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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 b.vei

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

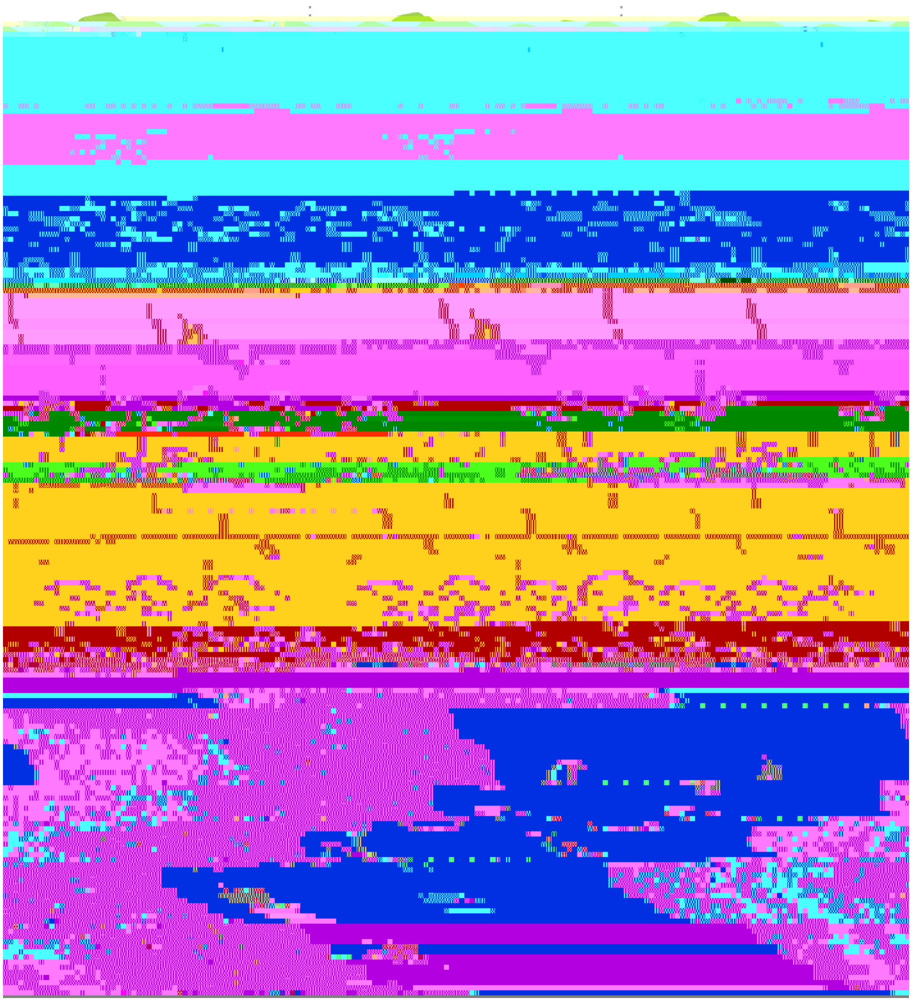
0.75 kPa fire-suppression threshold [36]. Such an increase in VPD can persist for years. For example, 5 years after a category 5 cyclone, VPD across tropical wet forests in Honduras remained higher in more disturbed areas [37]. In addition, more open canopies increase light availability and understory 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].

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

(A)



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, fi

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

(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 inten

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