas; http://www.wdpa.org/). This coverage is far too small to enable long-distance range shifts of forest-dependent organisms. Parts of the Brazilian Amazon might contain sufficient PA coverage to avert local climatic changes [49] and retain large-scale connectivity. Yet few other tropical regions or nations have sufficiently large 'megareserves' or linked-reserve networks along key environmental gradients to help buffer major climatic change [63]. To enhance reserve resilience, governments and conservation organizations should strive to protect or restore viable habitat linkages among existing PAs, and to fund and manage PAs and habitat corridors for biodiversity conservation adequately. Enhancing connectivity could be achieved via a combination of mechanisms, including national parks established by central governments, community-managed forests, international trans-boundary areas and carbon-financing projects.

In addition to maintaining dispersal corridors, PAs can be used to slow the advance of the agricultural frontier to retain large, contiguous forest tracts, within which range shifts of species can occur. Such a strategy is exemplified by the establishment of several large PAs in the Brazilian Amazon via a multiple-stakeholder strategic plan [64]. In the Amazon, however, forest loss is geographically concentrated in the southern and eastern parts of the basin, whereas in other tropical regions it is often more widespread [65]. For instance, Southeast Asia has already lost the majority of its original forested lands [66] and the remaining pockets of lowland forest, even inside many PAs, continue to be eroded by large- and small-scale agricultural expansion [67,68].

Strategic coordination to increase forest resilience to climate change

In parts of the tropics, efforts to expand PAs and limit fires are ongoing, but we argue that they should be coordinated at regional and international levels explicitly to increase the resilience of remaining forests and forest-dependent taxa to climate change [69]. Reducing Emissions from Deforestation and forest Degradation (REDD) initiatives, supported by international carbon trading, could be integrated into such strategies. The biodiversity benefits of REDD projects could be increased by strategically locating forest conservation efforts to increase effective coverage of PAs, protect habitat linkages and potential species migration routes, and limit expanding agricultural frontiers. This might require revising REDD-finance protocols if it turns out that opportunity costs for strategic placement of REDD sites are higher than simply conserving the most carbon-rich ecosystems. Ecological connectivity is also urgently needed between major eco-zones, such as between the Amazon lowlands and the uplands of the Andean Piedmont, Brazilian Shield and Guyana Shield [22], and to link PAs into large-scale networks, such as the forest complex of the Thailand–Myanmar border (spanning a latitudinal gradient of approximately 9°) or along the Annamite Mountains of Laos and Vietnam (spanning approximately 5.5° in latitude).

Concluding remarks

The coming decade will be crucial in determining the extent to which humankind can ameliorate the potentially devastating effects of climate change and rapidly expanding land use on tropical biodiversity. We argue that these two threats should not be treated in isolation. Human activities, such as logging and habitat fragmentation, degrade ecosystem resilience to climate change. Climatic shifts, in turn, enhance the destructive impacts of human-lit fires and facilitate habitat destruction. Concerted strategies at national, regional and international scales,

involving relevant stakeholders and a simultaneous focus on multiple conservation challenges, are vital for alleviating these synergistic threats to global biodiversity.

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