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Review

Altered cyclone–fire interactions are changing ecosystems

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Global change is altering interactions between ecological disturbances. We review interactions between tropical cyclones and fires that affect woody biomes in many islands and coastal areas. Cyclone-induced damage to trees can increase fuel loads on the ground and dryness in the understory, which increases the likelihood, intensity, and area of subsequent fires. In forest biomes, cyclone–fire interactions may initiate a grass–fire cycle and establish stable open-canopy biomes. In cyclone-prone regions, frequent cyclone-enhanced fires may generate and maintain stable open-canopy biomes (e.g., savannas and woodlands). We discuss how global change is transforming fire and cyclone regimes, extensively altering cyclone–fire interactions. These altered cyclone–fire interactions are shifting biomes away from historical states and causing loss of biodiversity.

Highlights

Tropical cyclone–fire interactions are key drivers of the distribution, composition, and dynamics of woody biomes on islands and in coastal regions.

Cyclone-induced damage to trees can increase fuel loads on the ground and dryness in the understory, which in turn increase the likelihood, intensity, and area of subsequent fires.

Historically, cyclone–fire interactions have been rare in closed-canopy forests, but have maintained open-canopy savanna and woodland biomes via cyclone-enhanced fires.

Global change is modifying cyclone and fire regimes worldwide, producing increased frequencies and intensities of cyclone–fire interactions that change biomes and their distributions.

Increased frequencies and intensities of cyclone–fire interactions shift closed-canopy forests into open, degraded biome states and open-canopy savannas and woodlands into treeless grasslands.

Interacting disturbances are key ecological and evolutionary drivers

Disturbances (see Glossary) such as **tropical cyclones** and fires recurrently affect many terrestrial woody ecosystems. These disturbances often damage or kill individual woody plants, but populations of most species usually persist [1]. At the ecosystem scale, a range of post-disturbance states and altered ecosystem dynamics can result [2,3]. Over the long term, recurrent disturbances may cause evolutionary adaptations of resident biota [1,2] and result in feedbacks on environmental drivers [4], which together create **disturbance regimes**. Such evolutionary responses may generate and maintain **alternative biome states** [3,5].

Co-occurring disturbances can produce interactive effects when a disturbance affects an ecosystem that has yet to fully recover from a previous disturbance (i.e., has not returned to some predisturbance state) [6] (Figure 1). These interactions can be synergistic (amplifying effect), antagonistic (buffering effect), or neutral [6]. The initial disturbance can change the likelihood and characteristics of the subsequent one ('linked' disturbances) or produce effects that change the **resistance** and **resilience** of ecosystems to the subsequent disturbance ('compound' disturbances) [7]. When disturbances co-occur frequently, their interactions may favor adaptations that maintain **biome** states. By contrast, when disturbances co-occur infrequently, synergistic interactions might cause greatly magnified effects that result in altered recovery trajectories or changed biome states [7–9].

Ongoing global changes are altering disturbance regimes and, hence, their interactive effects. Humans have directly altered natural disturbance regimes by introducing novel disturbances or suppressing historical disturbances [10] and indirectly by changing land use, local environments, and global climate [9]. As a consequence, new interactions among disturbances are emerging and increasing in frequency globally in the Anthropocene [11]. These changes in the frequency, extent, and nature of interactions among disturbances can influence the state, distribution, and

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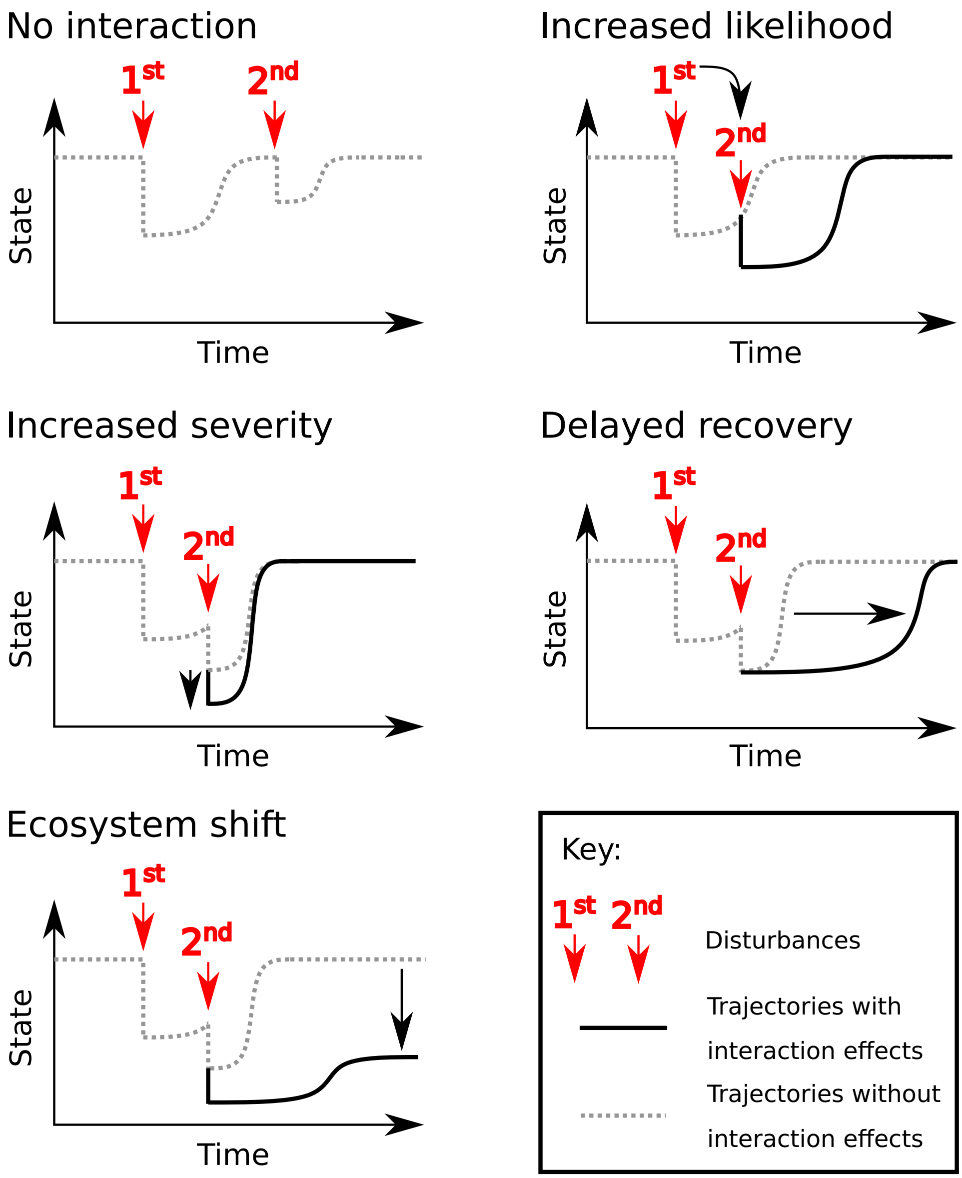

Figure 1. Example of potential synergistic interaction effects between two disturbances (e.g., a tropical cyclone and a fire) on an ecosystem (e.g., a forest). Disturbances affect the state of the ecosystem (i.e., its structure, e.g., number of standing, alive trees), composition (e.g., richness of species), and functioning (e.g., productivity).

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dynamics of ecosystems with long-lasting impacts on biodiversity [12] and ecosystem services [13] if **tipping points** are exceeded [14,15].

Here, we review the role of tropical cyclones and fires as major interacting disturbances in woody ecosystems. Previous reviews have considered tropical cyclones [16–18] and fires [3,19] in isolation, potentially missing important ecosystem impacts that result from their interactions. We first identify those regions where tropical cyclones and fires co-occur and then summarize evidence for interactive effects on woody ecosystems. We use this evidence to develop conceptual models of cyclone–fire interactions that provide mechanistic insights into how woody ecosystems might be impacted. We postulate that altered cyclone–fire interactions can alter the distribution and composition of ecosystems and biomes, especially on islands and in coastal regions where these disturbances occur frequently.

