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Review

Tropical Cyclone Ecology: A Scale-Link Perspective

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Tropical cyclones are increasing in intensity and size and, thus, are poised to increase in importance as disturbance agents. Our understanding of cyclone ecology is biased towards the North Atlantic Basin, because cyclone effects do differ across oceanic basins. Cyclones have both short and long-term effects across the levels of biological organization, but we lack a scale-perspective of cyclone ecology. Effects on individual trees, such as defoliation or branch stripping and uprooting, are mechanistically linked to effects at the community and ecosystem levels, including forest productivity and stand regeneration time. Forest dwarfing via the gradual removal of taller trees by cyclones over many generations illustrates that cyclones shape forest structure through the accumulation of short-term effects over longer timescales.

Highlights

Our understanding of cyclone ecology is biased toward the Atlantic Basin, but cyclone effects on forests differ among oceanic basins because of differences in storm frequency and strength.

Projected increases in cyclone frequency, intensity, and geographic distribution will threaten the tall old trees of the world, especially those in old-growth forests, which historically have few cyclones, such as those in the southeastern USA and southern Japan.

Cyclone effects on ecosystem processes, such as primary productivity and nutrient cycling, are mediated through the range of direct disturbance effects on individuals and species, such as defoliation and tree mortality.

Forest dwarfing, because of the gradual removal of tall trees by individual cyclones, illustrates the accumulative short-term effects of individual cyclones on shaping long-term forest structure.

Tropical Cyclones as Agents of Ecological Disturbance

Natural **disturbances** (see Glossary) have a key role in characterizing ecosystem structure and dynamics [1–4]. **Tropical cyclones**, as natural disturbances, influence ecosystem structure and function at the global scale. The increasingly warm sea surface temperatures that drive the convection necessary to produce and sustain tropical cyclones are likely to increase the intensity of tropical cyclones to unseen magnitudes [5–8], with increases in cyclone intensity potentially being strongest in the North Atlantic [9]. Moreover, the behavior of tropical cyclones is changing with climate change, with storms increasing in size [10] and geographic range [5,11], traveling at slower speeds [12] (Figure S1 and Table S1 in the supplemental information online), and carrying more rain, which increases their potential as agents of ecological disturbance.

Even though tropical cyclones are poised to have an increasingly important role in shaping ecosystems, we contend that most of our ecological understanding has come from studies that have focused on the most intense cyclones in the North Atlantic Basin. Moreover, a few cyclones dominate the literature on ecological disturbance, such as Hurricane Hugo (1989) in the Caribbean [13–16], Hurricane Katrina (2005) in the southeastern, USA [17,18], and Cyclone Larry (2006) in northeastern Australia [19,20], potentially biasing understanding toward the specifics of those storms. Between 1989 and 2018, 14% of cyclones (a total of 1490) occurred in the North Atlantic Basin; however, based on a search of published scientific papers using Web of Science, 67% of the studies (a total of 798) that investigated the impacts of cyclones on forests were conducted in the North Atlantic (Figure 1). In fact, the top eight most-studied cyclones, which comprise only 0.5% of cyclones occurring between 1989 and 2018, make up 36% of the studies on cyclone-induced forest disturbance, and are all North Atlantic Basin cyclones except for one, which was a Southwest Pacific Basin cyclone (Figure S2A in the supplemental information online). By contrast, during the same period, 32% of cyclones occurred in the Northwestern Pacific but only 18% of studies were conducted in this region, and only 5% of studies examined the effects of cyclones from the Indian Ocean, although 22% of the cyclones occurred in this region (Figure 1). The geographic bias toward the North Atlantic Basin is accompanied by a disproportional number of studies on intense cyclones. Cyclones in category 3 or greater on the Saffir-Simpson index

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comprise only 5.7% of cyclones globally but make up 66% of studies. Such a disproportional representation of intense cyclones is not present for other oceanic basins in the literature (Figure S2B in the supplemental information online). The bias is likely because intense cyclones tend to have greater effects on vegetation and, therefore, attract more studies (but see discussion on Ecosystem-Level Effects later).

