Interacting climate and local human disturbances drive ecological changes in tropical ecosystems

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Summary

Tropical forests and coral reefs host a disproportionately large share of global biodiversity and provide ecosystem functions and services used by millions of people. Yet, ongoing climate change is leading to an increase in frequency and magnitude of extreme climatic events in the tropics, which, in combination with other local human disturbances, is leading to unprecedented negative ecological consequences for tropical forests and coral reefs. Here, we provide an overview of how and where climate extremes are affecting the most biodiverse ecosystems on Earth, and summarize how interactions between global, regional and local stressors are affecting tropical forest and coral reef systems through impacts on biodiversity and ecosystem resilience. We also discuss some key challenges and opportunities to promote mitigation and adaptation to a changing climate at local and global scales.

Keywords: biodiversity, climate change, climate extremes, coral reefs, ecosystem functioning and resilience, tropical forests

1. Introduction

The tropics contain the overwhelming majority of Earth's biological diversity [1] disproportionately distributed in two key ecosystems: tropical forests and coral reefs. Tropical forests cover less than 12% of the planet's ice-free surface but host more than two-thirds of all terrestrial species [1]. They provide the largest contribution to Earth's productivity from any biome [2], and play a critical role in overall climate regulation by storing 25% of the carbon in the terrestrial biosphere [3]. Equally important are tropical coral reefs (hereafter 'coral reefs'), covering just 0.1% of the ocean surface yet holding the highest species diversity of any marine ecosystem [4]. They also sustain crucial ecosystem processes for more than 500 million people who use coral reefs and reef products for food provisioning, fisheries, and ecotourism [5,6], and through providing coastal protection against natural hazards [7].

Despite their global importance, tropical forests and coral reefs are subject to a complex mixture of more localized pressures such as overexploitation, habitat loss, pollution and global climate change [1,8]. Growing evidence also suggests that anthropogenic climate change is increasing the periodicity and intensity of some climate extremes (e.g. [9–11]), which can be defined as abrupt climatic events such as abnormally intense storms, hurricanes, floods, heatwaves, droughts and associated large-scale wildfires [12]. The ecological impacts of these extreme climate events can be exacerbated by ongoing gradual changes in temperature and precipitation, as well as local anthropogenic pressures, such as land-use change [13,14]. Understanding how tropical rainforests and coral reefs respond to climate extremes – and their interactions with other stressors – is therefore essential to achieve global conservation targets [15] and sustainable development goals [16].

Evidence of the influence of gradual climate changes and extreme climatic events is growing, and many studies explore their interactions with other more localized human pressures that threaten tropical forests and reefs (e.g. [1,13]). Yet, the existing literature is patchy and our ability to protect and manage these ecosystems is limited by two important knowledge gaps. First, no study to our knowledge has summarized where climate extremes are known to already affect both tropical forests and coral reefs worldwide, or which extreme events drive ecological changes in these two ecosystems. Second, despite a growing literature on the subject, it is not clear how interactions between gradual climate change, extreme climatic events, and local disturbance are influencing tropical forests and reefs. These two knowledge gaps motivate the first and second part of our review. The final part explores how our understanding of ecosystem responses to multiple pervasive pressures could be applied to inform management and conservation strategies. Although we primarily focus on tropical forests and coral reefs, the synergies among climate-related and local human-driven stressors are also major threats to other global ecosystems both in tropical and extratropical regions [17–19].

2. Where and how are climate extremes affecting tropical forests and reefs?

(a) Storms and floods

Climate change is causing more intense and frequent cyclonic storm systems (i.e. hurricanes, cyclones, and typhoons) [10], with more extreme events expected in regions already affected by tropical cyclones, including Central America and the Caribbean, East Africa, most of Asia, as well as in Australia and the Pacific islands [20]. Although their impacts on coral reefs are primarily physical, for example through reef structural damage [21], storms and hurricanes can strongly influence marine ecosystems [22,23]. On the Great Barrier Reef (GBR), for example, heavy rainfall was associated with negative trends in live coral cover, and storms emerged as the major driver of changes in inshore reef dynamics [24]. Not surprisingly, cyclonic storms have been shown to trigger regime transitions, from coral to macroalgal dominance, through interactions with local stressors (e.g. overfishing and diseases) that drive coral cover declines [25].