The co-occurrence of tropical cyclones and fires

Tropical cyclones originate over warm tropical oceans but commonly make landfall. They generate high intensity winds (from 119–153 $km.h^{-1}$ for category 1 cyclones to ≥252 $km.h^{-1}$ for category 5 cyclones [20]) and heavy rainfall over large areas. Immediate impacts on woody vegetation range from defoliation to extensive stem snapping or uprooting [13,21]. Tropical cyclones mainly occur in six well-defined basins (Figure 2A). Cyclone-prone terrestrial regions (defined here as regions located <150 km from the paths of category ≥1 tropical cyclones over the past 40 years) encompass more than 6.2 million km^2 (Mkm^2; i.e., about 4% of global land area;

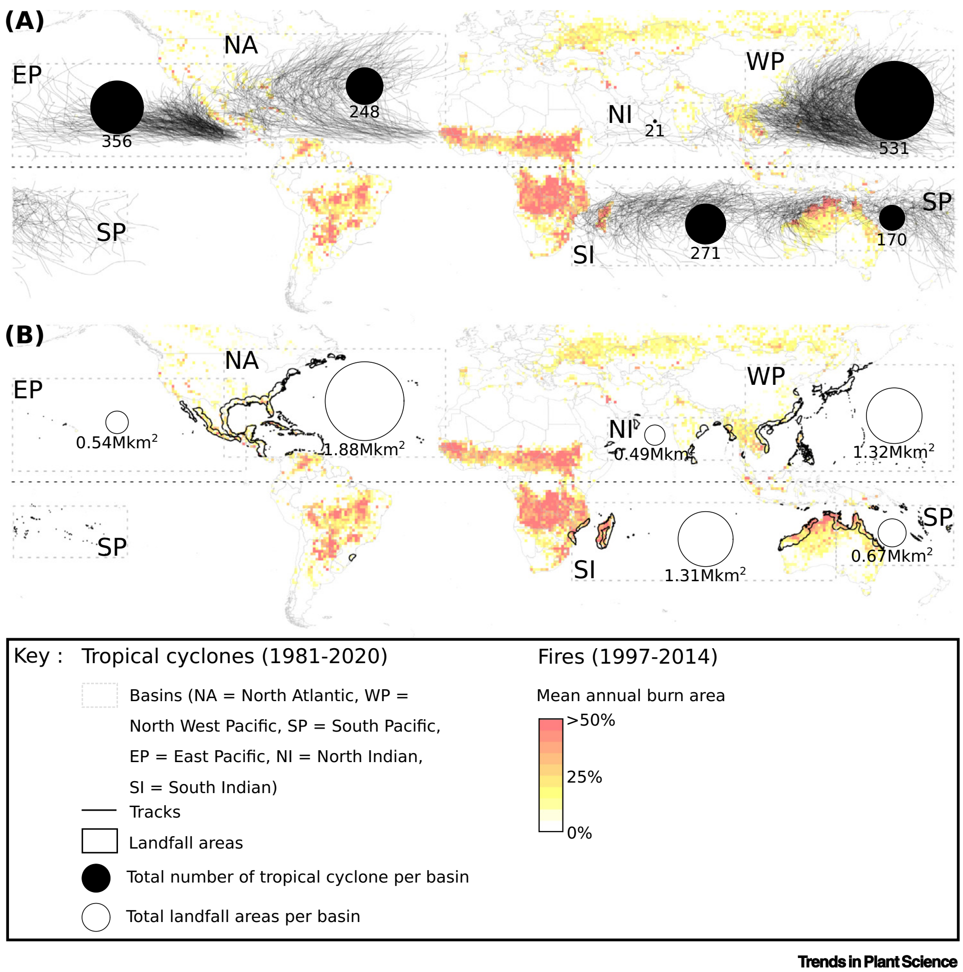

Figure 2. Tropical cyclone and fire co-occurrence. (A) Trajectories of tropical cyclones reaching category 1 or higher [20] at some point on their tracks between 1981 and 2020 [22]. (B) Landfall areas computed using a 150 km buffer area around the centers of ≥ category 1 tropical cyclones [102]. In (A) and (B) burn area represents the average annual burned area between 1997 and 2014 [103]. Maximum burned area was set as >50% to highlight contrasts among different regions. Abbreviation: Mkm^2, million km^2.

Glossary

Alternative biome states: the alternative biome states theory proposes that different biome states (e.g., tropical wet forest and savanna) can be stable in a given area (i.e., for a given climate). Biome states are stabilized by feedback processes but can shift from one state to another when certain ecological thresholds (see tipping point definition) are surpassed (e.g., canopy cover allowing or impeding the growth of flammable grasses).

Biomes: regional biogeographic areas of homogeneous vegetation types (e.g., tropical wet forest and savanna), which exist in equilibrium with climate (temperature and precipitation) and soil. Note that, on a smaller spatial scale, different stable biome states can exist for a given set of environmental conditions (see alternative biome states definition).

Disturbance regime: the spatio-temporal characteristics of disturbances in a given area or ecosystem (i.e., frequency, extent, intensity, timing).

Disturbances: discrete events in time and space that disrupt ecosystems, communities, and their populations, impacting vegetation structure and dynamics. Disturbances change resource availability (e.g., light in the understory) and the physical environment (e.g., microclimate).

Fire-trap: in frequently burned areas (e.g., tropical savannas), the fire-trap describes the repeated fire-induced death of above-ground biomass (topkill), preventing recruitment of woody plants into adult sizes.

Resilience: the capacity of an ecosystem to recover to its original state (composition, structure, function) after a disturbance. Ecosystem resilience depends on the ability of the ecosystem to both resist and recover from disturbance-induced change. Ecosystem resilience can be measured by recovery time, the time needed to reach the original state after a disturbance (the higher the resilience, the shorter the recovery time).

Resistance: the capacity of an ecosystem to be exposed to a disturbance without being disturbed.

Severity: the degree to which a disturbance affects an ecosystem. Disturbance severity can be measured by disturbance-induced mortality rate or reduction in vegetation biomass. Severity depends on both the characteristics of the disturbance (e.g., its intensity) and

Figure 2B), often with at least one cyclone per decade [22]. The North Atlantic basin contains the largest area of cyclone-prone land (1.88 Mkm^2 between 1981 and 2020), while the northwest Pacific has the greatest frequency of tropical cyclones (531 tropical cyclones between 1981 and 2020).

Fires are widespread disturbances in many terrestrial ecosystems. Lightning strikes are globally the most common natural (i.e., non-anthropogenic) cause of fires and occur most densely in the North Atlantic and East Pacific basins [23]. Climate and weather interact with vegetation to generate natural fire regimes [24–26]. However, fire regimes have become increasingly associated with human ignition and modified fuel loads in the Holocene and Anthropocene [3,27]. Notably, humans have altered fire regimes by introducing fire to locations where and at times when lightning-ignited fires were unlikely or, conversely, by suppressing fire at locations and at times that lightning-ignited fires were likely. For example, in northern coastal Australia, burned areas are larger than expected for the density of lightning given human ignition [13,28]. Conversely, in the North American Coastal Plain, burned areas are currently smaller than expected based on lighting density because of land-use changes and fire suppression, resulting in few naturally ignited fires and a high density of small, prescribed fires [26,27].

The likelihood and effects of interactions between tropical cyclones and fires are likely to differ among cyclone basins and dominant biomes, as a function of both the disturbance regime and how tropical cyclones can modulate the historic limits to fire in these biomes. For example, areas dominated by tropical wet forest, the most common biome in cyclone-prone regions (35% of the total area, see Figure S1 in the supplemental information online), are characterized by rare, small, low-intensity fires [29] primarily limited by high fuel moisture [30] maintained under closed tree canopies. Areas dominated by tropical savanna, which cover 15% of cyclone-prone regions, are characterized by frequent, larger, and higher-intensity fires [29] primarily limited by grass biomass and leaf litter fuel loads in more wooded savannas [30,31]. We therefore hypothesized that tropical cyclones, which mostly affect trees, should have greater effects on fires in tropical wet forests than in tropical savannas. Furthermore, given that fires are rare in tropical wet forests, tropical cyclone-driven fires should have much more dramatic effects in wet forests than in tropical savannas.