The effects of cyclones on ecosystems have been shown to differ among the different oceanic basins [21]. For example, three category 3 (Saffir-Simpson scale) typhoons caused only 1.4% tree mortality in a forest in northeastern Taiwan [22] compared with 7–50% tree morality in the Luquillo Experimental Forest of Puerto Rico due to Hurricane Hugo, which was also a category 3 hurricane when it impacted the forest [23]. Moreover, many studies in the Caribbean have reported negative relationships between wood density and cyclone-driven tree damage [15,24], but no difference in wood density was found between fallen trees induced by typhoons and living trees in forests in northeastern Taiwan [25]. The differences in cyclone effects on forests among oceanic basins suggest that the distributional bias of cyclone studies toward the Atlantic Basin and the Southwest Pacific Basin is leading to an incomplete and biased understanding of cyclone ecology at the global scale. This may also skew our understanding of how future changes in cyclone disturbance regimes will affect forest ecosystems globally.

Cyclone Disturbance and Forest Ecosystems

Several papers have reviewed the ecological impacts of cyclones on the structure of forests [26–30]. While these papers summarize much of our understanding of the effects of cyclones on forests from a disturbance perspective, they do not explicitly address the role of ecological scale. A scale perspective is particularly important in disturbance ecology [31–34], because many disturbance effects, such as the effect of habitat modification on species diversity [35] and the effect of windthrow on forest structure, are scale dependent [36]. Here, we synthesize our understanding of the effects of cyclones on forests from the perspective of scale, both in terms of the level of biological organization and the temporal scale of the effects.

Tropical cyclones affect forest ecosystems and their constituent biota at various levels. Damage to individual plants can affect species and community-level dynamics and, thus, influences both the speed and trajectory of **forest regeneration** [15,27,37]. Variation in rates of forest regeneration alters the spatial patterns of landscape-level ecosystem structure and function [38–40]. We can advance our understanding of scale-dependent processes by looking at the impacts of cyclones with an emphasis on the linkages between and within levels of biological organization. For example, although linking the short-term (days to a few years) and long-term (decades to millennia) effects (Figure 2) of cyclone disturbance has been difficult, we believe that highlighting the links among scale-dependent processes in a cause-effect manner will improve mechanistic understanding of how cyclones alter ecosystems. A deeper mechanistic understanding of the links among scale-dependent processes will enable us to predict how future changes in cyclone frequency or intensity will affect forest structure and function. We focus in depth on two important, but understudied aspects of cyclone disturbance and forest recovery dynamics for understanding forest primary productivity and carbon sequestration: forest dwarfing and defoliation.

Individual and Species-Level Effects

The effect of tropical cyclones on individual trees ranges from defoliation, branch and canopy damage to bole snapping and uprooting. The level of damage depends on the intensity of the cyclone, the resistance properties of the trees [41–43], and the successional status of the ecosystem [44]. High-intensity cyclones typically lead to greater levels of defoliation and have a greater chance of causing bole snapping and uprooting. Among individuals of a species, trees that are

Glossary

Disturbance: a short-term change in environmental conditions that causes a pronounced change in an ecosystem. Disturbances often act in a short and discrete time period and have the ability to alter the physical structure or arrangement of biotic and abiotic elements within an ecosystem.
Forest regeneration: process through which new tree seedlings become established after forest trees have been harvested or have died from fire, wind, insects, or disease.
Nutrient cycling: movement of nutrients among different components of an ecosystem so that they can be used and reutilized by some of these components.
Old-growth forest: natural forests that have developed over a long period of time, generally more than a century, without experiencing severe, stand-replacing disturbances, such as a fire, windstorm, or logging.
Resilience: the time required for an ecosystem to return to conditions that are indistinguishable from those before a disturbance represents the resilience of a system.
Resistance: reflects the degree to which ecosystem characteristics remain unaffected by disturbance.
Shade-intolerant species: plants that require high light levels to regenerate and grow. They tend to grow fast, have low wood density and leaf mass per area, and have low rates of seedling survival in the deeply shaded forest understory.
Sprouting: initiation of new stem growth from newly grown buds. In disturbance ecology, it is used in the context of a response to disturbance and implies the potential for vegetative regeneration from buds and meristems.
Tropical cyclone: generic term for a nonfrontal synoptic scale low-pressure system over tropical or subtropical waters with organized convection and definite cyclonic surface wind circulation. They have different names in different regions, a 'hurricane' in the North Atlantic Ocean and the Eastern Pacific Ocean, a 'typhoon' in the Northwestern Pacific Ocean, and a 'tropical cyclone' in the Southwestern Indian Ocean.