Tropical forests are also being affected – hurricanes frequently affect tropical forests in the Caribbean and Central America [26–28], and heavy storms have caused severe landslides in Venezuela [29] and floods in the Amazon basin (e.g. in Brazil and Peru [30–32]; figure 1). Some of the most extreme hydrological events have been associated with La Niña-induced changes in precipitation and river flow (e.g. 1989, 1999, 2009 and 2012) [32–34]. The 1998/99 La Niña, in particular, brought one of the strongest hurricane seasons ever recorded in the North Atlantic, while in the Indian Ocean over 50% of Bangladesh was flooded [35]. Consequently, a range of post-hurricane ecological consequences has been recorded in tropical forests, such as reductions in non-tree resources for nectarivorous and frugivorous fauna [36]; changes in plant-herbivore networks (e.g. negative effects on network size and specificity, but increased connectance and robustness) [37]; and >50% declines in rates of occupancy, and even local and global extinctions of forest birds on Caribbean Islands [26,38].

[Figure 1 here]

(b) Heatwaves and droughts

Extreme temperatures and droughts have been recently recorded across much of southern Africa, Southeast Asia and South America [39]. In recent decades, marine heatwaves have provoked widespread coral bleaching [40] (figure 1), leading to fundamental changes in coral reef ecosystems (e.g. [41–43]). In particular, the extremely high sea surface temperatures across most of the tropical and extratropical oceans during the 2015/16 record-breaking anomaly [44] caused one of the strongest mass bleaching events on a worldwide scale [45]; and resulted in unprecedented levels of coral mortality [46] and altered community composition of both corals and fish on the GBR [47]. Other heatwave-induced ecological impacts include flattening of reef structure [48] and loss of carbonate production [49], formation of persistent novel fish communities [41], shifts to macroalgal regimes [42], and synchronous multi-trophic ecological disruptions in terrestrial and marine ecosystems (e.g. tree die-off and coral bleaching) [50].

The combination of extreme high temperatures with longer and more severe dry seasons has also led to the spread of unprecedented and large-scale wildfires in tropical forests [51,52] (figure 1). For example, forests in the Amazon basin and Indonesia have witnessed at least four 'mega-droughts' in the last three decades [53,54]. Some of these heat and drought events were aggravated by the El Niño Southern Oscillations (ENSO), such as in 2015/16 when fires devastated around 1 Mha of Amazonian forests [55,56] and >4.6 Mha across Sumatra, Kalimantan and West Papua [52]. As a result of more frequent, extensive and intense drought and fire events, tropical forests have been affected through elevated tree mortality [57–59], impoverishment of biological communities [57,60–62] and loss of specific functional groups (e.g. evergreens and softwoods [63]). For instance, in Amazonia, thermally-enhanced dry seasons impose additional water-stress for trees even in the wetter environments [64], and tree recruitment has shifted towards more dry-affiliated individuals, accompanied by increased mortality of wet-affiliated species [65]. These drought-related impacts can go beyond taxonomic and functional changes to effects on ecosystem resilience and stability (Box 1), and in combination with wildfires, have led to reduced plant growth (e.g. [66] but see [67]) and ecosystem primary production [66,68] – all of which negatively affects the forest carbon cycling [69,70].

Box 1. Empirical examples of how climate extremes impact taxonomic and functional diversity, affecting the resilience and stability of tropical forests and coral reefs

Securing functionally stable and resilient ecosystems is a pressing issue under ongoing global change. It is assumed that biodiversity increases ecosystem functioning and climate-resistance [71], and that functional trait-based approaches can better quantify disturbance consequences on ecological function and ecosystem stability [72]. However, the literature lacks evidence from the tropics [73,74]. To explore how an El Niño-related extreme drought and marine heatwave can affect the functional stability and ecosystem functioning of tropical forests and coral reefs, we used empirical data from dung beetles – which are important insects for secondary seed dispersal and seedling establishment processes in tropical forests [75,76] – within primary Amazonian forests and herbivore parrotfish within reefs throughout the inner Seychelles. We measured functional traits of dung beetles and parrotfish, along with two key ecosystem functions: secondary seed dispersal rates by dung beetles in forests and grazing rates by herbivorous parrotfishes on reefs. All datasets were sampled before and after the onset of the 2015-16 El Niño (forest: 2010 and 2016; reef: 2014 and 2017; for further details see supplementary material and Refs. [42,77]). We, hence, compared post-El Niño functional diversity metrics and biodiversity-ecosystem function (BEF) relationships with those from pre-El Niño surveys.