Interactions between tropical cyclones and fires

Determining the nature of the interactions between tropical cyclones and fires is challenging. For example, although fires that follow tropical cyclones increase tree mortality rates in forests [32,33], it is unclear if the cyclone- and the fire-induced mortality is additive or if there are interactions. Furthermore, the type of interaction can vary. Cyclone-caused mortality and fallen debris could add flammable fuels, thereby augmenting fire intensities and fire-induced mortality (linked interaction). Alternatively, a cyclone or a fire could render the subsequent disturbance more severe because damage caused by the first disturbance lowered the resistance of established trees or favored the establishment of less resistant trees (compound interaction). Therefore, disentangling the nature of interactions may require considering the temporal order of the two disturbances.

Tropical cyclone followed by fire

Tropical cyclones open forest canopies. This often results in a drier microclimate in the understory [34], which decreases fuel moisture and promotes fire spread. This process is particularly critical in tropical wet forest, where fires are typically rare and fuel moisture is the principal factor limiting fires [30]. Fuel moisture is strongly associated with vapor pressure deficits (VPD). VPD lower than 0.75 kPa strongly inhibit the spreading of fires into forest understory [35]. In an Australian tropical wet forest, VPD more than doubled after a category 2 cyclone, with values exceeding the

of the species (their capacity to resist the disturbance or avoid it).
Tipping point: a threshold at which, after a disturbance, a self-propagated change causes a rapid shift from one ecosystem or biome state to another.
Tropical cyclones: disturbances also referred to as hurricanes in the Atlantic and northeast Pacific and typhoons in the northwest Pacific. Tropical cyclones are intense windstorms that originate over warm tropical oceans. They are characterized by a circular rotating structure with warm cores, an ‘eye’ of low pressure, and radii that can reach 200 km or more. They affect the entire troposphere, generating very high wind speeds (>33 $m.s^{-1}$ within 150 km from the cyclone eye) and large rainfall bands.

0.75 kPa fire-suppression threshold [36]. Such an increase in VPD can persist for years. For example, 5 years after a category 5 cyclone, VPD across tropical wet forests in Honduras remained higher in more disturbed areas [37]. In addition, more open canopies increase light availability and understory light levels may take 2–10 years to decline to precyclone levels [38,39]. Prolonged increased in light levels at ground level may promote the establishment and growth of light-demanding flammable grasses in wet forest [40], with potentially large impacts on the fire regime [1].

Damage caused by tropical cyclones can also generate large amounts of dead fuel for fires. In wet and dry forests, major cyclones (≥ category 3) increase annual fall of litter and woody material more than threefold compared with years without cyclones [33,39,41]. Furthermore, 3 years after a tropical dry forest in Mexico was disturbed by a category 5 cyclone, the mass of fine woody debris on the forest floor generated by the cyclone remained more than twice that of undisturbed areas [42]. Greater fuel loads and altered microclimates caused by cyclones have been widely suggested to increase the likelihood of fires in cyclone-affected woody ecosystems [32,33,43–50]. So far, the only evidence supporting this was reported from northern Australian savannas, where the fuel load generated by a category 5 cyclone increased fire frequency over 10 400 km^2 for 4 years after the cyclone [51].

Tropical cyclones can also indirectly increase the likelihood of fires by increasing the incidence of human ignition and the likelihood of grassland fires being carried into forests. This phenomenon is common where people depend on slash-and-burn agriculture or forest resources for livelihoods (e.g., in Samoa [32], Madagascar [50], Papua New Guinea [49], and the Philippines [47]). After cyclones, damaged forests may be burned to provide ash beds for planting new crops and for easier access to forest resources. Fire might also be used to control invasion by non-native grasses after cyclones and these fires can spread into nearby forest [49]. Cyclone–fire interactions can also be exacerbated by timber extraction, which leaves additional coarse woody debris in forests after logging (e.g., when a cyclone and fire affected tropical dry forests in the Yucatán Peninsula [33]).

Postcyclone fires can arrest or retard natural recovery processes, produce transitions from forests to more open biomes types, and facilitate invasion by non-native plant species (Figure 3). For instance, cyclone–fire interactions due to fires following a category 4 cyclone in Madagascar resulted in extensive tropical dry forest loss in Kirindy-Mitea National Park (KMNP) [52]. The cyclone affected a large area of forest in KMNP, damaging most trees and killing about 14% of trees larger than 10 cm in diameter [53]. However, most forest loss was caused by uncontrolled fires during the dry season that spread from adjacent agricultural land into cyclone-damaged forest [50]. Similar processes of forest loss occurred in the Mikea National Park (200 km south of KMNP) after a category 3 cyclone [50].

Cyclones followed by fires in tropical wet forests can also result in greater incidence of invasions by non-native plant species than occurs after cyclone disturbance alone [54]. For example, part of a lowland tropical wet forest in Samoa that was affected by a category 3 cyclone was subsequently burned. Mortality of native trees was up to 90% in areas affected by the cyclone and fire versus only up to 50% in areas not affected by the fire [32]. Non-native trees colonized over the next 5 years and were abundant 10 years later in areas affected by the cyclone and fire (G. Keppel, personal observation). In Australian tropical wet forests, non-native flammable grasses colonized areas affected by cyclones and subsequent fires, supporting an enduring fire–grass cycle [55].

Slower recovery and altered recovery trajectories of forests after cyclones and subsequent fires are also documented in paleoecological records. In savannas of the North American Coastal