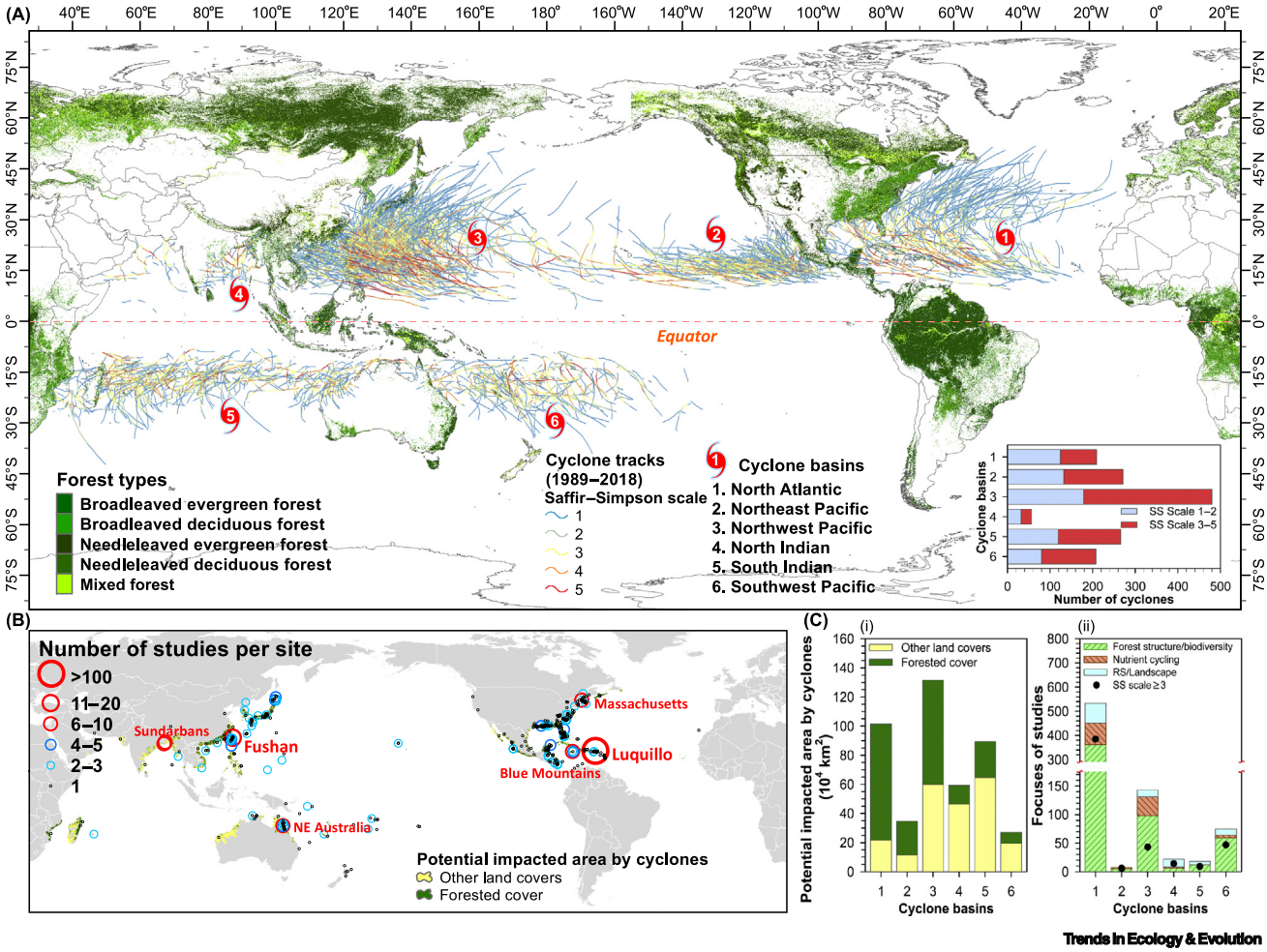

Figure 1. Imbalanced Global Distributions between Tropical Cyclones and Studies of Cyclone Effects on Forest Ecosystems. (A) The global distribution of forests and tropical cyclone tracks; (B) the number of studies at different sites; (C) potential impacted area by cyclones (i) and focus of studies (ii) of ecological effects of cyclones on forest ecosystems in the six tropical cyclone regions between 1989 and 2018. We categorized the focus of the studies into: (1) forest structure and biodiversity; (2) nutrient cycling; and (3) whole-landscape studies, typically carried out using remote-sensing approaches (RS). Data were derived from a Web-of-Science search (1989–2018) using the keywords 'hurricane and forest', 'typhoon and forest', and 'cyclone and forest' (see all references in the supplemental information online). The number of studies of cyclones ≥ category 3 are marked with a solid circle for each cyclone region in (B). The potential impacted area (Ci) was analyzed by overlaying a 100-km buffer layer of tropical cyclone tracks (A) on the global forest distribution [the background of (A)], using Buffer in Proximity and Clip in Extract toolsets of ArcGIS v10.6. Data from ESA DUE GlobCover (http://due.esrin.esa.int/page_globcover.php) and IBTrACS (www.ncdc.noaa.gov/ibtracs/index.php?name=ib-v4-access) (A).

taller, have larger crowns, less dense wood, grow in more exposed sites, or are in poor health (e.g., infected by pathogens, drought stressed, or with high liana load) are more likely to be severely damaged by cyclones [27,45,46].

Variation in cyclone damage among individual trees is directly linked to cyclone effects at the species and population levels. For example, variability in cyclone damage to trees of different sizes and species will cause immediate changes in population demography. If plant health has a genetic basis (e.g., pathogen susceptibility), then the removal of individuals in poor health will alter population genetics. Variation in cyclone damage to individuals growing in different locations will affect the spatial distribution of the species. In addition, the commonly observed increase in seedlings during the first couple of years following cyclone disturbance [47] also alters population demography.