Our findings suggest that climate extremes could reveal the importance of tropical biodiversity for ecosystem functioning, increasing the range of ecological niches occupied by functional groups (functional richness), and reducing the trait dissimilarity among communities (functional dispersion) – but these impacts are ecosystem-dependent [78] (figure 2). Lower seed dispersal rates occurred in forests with reduced beetle richness after the 2015-16 El Niño drought (figure 2a-b), while positive BEF relationships were found in both pre- and post-El Niño surveys on Seychelles reefs (figure 2e-f). Although focusing only on the short-term responses, these findings provide empirical evidence suggesting that disturbances may emphasize the value of higher biodiversity in maintaining ecosystem functioning [79], at least in tropical forests; while demonstrating that not only climate change, but also climatic extremes, may have filtering effects for terrestrial biological communities [17]. In addition, the maintenance of high post-disturbance grazing rates – under some specific ecological contexts [80] – may promote long-term coral recovery and stability by controlling competitive algae and reducing the likelihood of ecosystem transitions to algal-dominated states [42].

After the El Niño event in the Amazon, dung beetle functional richness was higher (figure 2c) and functional dispersion was lower (figure 2d). Similar results were found for flood disturbance effects on ground beetle functional responses in German grasslands [81], which could be explained by the loss of species with unique traits and increased dominance of functionally similar species such as generalists (often found in more disturbed environments [37,82,83]). It is therefore likely that the El Niño drought-induced compositional changes in dung beetle communities resulted in lower seed dispersal rates within forests with lower species richness – which may affected functioning insurance through lowering functional redundancy [84,85]. In contrast, the lack of changes in functional richness and dispersion in the marine example (figure 2g-h) indicates no overall variation in the number of different functional traits and groups in parrotfish communities. Thus, the high taxonomic richness on coral reefs may support high functional redundancy, enabling functional groups to persist despite the El Niño event. Previous studies have similarly found no change in functional indices, including richness and dispersion, of coral-reef fishes following habitat degradation due to storms or bleaching [47,86]. However, functional originality of coral-reef fishes often decreases following climate extremes [47,86], which could make them more susceptible to future disturbances and to the interacting effects of climate change, climate extremes, and local stressors (figure 3).

[Figure 2 here]

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3. How do interactions among climate change, extreme climatic events and multiple human-driven stressors affect the resilience of studied ecosystems?

Following the framework proposed by Didham et al. [18], the interactions between climate-related stressors and local disturbances can result in 'chain' and 'modification' effects (figure 3). The interaction chain effects occur when multiple stressors have direct ecological impacts, with one driver amplifying the magnitude of another (a direct and synergistic interaction; e.g. land-use change increases climate warming via albedo effects or carbon release [87]). In contrast, interaction modification effects occur when the per-unit or per-capita influence of one stressor is modified by another (an indirect interaction), such as when habitat fragmentation prevents species from migrating to track their preferred climate niche [88]. These modification effects can occur through additive, antagonistic, or synergistic interactions between stressors (reviewed by Côté et al. [89]). Regardless of how they interact and the scale on which they operate (figure 3), climate change, extreme climate events and local stressors are likely to act as strong and interacting environmental filters [72,90]. As only a small subset of the original species pool is likely to respond positively to multiple stressors [1,91], this potential filtering of biological communities can result in subsequent effects on ecosystem functioning and functional stability of tropical coral reef and forest systems. These impacts, however, are likely to be ecosystem-dependent, as demonstrated by the empirical evidence from Brazilian Amazon forests and Seychelles coral reefs (Box 1).

[Figure 3 here]

(a) Climate and deforestation interactions threaten tropical forests and coral reefs

Climate stressors and land use change, principally for food production and human settlement provision, have been exerting multi-taxa and -trophic effects on terrestrial and marine systems [1,92–95], and causing disproportionate biodiversity loss – particularly in the tropics [13]. Although climate change is considered the most important threat to coral reefs [80], deforestation impacts are also projected to outweigh future climate change-driven declines in river flow and sediment load to reef systems in some regions [95]. However, the complex interactions between these stressors can make it challenging to tease apart their independent effects [89,96].