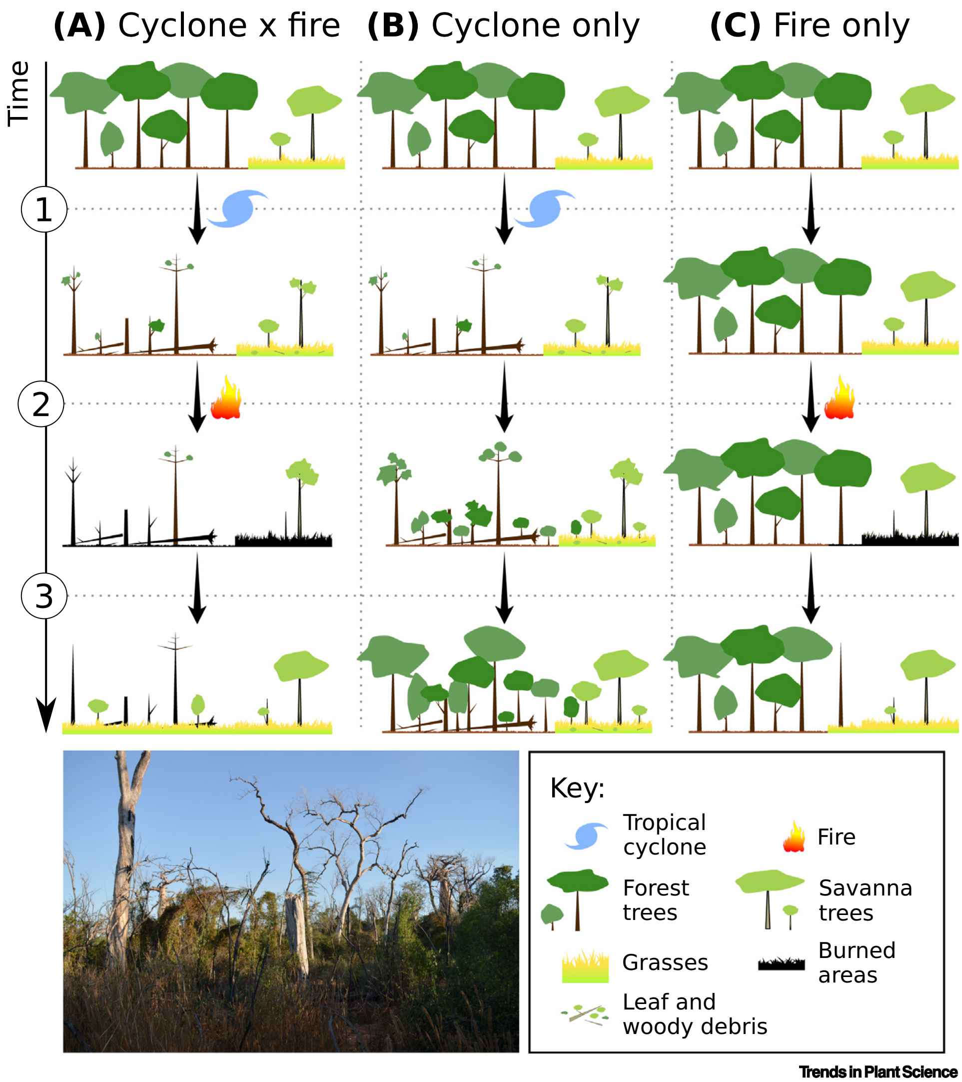

Figure 3. Effects over time of a tropical cyclone followed by a fire (A), a cyclone alone (B), or a fire alone (C) on a forest located adjacent to a savanna woodland. Vertical sequences indicate postulated changes beginning with an intact forest. (A) A tropical cyclone opens the canopy of a forest (A1), increasing the fuel load and lowering fuel moisture. If a fire is ignited or spreads into the forest from the savanna it further increases forest tree mortality (A2). The altered forest might shift to an alternative savanna biome state if invaded by flammable vegetation supporting recurrent fires (A3). (B) A tropical cyclone opens the canopy of a forest (B1), increasing the fuel load and lowering fuel moisture. Without the subsequent fire, the forest recovers by resprouting of surviving trees and recruitment of new trees (B2), reforming a closed canopy forest, and potentially spreading into adjacent savanna woodland (B3). (C) Without the tropical cyclone (C1), fire burns adjacent savanna woodland, but spreads only into the edge of the forest (C2), potentially shifting the savanna–forest transition with recurrent fires (C3). The photograph shows standing dead trees and regrowing low vegetation 7 years after the passage of tropical cyclone Fanele (category 4, 2009) and subsequent fires (within a year after the cyclone) that shifted the dry forest toward savanna in the Kirindy-Mitea National Park (Madagascar).

Plain, the recovery of pine populations from intense cyclones has been retarded at times during the past 1200 years by subsequent intense fires [56]. In Nicaragua, recovery of a tropical lowland wetland forest from cyclone damage 3350 years ago took over 500 years because of subsequent repeated fires [57].

Fire followed by tropical cyclone

Fires can directly increase impacts of subsequent tropical cyclones by damaging trees and changing the composition and structure of tree communities, reducing their resistance to cyclones. In New Caledonian tropical wet forests and shrublands, trees affected by earlier fires appeared to be less resistant to cyclonic winds than unburned trees, perhaps because of damage to their wood structure. In populations of two *Araucaria* species, only a third of trees had fire scars, but all the trees snapped or uprooted by two category 4 cyclones had fire scars [58]. In Tonga, tree mortality related to a category 3 cyclone was higher in previously burned than unburned tropical wet forests [45,54]. This synergistic interaction was attributed to a precyclone fire favoring the recruitment of fast-growing pioneer species with low wood density, which then exhibited higher cyclone-induced damage and mortality. Fires can also increase spacing among trees, which could make them more susceptible to wind damage, as suggested by higher mortality of oaks in burned compared with unburned Florida panhandle savannas during and after cyclones (categories 2 and 4) [59].

The effects of fires on the **severity** of impacts by a subsequent tropical cyclone may change with environmental conditions. For example, in south Florida, the mortality of savanna pines after a category 5 cyclone was higher in areas that had been burned during the dry season than in those that had been burned in the wet season or not burned at all [60]. Pines in savannas burned during the dry season exhibited faster growth, resulting in lower-density wood, and lower resistance to cyclonic winds. Another potential indirect effect is that fires are more likely to kill smaller, shorter trees, leaving a higher proportion of taller trees, which in turn are more likely to be killed by cyclones.

Cyclone–fire interactions and the maintenance and shifts of biome states

Together with climate, disturbances have long been recognized as influencing species distributions and biome states. In tropical and warm temperate regions, the role of disturbances by fires in maintaining open savannas and woodlands over closed forests in areas receiving intermediate or seasonal rainfall is well established [5,26,61–63], but the role of cyclones in this dynamic is less clear. Open-canopy, woody biomes with flammable grass layers often support frequent fires during dry seasons. These fires reduce tree establishment to the extent that open canopies are maintained, which in turn supports flammable grass layers and results in a phenomenon known as the **fire-trap** [64,65]. In more woody savannas leaf litter and woody debris contribute to a substantial proportion of the fuel load [31], especially after tropical cyclones [66,67]. By increasing fuel load and continuity, cyclones increase the intensity and size of subsequent fires. In regions where cyclones and fires are frequent, resultant cyclone-fueled fire regimes are likely to play a key role in producing and maintaining savannas and woodlands by opening the canopy and promoting the recruitment of shade-intolerant species (Figure 4).

However, open-canopy woody biomes can shift toward closed canopy states during extended intervals without fires, either as a result of natural phenomena (e.g., climatic fluctuations, variation in the number of lightning strikes, or successive exceptionally wet years) or because of fire suppression by humans. Trees then escape the fire-trap and grow in size. In absence of fire, a 'fire suppression threshold' is reached [67], where the canopy is sufficiently closed to suppress the flammable grass layer and maintain cooler and wetter understory microclimates, which greatly reduces the likelihood of fire and allows a closed canopy to be maintained. Such dynamics can result in patches of forest imbedded in savannas or can result in dynamic boundaries between savanna woodland and forest habitats (Figure 4).

Such closed-canopy biomes have been suggested to shift back to open-canopy ecosystems when, during exceptionally dry periods, multiple fires occur and kill enough trees to allow a