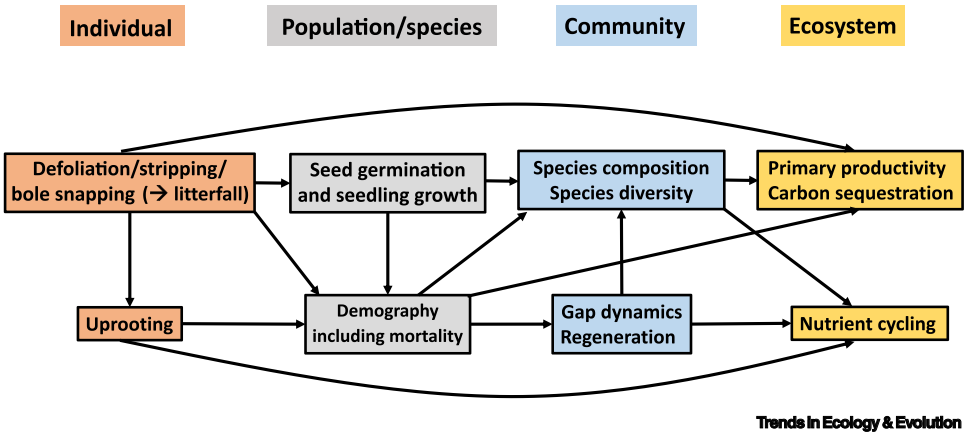

Figure 2. Cyclone Effects on Forest Ecosystems Highlighting the Linkages within and between Various Levels of Ecosystem Organization, from Individual Trees to the Ecosystem (Not All Possible Cyclone Effects or Linkages Are Included). Tropical cyclone effects on lower levels of biological organization have both direct effects (i.e., those that do not span multiple levels) and indirect effects on higher organizational levels. Cyclone effects at the individual level may lead to multiple effects at higher levels of biological organization. For example, at the population level, defoliation affects seed germination and seedling growth, and primary production and nutrient cycling at the ecosystem scale (see Box 1 in the main text). Multiple aspects of cyclone disturbance on tree individuals can interact to influence a response at a higher level of biological organization. For example, defoliation, branch striping, bole snapping, and uprooting all affect seed germination and seedling growth via an increase in understory light availability. Linkages can also occur within levels of biological organizations. For example, defoliation reduces the risk of bole snapping and uprooting.

Community-Level Effects

Cyclone disturbance effects at the individual and species levels scale to the effects at the community level. Species in a community differ in wood traits, degree of exposure, and tree or crown size, leading to differential vulnerability to cyclones, through which cyclone disturbance alters community species composition [16,48]. Cyclones increase wood density and decrease average tree height at the community level, due to the removal of trees with low wood density [49] and of taller, more exposed trees [50,51]. In addition, the increased establishment and growth of seedlings associated with enhanced resource availability, especially light, following cyclone disturbance, differs among species due to different light requirements. As predicted by the gap-phase regeneration theory [52–56], seedlings of **shade-intolerant species** disproportionally benefit from the enhanced resource availability caused by cyclone disturbances.

Sprouting is a common response to disturbance [57], through which many tree species maintain their presence and develop multiple-stem morphologies in forests affected by cyclones [24,58]. Differences in sprouting ability may lead to changes in the basal area and species composition of forests as they recover. Thus, overall, cyclones can affect plant community composition through the differential damage to adult tree species, the variable responses of seedlings of different species to the altered understory environment, and variation in postcyclone sprouting among different tree species.

The effects of tropical cyclones on the community composition of tropical forests over time are largely dependent on cyclone frequency. In regions where cyclones occur at decadal or longer intervals, cyclones are known to cause shifts in the relative abundances of different tree species (e.g., pioneer versus late-successional species) [15], while in regions with annual cyclone disturbance, such differential effects are diminished, if found at all [22,25]. However, over evolutionary timescales, all trees in cyclone-prone regions are subjected to the selection pressures of strong, damaging cyclonic windstorms. Some trees can tolerate cyclone disturbance better than others

(i.e., are damaged less and survive and recover better). This differential response in terms of performance acts as driver of natural selection to increase tree resistance to cyclone storm wind damage. A study in northern Queensland proposed that an increased frequency of intense cyclones restricts the distribution of tree species susceptible to cyclone damage in sites prone to intense cyclone disturbance [59]. Additionally, a summary of studies in the Luquillo Experimental Forest in Puerto Rico reported long-lasting effects of cyclone disturbance on fundamental forest structure [60]. Thus, over evolutionary timescales on which cyclones have exerted selection pressure, it is likely that individual trees and species that are vulnerable to cyclone disturbance are selectively culled from the community, leaving the species that are resistant to cyclonic disturbance.

Therefore, it is inappropriate to infer that cyclone disturbance has no effect on tree species composition in very frequently disturbed forests. The lack of any immediate disturbance effect on the forest community is the result of the cumulative effect of the greater historical cyclonic storm regime. The return time of damaging cyclone disturbances is the principle governing factor. Return time matters because the amount of damage a cyclone exerts on a forest is largely dependent on the time the ecosystem has to develop in the absence of a damaging cyclone (Box 1). Generally, if forests have over 40 years to develop between damaging cyclones, they can regenerate and add substantial biomass, making each storm a strong reset for the system [48]. As the return interval shortens, there is less time for the forest to regenerate and accumulate biomass. It is as though the overall disturbance regime at frequently disturbed sites dominates the disturbance dynamic, with a diminished effect of any single storm. By contrast, at sites with infrequent cyclones, a single disturbance event may greatly influence the overall disturbance regime.