Forest clearance constitutes a chain interaction when it favours climate change through effects on greenhouse gas emissions and surface fluxes of radiation, moisture and heat [87]; and it increases the likelihood, intensity and extent of regional climatic extremes [97,98]. On the other hand, many ecological responses to deforestation and fragmentation likely result from interaction modifications with climate. For instance, a global terrestrial analysis of 1319 papers found that habitat loss impacts on biodiversity were greatest in regions experiencing higher temperatures and lower rainfall [99]. Interaction modifications would also imply that climate extremes occur under conditions of altered resilience generated by previous forest conversion. For example, deforestation can indirectly reduce the ability of tropical forest and reef biota to resist further climate disturbances by creating hostile landscapes and ocean conditions that hinder species capacity to track and achieve climate envelopes with more suitable conditions [88,100,101]. Moreover, habitat area, quality, heterogeneity, and configuration can also affect the biota sensitivity and recovery after climatic disturbances [96,102,103].

(b) Enhanced heat- and drought-vulnerability within human-modified tropical forests

Most remaining tropical forests are currently subject to some form of anthropogenic disturbance [104]. Many of these alter forest microclimates – selective logging and wildfires, for example, increase tree mortality, which result in greater canopy openness [105,106] and drier understoreys [107]. These processes, combined with increasingly hotter and longer dry seasons, enhance forest flammability [108] and the likelihood of escaped fires ignited on agricultural lands [109] to burn neighbouring forests [110,111]. Although many tree species have molecular and physiological mechanisms that help them resist short-lived heat and drought [68], tropical rainforests are fire-sensitive and have few fire-resistant species [112]. Post-disturbance changes in carbon cycles [104] and evapotranspiration rates – a key source of aerial moisture – are also likely to affect atmospheric circulation patterns through biogeochemical feedbacks mediated by pollution through the release of CO_2 and other aerosols [113,114], which have been shown to suppress cloud formation and regional precipitation [115,116]. Another example of an interaction modification effect occurs when climate change exacerbates the many negative impacts of ongoing forest degradation through declines in rainfall [57,117] that can enhance tree mortality through physiological mechanisms related to carbon starvation and hydraulic failure [68,118]. As rising global temperatures promote the occurrence and severity of extreme droughts [119] and wildfires [120], their interaction chain effects are also likely to be common in tropical forests (figure 3). Climate changes can also indirectly modify the susceptibility of tropical forests to climate extremes. For example, if cloud cover is declining over mid-latitudes [121] and elevated CO_2 levels are enhancing liana biomass [122], then this could increase the mortality rates of drought-stressed trees even in otherwise undisturbed tropical forests [123].

(c) Climate-induced disturbances exacerbate impacts of local stressors on coral reefs

The current coral crisis is the result of a combination of large-scale climatic stressors and localized non-climatic disturbances [124]. Coral reef ecosystems are already widely threatened by local stressors such as overharvesting, land-based pollution, diseases, sedimentation and nutrient loading [124]. At a global scale, climate change is increasing the frequency, duration and intensity of marine heatwaves [44], resulting in interaction chain effects (figure 3) that are pushing coral communities towards their physiological stress limits [125] and causing widespread coral bleaching (figure 1). For example, the 1997/98 and 2015/16 bleaching events affected ~75% of well-studied coral reefs globally

[45] and, in some regions, led to >90% declines in live coral cover [126]. The individual effects of local and global stressors on coral reefs are relatively well-understood, but recent insights suggest that the impacts of climate extremes can also be exacerbated by local stressors. Corals on the GBR, for example, contend with multiple disturbances including sedimentation, nutrient run-off, and crown-of-thorns starfish outbreaks [22] – and interactions between these disturbances determine coral resilience to bleaching (figure 3). For instance, coral declines are greatest and coral recovery is slowest on reefs where overfishing has compromised ecosystem processes such as predation and herbivory [127]. Furthermore, reefs adjacent to turbid river outflows have a lower probability of bleaching mortality due to lower light stress – an antagonistic interaction modification effect; while elevated nutrient levels have reduced coral recovery rates by 12-27% [23], which signals an additive or synergistic interaction.