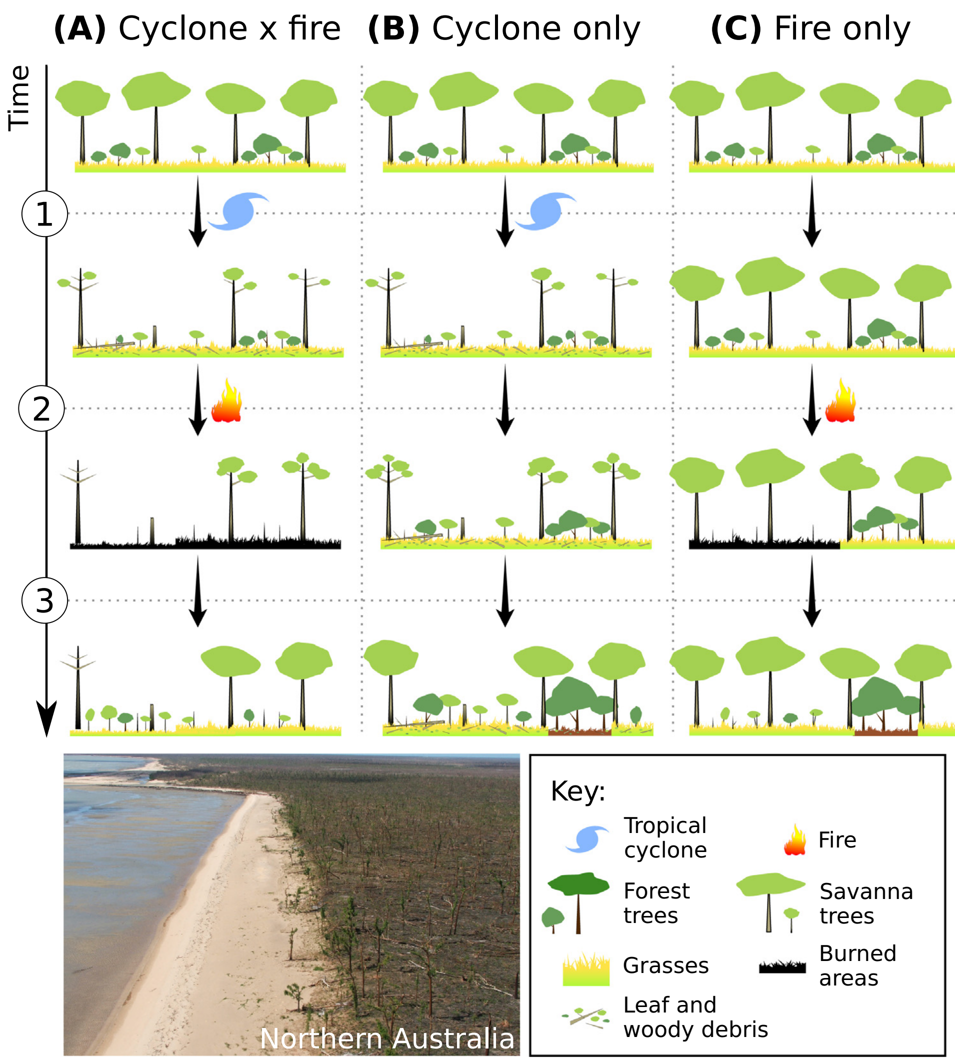

Figure 4. Effects over time of a tropical cyclone followed by a fire (A), a cyclone alone (B), or a fire alone (C) on a savanna woodland with imbedded patches of forest. Vertical sequences indicate postulated changes beginning with an intact savanna woodland. (A) A tropical cyclone opens the canopy of a savanna woodland (A1), increasing fuel loads and continuity. Cyclone-enhancement of fires ignited or spreading into the savanna woodland increases fire intensity and continuity across the landscape, consuming most fuels and depressing ground-layer vegetation (A2). Therefore, subsequent fires are fuel limited and less intense, promoting recruitment of new cohorts of savanna trees and potential spread of savanna woodland into adjacent forest (A3). (B) A tropical cyclone opens the canopy of a savanna woodland (B1). Without subsequent fire, most trees survive and recover. Regrowth and recruitment of canopy savanna woodland trees occurs and recruitment of forest trees occurs in patches, especially close to adjacent forest (B2). If the interval between two fires is long enough, the canopy suppresses the flammable ground-layer vegetation, shifting the system toward forest, especially in patches colonized by forest trees (B3). (C) Without the tropical cyclone (C1), the fire is less intense, top-killing small or less resistant trees. Such fires often leave some unburned patches, especially close to forests (C2). Such fires thus can result in patches of forest trees in savanna woodlands (C3). The photograph shows coastal savanna woodlands in northern Australia where the impacts of category 5 tropical cyclone Monica in 2006 followed by fires maintained an open canopy.

more flammable vegetation to re-establish [5]. We propose that, in cyclone-prone regions with seasonal climate, tropical cyclone disturbances should be a key driver of maintaining open canopies or reopening more closed canopies, thereby promoting subsequent fires [26,68].

Box 1. Tropical cyclone modifications of frequent fires drive tree population dynamics in North American Coastal Plain savannas

Historically, pine-dominated savanna-woodland habitats (Figure IA) characterize southeastern upland regions in the North American Coastal Plain biodiversity hotspot [12]. In this biome, multiple lightning-ignited, ground-layer fires occur per decade [93]. These low-intensity fires are modified by tropical cyclones that make landfall every few years [93,94]. Recurrent cyclone–fire interactions alter fire characteristics across landscapes [60,66] and localized effects produced during more intense cyclones generate discrete patches in the ground layer at decade-long intervals [68,90]. These cyclone-altered fire regimes affect tree dynamics.

Tropical cyclone winds considerably augment litterfall of pyrogenic pine needles [66,95] across landscapes. Elevated fuel loads, as much as 50% [68,96], increase intensities and durations of heating at ground level during subsequent fires [68], generating pervasive fire-traps for small trees [67]. Juvenile pines experience high mortality (up to 75% per fire) until they reach stages where terminal buds are protected [97,98]. Many hardwood species only recruit during infrequent longer fire-free intervals, reaching 1–2 meters in height before being top-killed by fires, but persist indefinitely via resprouting or clonal growth [99]. Some woody species may reach tree size in patches with lengthened fire return intervals [44,100]; others occur only as flowering shrubs in the ground layer [12,94]. In this biome, frequent cyclone-enhanced fires restrict hardwoods and pines to the ground layer, with only infrequent recruitment into the overstory.

Cyclone–fire interactions result in nonclonal, long-lived savanna pines being the predominant trees in this biome. Large pines typically experience almost no mortality from frequent, low-intensity fires [94,101]. During intense tropical cyclones, however, mortality of large savanna pines (Figure IB) reaches 25–50% [89,101]. Then, within the broadscale matrix of post-cyclone fires, smaller patches with pine stumps, branches, and crowns, which tend to contain large needle and wood mass, burn intensely (Figure IC), killing more large trees and suppressing ground-layer vegetation [90]. Subsequently, these cyclone-generated patches burn at much lower intensity [90], facilitating pine recruitment (Figure ID) and generating patches of overstory trees (Figure IE).

Cyclone-modified fire regimes maintain an open, fiery biome in the North American Coastal Plain. Frequent fires of cyclone-elevated intensity burn almost annually across landscapes, within which local patches of high-intensity fires periodically generate conditions facilitating recruitment and growth of pyrogenic savanna pines into the overstory. The resulting savanna–woodland ecosystems contain towering seas of signature pines above mega-diverse and flammable ground layers rich in complex arrays and mosaics of endemic C_4 grasses, forbs, and shrubs [12,64].

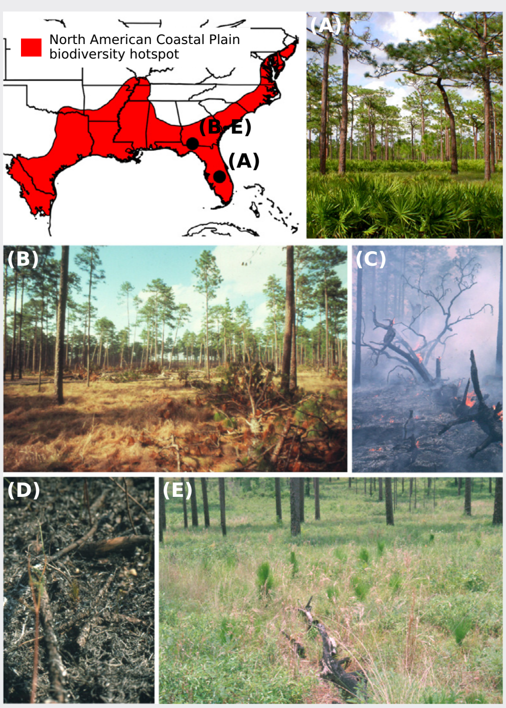

Figure I. Fire–tropical cyclone Interactions facilitate pines as the signature trees in the overstory of North American Coastal Plain savannas. (A) Old-growth longleaf pine savanna dominated by longleaf pine (*Pinus palustris*) and ground layer dominated by saw palmetto (*Serenoa repens*) and C_4 grasses in the Avon Park Air Force Range (Highlands County, FL, USA). (B) Category 2 tropical cyclone Kate (1985) increased fine fuel loads and killed ~15% of trees >50 cm diameter at breast height (the equivalent of 7–8 years of annual mortality) in the old-growth Wade Tract stand (Thomas County, GA, USA). (C) Aftermath of an intense ground-layer fire in the crown of a Kate-felled longleaf pine 2 years later (1987). (D) Two-year old pre-grass stage longleaf pine juvenile that germinated in the fall of 1987, following an intense fire that burned the crown of a Kate-felled pine in the spring of 1987 and then survived a low-intensity fire in 1989. (E) Cluster of grass-stage juveniles (inside crown of Kate-felled pine) emerging from ground layer and initiating height growth 15 years post-Kate (2000). Over three decades post-Kate, clusters of juveniles associated with Kate-felled trees that burned intensely have formed patches of overstory trees on the Wade Tract. High-intensity fires generated by the felling of trees during tropical cyclones shorten times between death of large pines and recruitment of new cohorts and shift stand structures toward smaller size classes. Such interactions modify pine population dynamics in ways that facilitate pines dominating the southeastern savanna-woodland biome. Photographs: W.J. Platt.