Although the magnitude of impacts of climate extremes will depend on the direct and indirect interactions with local and global pressures (figure 3), even isolated and relatively-pristine reefs are vulnerable to both climate change and extremes [45,128]. Thus, local management alone is not expected to promote coral reef resilience in the face of climate stressors [129,130], although limited evidence shows that local stressor alleviation favoured post-bleaching recruitment and coral recovery in the GBR [127], Caribbean [131], Mesoamerican [132] and Kenyan reef systems [133]. In other regions, ecosystem protection of coral reefs can fail to mitigate bleaching impacts when compliance is weak and protected areas are small [134,135].

4. The way forward

We have herein outlined various examples of how climate extremes pose a broad range of challenges to tropical forests and coral reefs (figure 1; Box1), particularly when combined with or overlain ongoing climate change and more localized human pressures (figure 3). Guarding against negative impacts to the world's most biodiverse ecosystems will be challenging and dependent on local and global actions for climate adaptation and impact mitigation, while more traditional conservation strategies will need to be renewed to ameliorate the impacts of multiple interacting threats.

(a) Climate-smart protected areas

Networks of connected protected areas have been the cornerstone of efforts to conserve biodiversity, however interactions between local and climatic stressors (figure 3) require a new focus on functional and climate connectivity, with the particular aim of allowing species range shifts along climate gradients [88]. The global extent of marine protected areas protects just 7.66% of the ocean, and the size of the tropical network is far smaller than in the rest of the world [136]. Although the largest percentage of forest area under protected status (>26%) is found in the tropics [137], most tropical reserves are smaller than 100 km^2 [138]. The coverage of tropical forest and marine protected areas is therefore too small to permit species long-distance range shifts, and over 62% of the tropical forests have been shown to be likely to fail in facilitating species movements to analogous future climates [88].

To enhance climate connectivity and hence resilience, decision-makers should also focus on viable patch-linkages and habitat corridors among protected areas preferably distributed along climate gradients and where species vulnerability to climate and connectivity loss are high [88]. Achieving successful reserves will also require the protection of habitat in the wider landscape – such as private lands – to ensure reserves remain functionally connected if climate changes and extreme events result in enhanced environmental stochasticity [139], and species need to travel longer to find suitable bioclimatic conditions [88,140]. In addition, protected areas may also play a key role for both climatic mitigation and adaptation through reducing emissions from tropical deforestation [141], alleviating regional flood (drought) occurrence during extremely rainy (dry) seasons [142–144], and avoiding overexploitation and loss of organisms and processes important for post-disturbance ecosystem recovery (e.g.[127,145]). However, to fulfil their role as an insurance policy for biodiversity and climate-mitigation, current protected area networks need to be well enforced and funded [146], while new marine and forest reserves should be strategically placed where they increase climate connectivity [88] and/or are predicted to escape the burden of climate-associated stressors [129]. This is important because even regions under low direct anthropogenic stress may be subject to impacts from regional and global stressors [80] (figure 3).

(b) We are all in the same boat: multi-level actions to tackle different stressors

As human populations continue to grow, the fate and future benefits provided by tropical forest and reef systems will also depend greatly on how well these ecosystems are managed. Their long-term resilience to climate change and extremes will require the collective effort of a broad range of stakeholders at distinct levels. Acting locally is important, and there are different approaches to avoid further on-the-ground disturbance. For instance, the post-disturbance resilience of tropical ecosystems and biota may be enhanced through approaches for climatic adaptation such as the implementation of well-planned landscapes, reinstatement of connectivity and energy flows among ecosystems [147], and improvements in habitat quality through ecological restoration (e.g. green firebreaks in China [148]). Addressing the many distal drivers of degradation in tropical ecosystems is essential to foster the effectiveness of these approaches [1,124]. Research and climate-mitigation strategies are also more likely to have an effect if engaging with local actors such as tropical scientists, managers, and institutions [149–151], and encouraging land- and marine-use practices that respect local needs and diverse socio-ecological conditions (e.g. fire-safe agriculture in tropical forests [152] and community-based management programs for coastal populations that depend on corals and small-scale fisheries [153]).

Managing locally may not be enough if we do not tackle global climate change issues [80]. Redoubling efforts to limit anthropogenic climate changes remains critical and is the most important mitigation option we have where climate stressors cause widespread damage independent of other local non-climatic disturbances. This issue needs to be addressed by local, national and international stakeholders, while balancing the needs for economic growth and environmental sustainability, a particular challenge for tropical nations [154]. For this, both tropical and extratropical decision-makers will need to develop strategies such as low-carbon technologies to reduce the emissions of greenhouse gases while avoiding forest destruction to increase carbon intake [104]. If it is not already too late, controlling climate change may also reduce the risks of more severe and frequent weather extremes [44,155], and, consequently, the need for a considerable amount of investments to prepare regions that are more vulnerable to them.

6. Conclusions

Our review shows that climate extremes are impacting forests and reefs throughout the tropics (figure 1), but their ecological consequences for ecosystem resilience and stability are likely to differ across realms (Box 1). The fate of these ecosystems will be determined by a complex interplay between the impacts of local and climate-associated stressors [1,17] (figure 3). Ecological studies on species-specific physiological tolerance [156], changing species composition [58,157] and ecosystem recovery trajectories [27,46] may help us to inform management decisions where climatic stressors are the main drivers of disturbance. However, where local and climate-related stressors are jeopardising ecosystems services, we need to develop better predictive models to understand how chain and modification interactions with local stressors can mediate the ecological consequences of climate change and climate extremes. Such integrated approaches can better inform policy and climate-adjusted management solutions to ameliorate further disturbance impacts, helping to promote ecosystem adaptation and resilience. We urge the creation of conservation initiatives to develop interventions that effectively curb local disturbances, but these will be of limited success if they are not accompanied by international actions to decrease CO_2 emissions and therefore slow global climate changes. Only through multinational cooperation between a broad range of stakeholders and levels will we ensure that tropical forests and coral reefs are adequately protected and maintained for future generations.

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Figure captions

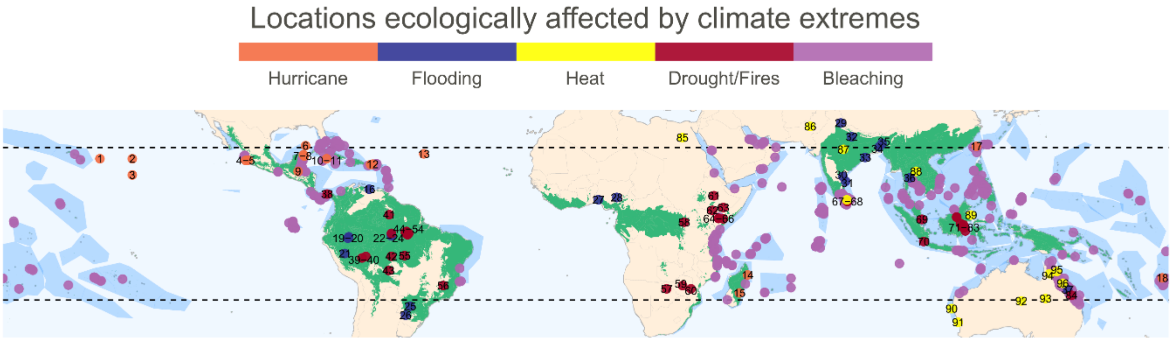

Figure 1. Locations where extreme climate events have ecologically affected tropical forests and coral reefs. Tropical forest biome (green) was defined following the ecoregions "Tropical & Subtropical Dry Broadleaf Forests" and "Tropical & Subtropical Moist Broadleaf Forests" [158]. The tropical marine biome (darker blue polygons) was defined as the extent of shallow-water coral-forming ecoregions [159] on the basis of sea surface temperature (mean minimum monthly 18° C sea-surface isotherm between 1988-2018; [1]). Color-coding of the dots on the map indicates different extreme climatic events: Drought/fires (red), floods (blue), heatwaves (yellow) and hurricane/cyclones (orange). Purple-coloured dots show high-intensity bleaching reports from ReefBase (www.reefbase.org) between 1990 and 2010. Data sources and references for each number are presented in Supplementary Tables 1 and 2, respectively.