Therefore, cyclone–fire interactions may play a key role in maintaining biome states in these regions. Indeed, over 50% of the land area located in cyclone-prone regions (i.e., >3.1 Mkm^2 or ~2% of the total global land area) is equally likely to support open- (e.g., savannas, woodlands) or closed-canopy biomes (i.e., forests), according to the climate envelopes of global biomes [69].

The hypothesis that cyclone–fire interactions maintain open-canopy biomes with shade-intolerant tree populations as an alternative biome state to closed forest has been mostly studied in the North Atlantic basin. Here, tropical cyclones and fires generate very frequent interactive effects that drive biome states in the North American Coastal Plain (Box 1). Such interactions likely explain the persistence of pine savannas or woodlands along the coasts and islands of the North Atlantic basin [48,70–73], as well as the presence of shade-intolerant, wind-dispersed, native hardwood species in the forests of this region (e.g., mahogany trees in the Yucatán Peninsula forests; L. Snook, PhD thesis, Yale University, 1993). Similar interactive mechanisms could also maintain distinct biome states in other regions with frequent cyclones and fires and seasonal climates, particularly south-east Africa (Mozambique and Madagascar) and northern Australia, but further studies are required to confirm this.

Cyclone–fire interactions in a changing world

Over the past 40 years, the proportion of major tropical cyclones (categories 3–5) has increased and this trend is predicted to continue [74]. Observed poleward shifts in cyclone intensity maxima and landfalls [75,76] also appear to result directly from human-induced climate change [77,78]. These forecast changes in tropical cyclone trajectories and intensities might bring these disturbances to fire-prone ecosystems with little or no past experience of cyclones. For instance, winds generated by a tropical cyclone (Ophelia, category 2, in 2017) fueled massive fires in temperate and Mediterranean forests in the Iberian Peninsula [25], an area not historically prone to cyclones. Furthermore, climate change-related droughts are increasing fire frequencies and areas burned in many regions [79,80] and are producing more severe and widespread mega-fires [81,82].

Therefore, droughts and human actions are important factors likely to modulate tropical cyclone–fire interactions [83]. For instance, fires that occurred after wet forests on the Yucatán Peninsula were affected by a category 5 cyclone in 1988 would have been unlikely to be as large (c. 90 000 ha) or as intense without the effects of a postcyclone drought that dried the fuel and without uncontrolled fires in adjacent agricultural land that ignited the fire [84]. The general trends in both disturbance types suggest that tropical cyclone–fire interactions will occur more frequently, more intensely, and over expanded areas as climate change intensifies.

Cyclone-driven fires should have increasing effects in many temperate and tropical wet forests that historically only rarely experienced fires and therefore are mostly composed of fire-intolerant species. Such forests comprise the dominant biome in cyclone-prone regions globally. Increased cyclone–fire interactions in these forests are further promoted by continuing forest loss and fragmentation [85]. Indeed, fragmentation expands the interface between forests and open, fire-prone ecosystems, increasing the risk of fire entering forests, as well as promoting invasions of non-native plant species. Although impacts of cyclones on forest structure and fuel availability were identified as a potential source of changes in fire regimes more than 20 years ago [84], we still know little about the effects of changing cyclone–fire interactions on forests, especially in human-affected forests.

Human actions can modify the expected outcomes of cyclone–fire interactions through either increasing ignition rates or suppressing fires. For instance, in the North American Coastal Plain

(Box 1) predicted increases in lightning strikes [86] should interact with reduced and more variable precipitation to increase the length of lightning-ignited fire seasons [87,88]. Both increased lightning strikes and more intense tropical cyclones should increase mortality of large pine trees that dominate savannas [89] and, hence, promote the recruitment of new pines [90]. As fire frequencies and tropical cyclone intensities increase, a tipping point could be reached in which pine populations can no longer persist [91]. However, human actions such as fire suppression and altered fire regimes [26] diminish the cyclone–fire interactions that have maintained pine populations. Management practices, such as fire control, have been predicted to shift pine savannas toward hardwood forests due to decreases in prescribed fires [91,92] and changes in timing of ignition from natural lightning fires at the beginning of the wet season to anthropogenic fires occurring during the dry season [46,60]. As noted for other biomes [25], coastal plain pine savannas are therefore being transformed or lost as fire regimes are altered by humans.

Concluding remarks and future perspectives

Cyclone–fire interactions are changing worldwide in two ways. First, in forests where fires have been uncommon historically, increased fuel loads and dryness in the understory after canopy opening by tropical cyclones support fires that may convert forests into open biomes. Human ignitions are increasing fire frequencies and human activities that fragment forests and introduce flammable plants further increase fire intensity and frequency, making shifts to an alternative open biome more likely. With ongoing changes in tropical cyclone regimes due to climate change, understanding the local, regional, and global effects of tropical cyclones on the probability, extent, and intensity of subsequent fires is critical (see Outstanding questions). Second, historical interactions between tropical cyclones and fire have generated and maintained open biomes such as savannas and woodlands in fire- and cyclone-affected coastal and island regions worldwide. Although this hypothesis has been well studied in the North Atlantic basin, further investigations are needed to better understand the broader role of these interactions in maintaining open biomes across regions worldwide. Studies from the North Atlantic basin suggest that biomes influenced by cyclone–fire interactions are at conservation risk due to climate change and human manipulation of fire regimes. Generally, there is a critical need to develop concepts and approaches to manage both open- and closed-canopy woody biomes in the context of changing tropical cyclone and fire regimes.

Outstanding questions

How likely are tropical cyclone–fire interactions in closed- and open-canopy biomes in cyclone basins worldwide?

To what degree and under which environmental conditions (e.g., magnitudes of drought) do tropical cyclones increase the likelihood, intensity, and area of subsequent fires in closed- and open-canopy biomes?

How do climate change and human-induced changes in fire regimes alter cyclone–fire interactions? Are tropical cyclones more (or less) likely to increase the probability, extent, and/or intensity of subsequent fires in the future? If so, where?

What is the relative importance of cyclone–fire interactions in maintaining open-canopy biomes across tropical cyclone basins? How will changing frequencies and severities of fires and cyclones change the distribution of biomes?

How, where, and to what extent do fire-induced damages to trees increase the severity of subsequent tropical cyclones? Are fire-resistant species more or less susceptible than non-fire-adapted species?

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Declaration of interests

No interests are declared.