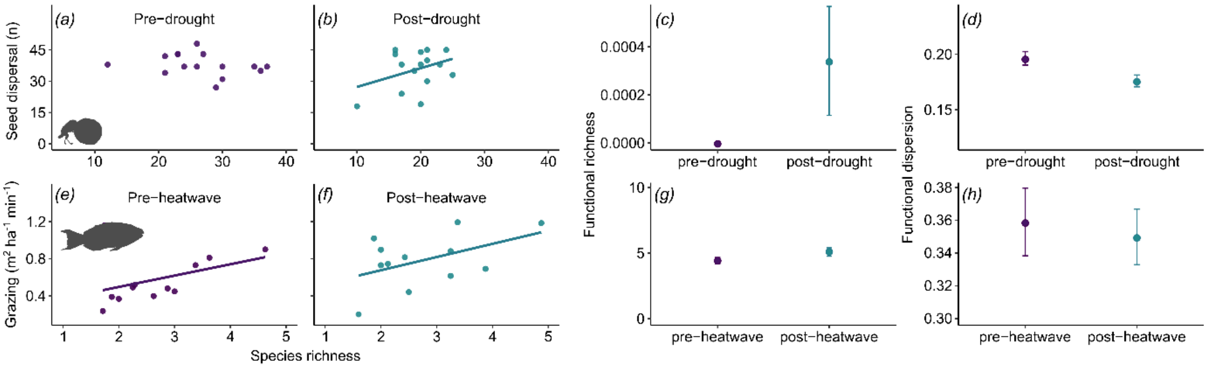

Figure 2. Drought and bleaching impacts on tropical biodiversity-ecosystem functioning links, functional richness, and functional dispersion in tropical forests and coral reefs, respectively. Dung beetle (a-d) and herbivore parrotfish communities (e-h) were surveyed before (purple) and after (blue) the 2015/16 El Niño drought within Brazilian Amazonian forests and heatwave in Seychelles reefs, respectively. The x-axis shows dung beetle (a-b) and parrotfish (e-f) richness, and pre- and post-drought/heatwave surveys (c-d/ g-h). The y-axis represents rates of dung beetle-mediated secondary seed dispersal (a-b), grazing rates (e-f), functional richness (c, g), and functional dispersion (d, h). Further details on functional traits, analyses and results are described in the supplementary material.

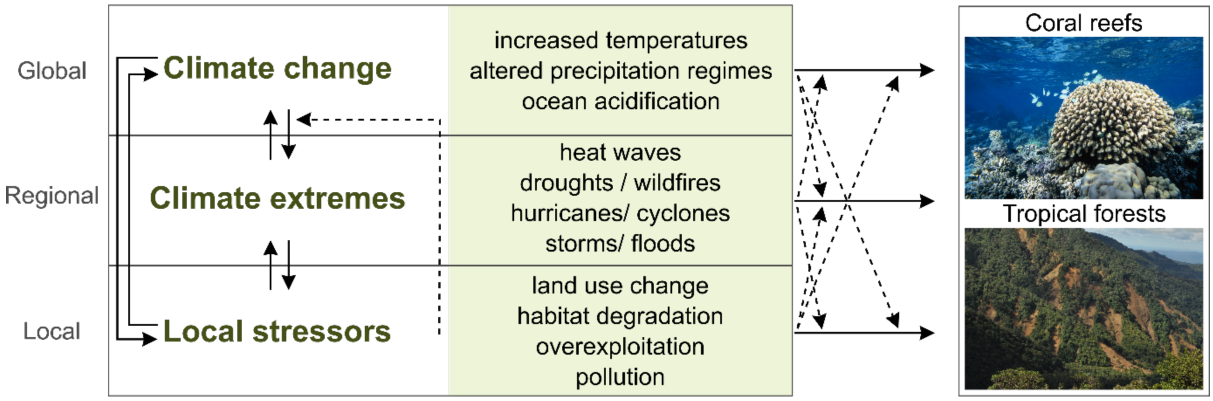

Figure 3. Framework of interactive effects between climatic and anthropogenic stressors on tropical forests and reefs. Interactions may occur through modification effects, whereby the impacts per capita/per unit of one stressor is influenced by another pressure (dashed arrows), or through chain effects that may occur when both stressors have a direct influence, with one amplifying the severity of the other (adapted from the framework proposed by Didham et al.[18]). Photos represent a coral bleaching event in Moorea and landslides after massive thunderstorms in Peruvian cloud forests, by K. Chong-Seng and M. Dehling, respectively.