Supplemental information

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References

1. Johnstone, J.F. *et al.* (2016) Changing disturbance regimes, ecological memory, and forest resilience. *Front. Ecol. Environ.* 14, 369–378
2. Lin, T.-C. *et al.* (2020) Tropical cyclone ecology: a scale-link perspective. *Trends Ecol. Evol.* 35, 594–604
3. McLauchlan, K.K. *et al.* (2020) Fire as a fundamental ecological process: Research advances and frontiers. *J. Ecol.* 108, 2047–2069
4. Pausas, J.G. and Bond, W.J. (2022) Feedbacks in ecology and evolution. *Trends Ecol. Evol.* 37, 637–644
5. Pausas, J.G. and Bond, W.J. (2020) Alternative biome states in terrestrial ecosystems. *Trends Plant Sci.* 25, 250–263
6. Buma, B. (2015) Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere* 6, art70

7. Paine, R.T. *et al.* (1998) Compounded perturbations yield ecological surprises. *Ecosystems* 1, 535–545
8. Platt, W.J. and Connell, J.H. (2003) Natural disturbances and directional replacement of species. *Ecol. Monogr.* 73, 507–522
9. Turner, M.G. (2010) Disturbance and landscape dynamics in a changing world. *Ecology* 91, 2833–2849
10. Song, X.-P. *et al.* (2018) Global land change from 1982 to 2016. *Nature* 560, 639–643
11. Lewis, S.L. and Maslin, M.A. (2015) Defining the Anthropocene. *Nature* 519, 171–180
12. Noss, R.F. *et al.* (2015) How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. *Divers. Distrib.* 21, 236–244
13. Russell-Smith, J. *et al.* (2019) Tree recruitment dynamics in fire-prone eucalypt savanna. *Ecosphere* 10, e02649
14. Scheffer, M. *et al.* (2009) Early-warning signals for critical transitions. *Nature* 461, 53–59
15. van Nes, E.H. *et al.* (2016) What do you mean, 'tipping point'? *Trends Ecol. Evol.* 31, 902–904
16. Everham, E.M. and Brokaw, N.V.L. (1996) Forest damage and recovery from catastrophic wind. *Bot. Rev.* 62, 113–185
17. Lugo, A.E. (2008) Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecol.* 33, 368–398
18. Xi, W. (2015) Synergistic effects of tropical cyclones on forest ecosystems: a global synthesis. *J. For. Res.* 26, 1–21
19. Pausas, J.G. *et al.* (2017) Flammability as an ecological and evolutionary driver. *J. Ecol.* 105, 289–297
20. Simpson, R.H. (1974) The hurricane disaster potential scale. *Weatherwise* 27, 169–186
21. Uriarte, M. *et al.* (2019) Hurricane María tripled stem breaks and doubled tree mortality relative to other major storms. *Nat. Commun.* 10, 1362
22. Knapp, K.R. *et al.* (2010) The international best track archive for climate stewardship (IBTrACS). *Bull. Am. Meteorol. Soc.* 91, 363–376
23. Cecil, D.J. *et al.* (2014) Gridded lightning climatology from TRMM-LIS and OTD: dataset description. *Atmos. Res.* 135–136, 404–414
24. Archibald, S. *et al.* (2018) Biological and geophysical feedbacks with fire in the Earth system. *Environ. Res. Lett.* 13, 033003
25. Pausas, J.G. and Keeley, J.E. (2021) Wildfires and global change. *Front. Ecol. Environ.* 19, 387–395
26. Platt, W.J. *et al.* (2015) Seasonality of fire weather strongly influences fire regimes in South Florida savanna-grassland landscapes. *PLoS One* 10, e0116952
27. Syphard, A.D. *et al.* (2017) Human presence diminishes the importance of climate in driving fire activity across the United States. *Proc. Natl. Acad. Sci. U. S. A.* 114, 13750–13755
28. Russell-Smith, J. *et al.* (2007) Bushfires 'down under': patterns and implications of Australian landscape burning. *Int. J. Wildland Fire* 16, 361–377
29. Archibald, S. *et al.* (2013) Defining pyromes and global syndromes of fire regimes. *Proc. Natl. Acad. Sci. U. S. A.* 110, 6442–6447
30. Kelley, D.I. *et al.* (2019) How contemporary bioclimatic and human controls change global fire regimes. *Nat. Clim. Chang.* 9, 690–696
31. Russell-Smith, J. *et al.* (2021) Opportunities and challenges for savanna burning emissions abatement in southern Africa. *J. Environ. Manag.* 288, 112414
32. Elmqvist, T. *et al.* (1994) Effects of tropical cyclones Ofa and Val on the structure of a Samoan lowland rain-forest. *Biotropica* 26, 384–391
33. Whigham, D. *et al.* (1991) The impact of hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatán Peninsula. *Biotropica* 23, 434–441
34. Frenne, P.D. *et al.* (2021) Forest microclimates and climate change: importance, drivers and future research agenda. *Glob. Change Biol.* 27, 2279–2297
35. Ray, D. *et al.* (2005) Micrometeorological and canopy controls of fire susceptibility in a forested Amazon landscape. *Ecol. Appl.* 15, 1664–1678
36. Turton, S.M. and Siegenthaler, D.T. (2004) Immediate impacts of a severe tropical cyclone on the microclimate of a rain-forest canopy in north-east Australia. *J. Trop. Ecol.* 20, 583–586
37. Batke, S.P. and Kelly, D.L. (2014) Tree damage and microclimate of forest canopies along a hurricane-impact gradient in Cusuco National Park, Honduras. *J. Trop. Ecol.* 30, 457–467
38. Bellingham, P.J. *et al.* (1996) Changes in light below the canopy of a Jamaican montane rainforest after a hurricane. *J. Trop. Ecol.* 12, 699–722
39. Lin, K.-C. *et al.* (2017) Impacts of increasing typhoons on the structure and function of a subtropical forest: reflections of a changing climate. *Sci. Rep.* 7, 4911
40. Murphy, H.T. and Metcalfe, D.J. (2016) The perfect storm: weed invasion and intense storms in tropical forests. *Austral Ecol.* 41, 864–874
41. Imbert, D. and Portecop, J. (2008) Hurricane disturbance and forest resilience: assessing structural vs. functional changes in a Caribbean dry forest. *Forest Ecol. Manag.* 255, 3494–3501
42. Harmon, M.E. *et al.* (1995) Decomposition and mass of woody detritus in the dry tropical forests of the northeastern Yucatán Peninsula, Mexico. *Biotropica* 27, 305–316
43. Stocker, G.C. (1981) Regeneration of a North Queensland rain forest following felling and burning. *Biotropica* 13, 86–92
44. Myers, R.K. and van Lear, D.H. (1998) Hurricane-fire interactions in coastal forests of the south: a review and hypothesis. *Forest Ecol. Manag.* 103, 265–276
45. Franklin, J. *et al.* (2004) The effects of cyclone Waka on the structure of lowland tropical rain forest in Vava'u, Tonga. *J. Trop. Ecol.* 20, 409–421
46. Gilliam, F.S. *et al.* (2006) Natural disturbances and the physiognomy of pine savannas: a phenomenological model. *Appl. Veg. Sci.* 9, 83–96
47. Huigen, M.G.A. and Jens, I.C. (2006) Socio-economic impact of super typhoon Harurot in San Mariano, Isabela, the Philippines. *World Dev.* 34, 2116–2136
48. Gannon, B.M. and Martin, P.H. (2014) Reconstructing hurricane disturbance in a tropical montane forest landscape in the Cordillera Central, Dominican Republic: implications for vegetation patterns and dynamics. *Arct. Antarct. Alp. Res.* 46, 767–776
49. Goulding, W. *et al.* (2016) Cascading effects of cyclones on the biodiversity of Southwest Pacific islands. *Biol. Conserv.* 193, 143–152
50. Vieilledent, G. *et al.* (2020) It's not just poverty: unregulated global market and bad governance explain unceasing deforestation in Western Madagascar. *bioRxiv* Published online July 31, 2020. https://doi.org/10.1101/2020.07.30.229104
51. Hutley, L.B. *et al.* (2013) Impacts of an extreme cyclone event on landscape-scale savanna fire, productivity and greenhouse gas emissions. *Environ. Res. Lett.* 8, 045023
52. Vieilledent, G. *et al.* (2018) Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biol. Conserv.* 222, 189–197
53. Lewis, R.J. and Bannar-Martin, K.H. (2012) The impact of cyclone Fanele on a tropical dry forest in Madagascar. *Biotropica* 44, 135–140
54. Franklin, J. (2007) Recovery from clearing, cyclone and fire in rain forests of Tonga, South Pacific: vegetation dynamics 1995–2005. *Austral Ecol.* 32, 789–797
55. D'Antonio, C.M. and Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23, 63–87
56. Liu, K. *et al.* (2008) A 1200-year proxy record of hurricanes and fires from the Gulf of Mexico coast: testing the hypothesis of hurricane–fire interactions. *Quat. Res.* 69, 29–41
57. Urquhart, G.R. (2009) Paleoecological record of hurricane disturbance and forest regeneration in Nicaragua. *Quat. Int.* 195, 88–97
58. Rigg, L.S. (2005) Disturbance processes and spatial patterns of two emergent conifers in New Caledonia. *Austral Ecol.* 30, 363–373
59. Provencher, L. *et al.* (2001) Restoration fire and hurricanes in longleaf pine sandhills. *Ecol. Restor.* 19, 92–98

60. Platt, W.J. *et al.* (2002) Interactions of large-scale disturbances: prior fire regimes and hurricane mortality of savanna pines. *Ecology* 83, 1566–15721
61. Bond, W.J. *et al.* (2005) The global distribution of ecosystems in a world without fire. *New Phytol.* 165, 525–538
62. Staver, A.C. *et al.* (2011) The global extent and determinants of savanna and forest as alternative biome states. *Science* 334, 230–232
63. de Dantas, V.L. *et al.* (2016) Disturbance maintains alternative biome states. *Ecol. Lett.* 19, 12–19
64. Beckage, B. *et al.* (2011) Grass feedbacks on fire stabilize savannas. *Ecol. Model.* 222, 2227–2233
65. Hempson, G.P. *et al.* (2019) Alternate grassy ecosystem states are determined by palatability–flammability trade-offs. *Trends Ecol. Evol.* 34, 286–290
66. Ellair, D.P. and Platt, W.J. (2013) Fuel composition influences fire characteristics and understory hardwoods in pine savannas. *J. Ecol.* 101, 192–201
67. Hoffmann, W.A. *et al.* (2012) Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecol. Lett.* 15, 759–768
68. Platt, W.J. *et al.* (2016) Pyrogenic fuels produced by savanna trees can engineer humid savannas. *Ecol. Monogr.* 86, 352–372
69. Whittaker, R.H. (1975) *Communities and Ecosystems* (2nd edn), Collier Macmillan
70. Martin, P.H. *et al.* (2007) Tropical montane forest ecotones: climate gradients, natural disturbance, and vegetation zonation in the Cordillera Central, Dominican Republic. *J. Biogeogr.* 34, 1792–1806
71. Myers, R.L. and Rodríguez-Trejo, D.A. (2009) Fire in tropical pine ecosystems. In *Tropical Fire Ecology: Climate Change, Land Use, and Ecosystem Dynamics* (Cochrane, M.A., ed.), pp. 557–605, Springer
72. Franklin, J. and Steadman, D.W. (2013) Winter bird communities in pine woodland vs. broadleaf forest on Abaco. *Caribb. Nat.* 3, 1–18
73. Crausbay, S.D. and Martin, P.H. (2016) Natural disturbance, vegetation patterns and ecological dynamics in tropical montane forests. *J. Trop. Ecol.* 32, 384–403
74. IPCC (2021) In *Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change* (Masson-Delmotte, V. *et al.*, eds), pp. 1–3949, Cambridge University Press
75. Kossin, J.P. *et al.* (2014) The poleward migration of the location of tropical cyclone maximum intensity. *Nature* 509, 349–352
76. Altman, J. *et al.* (2018) Poleward migration of the destructive effects of tropical cyclones during the 20th century. *Proc. Natl. Acad. Sci. U. S. A.* 115, 11543–11548
77. Knutson, T. *et al.* (2019) Tropical cyclones and climate change assessment: part I: detection and attribution. *Bull. Am. Meteorol. Soc.* 100, 1987–2007
78. Knutson, T. *et al.* (2020) Tropical cyclones and climate change assessment: part II: projected response to anthropogenic warming. *Bull. Am. Meteorol. Soc.* 101, E303–E322
79. Flannigan, M.D. *et al.* (2009) Implications of changing climate for global wildland fire. *Int. J. Wildland Fire* 18, 483–507
80. Mariani, M. *et al.* (2018) Climate change amplifications of climate-fire teleconnections in the southern hemisphere. *Geophys. Res. Lett.* 45, 5071–5081
81. Jones, G.M. *et al.* (2016) Megafires: an emerging threat to old-forest species. *Front. Ecol. Environ.* 14, 300–306
82. Gallagher, R.V. *et al.* (2021) High fire frequency and the impact of the 2019–2020 megafires on Australian plant diversity. *Divers. Distrib.* 27, 1166–1179
83. Smith-Martin, C.M. *et al.* (2022) Hurricanes increase tropical forest vulnerability to drought. *New Phytol.* 235, 1005–1017
84. Goldammer, J.G. (1992) Tropical forests in transition. Ecology of natural and anthropogenic disturbance processes — an introduction. In *Tropical Forests in Transition: Ecology of Natural and Anthropogenic Disturbance Processes* (Goldammer, J.G., ed.), pp. 1–16, Birkhäuser
85. Fischer, R. *et al.* (2021) Accelerated forest fragmentation leads to critical increase in tropical forest edge area. *Sci. Adv.* 7, eabg7012
86. Romps, D.M. *et al.* (2014) Projected increase in lightning strikes in the United States due to global warming. *Science* 346, 851–854
87. Prestemon, J.P. *et al.* (2016) Projecting wildfire area burned in the south-eastern United States, 2011–60. *Int. J. Wildland Fire* 25, 715–729
88. Fill, J.M. *et al.* (2019) Climate change lengthens southeastern USA lightning-ignited fire seasons. *Glob. Change Biol.* 25, 3562–3569
89. Gilliam, F.S. (2021) Impacts of tropical cyclones on longleaf pine ecosystems of Florida: tropical cyclogenesis, landfall frequencies, and climate change. *Front. Ecol. Evol.* 9, 8
90. Blanchard, M.D. and Platt, W.J. (2021) Ground layer microhabitats influence recruitment of longleaf pine in an old-growth pine savanna. *Am. Midl. Nat.* 185, 15–31
91. Beckage, B. *et al.* (2006) Modelling responses of pine savannas to climate change and large-scale disturbance. *Appl. Veg. Sci.* 9, 75–82
92. Kupfer, J.A. *et al.* (2020) Climate change projected to reduce prescribed burning opportunities in the south-eastern United States. *Int. J. Wildland Fire* 29, 764–778
93. Platt, W.J. (1999) Southeastern pine savannas. In *The Savanna, Barren, and Rock Outcrop Communities of North America* (Anderson, R.C. *et al.*, eds), pp. 23–51, Cambridge University Press
94. Platt, W.J. *et al.* (1988) The population dynamics of a long-lived conifer (*Pinus palustris*). *Am. Nat.* 131, 491–525
95. Gagnon, P.R. *et al.* (2010) Does pyrogenicity protect burning plants? *Ecology* 91, 3481–3486
96. Harms, K.E. *et al.* (2017) Groundcover community assembly in high-diversity pine savannas: seed arrival and fire-generated environmental filtering. *Ecosphere* 8, e01716
97. Grace, S.L. and Platt., W.J. (1995) Effects of adult tree density and fire on the demography of pre-grass stage juvenile longleaf pine (*Pinus palustris* Mill.). *J. Ecol.* 95, 75–86
98. Knapp, B.O. *et al.* (2018) Fire effects on a fire-adapted species: response of grass stage longleaf pine seedlings to experimental burning. *Fire Ecol.* 14, 2
99. Drewa, P.B. *et al.* (2002) Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. *Ecology* 83, 755–767
100. Gilliam, F.S. and Platt, W.J. (1999) Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (Longleaf pine) forest. *Plant Ecol.* 140, 15–26
101. Platt, W.J. *et al.* (2000) Effects of hurricane Andrew on stands of slash pine (*Pinus elliottii* var. *densa*) in the everglades region of south Florida (USA). *Plant Ecol.* 146, 43–60
102. Chavas, D.R. and Emanuel, K.A. (2010) A QuikSCAT climatology of tropical cyclone size. *Geophys. Res. Lett.* 37, 1–4
103. Randerson, J.T. *et al.* (2015) *Global Fire Emissions Database, Version 4.1 (GFEDv4)*, ORNL DAAC