The disproportional removal of taller and more exposed trees at the individual and species levels may contribute to the dwarfing of forest communities [50,60] (Box 1). Cyclone-induced dwarfing has been suggested as the cause of the lower canopy height of lowland forests in Madagascar, where canopy heights measure 23–26 m relative to 40–50-m canopies for neighboring Africa forests [30,61,62]. In Taiwan, low-elevation forests have shorter canopies than higher elevation forests because of the greater severity of cyclone damage in low-elevation forests [40]. The increase in forest height with elevation in Taiwan is contrary to the decreases in forest height with elevation that are common among other tropical forests (e.g., in Caribbean islands or the Peruvian Andes) [60,63] and is a direct result of frequent cyclones.

Defoliation has major consequences at multiple scales, but its ecological importance is often overlooked (Box 2). Given that defoliation reduces wind resistance, is defoliation is a critical adaptation to frequent cyclone disturbance? For defoliation to be an adaption to wind disturbance, it must occur early in a cyclone event, before the wind reaches speeds that cause greater tree damage (e.g., canopy breakage or whole-tree tip up). New technologies that record litterfall at fine temporal resolutions (e.g., hourly) coupled with on-site meteorological records could help to evaluate whether defoliation is an adaptation to frequent cyclone disturbance.

The effect of cyclone disturbance on forest regeneration dynamics is another aspect of cyclone–forest interactions. Since cyclone disturbances create gaps for tree recruitment and, therefore, forest regeneration, regions with more frequent cyclone disturbance should have shorter forest regeneration times [64]. Thus, it is not surprising, but important, that increases in cyclone intensity or frequency will speed up forest regeneration and, therefore, reduce the maximum possible age of the trees. Despite inconsistent projections on future changes in cyclone frequency, studies consistently project the poleward movement of cyclones (Figure S1 and Table S1 in the supplemental information online). Thus, it is likely that cyclone disturbances will become more frequent in **old-growth forests** that currently experience few cyclones, such as those in the southeastern

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Box 1. Tropical Cyclone Disturbance Effects on Forest Height

During a tropical cyclone, taller, more exposed trees are disproportionally affected (e.g., either removed from the community via mortality or damaged more severely). In forests with frequent cyclone disturbance, there may be insufficient time for full forest-canopy recovery before the next disturbance (the orange arrow in Figure I) so that the forest may gradually decrease in total canopy volume or tree stature over time (i.e., dwarfing, Figure IA). By contrast, for forests experiencing infrequent cyclone disturbance, there is likely to be enough time for full recovery of canopy and forest structure before the next disturbance and possibly time for further forest development. As a result, in areas with very frequent cyclone disturbance, the tropical cyclone regime potentially has less of an overall effect on forest stature over time, compared with areas with infrequent cyclone disturbance (Figure IB). However, if cyclone frequency increases, the time interval between successive cyclones will shorten, and may approach the time required for full recovery (Figure IC, third panel from the left); beyond this critical point, there is not enough time for the full recovery of forest structure, and trees will not reach their previous maximum height, resulting in forest dwarfing (Figure IC). Alternatively, if cyclone intensity increases, the effect of each cyclone will be more severe and the time required for full recovery will be longer and may approach the occurrence of the next cyclone disturbance (Figure ID, fourth panel from the left); beyond this critical point, there may not be enough time for the full recovery of the total canopy volume or forest structure, and trees may not reach their previous maximum height, leading to forest dwarfing (Figure ID). If both the frequency and intensity of tropical cyclones increase, the time required for full recovery becomes even longer, while the time between successive cyclone events shortens, potentially resulting in even more-severe dwarfing pressure (Figure IE).

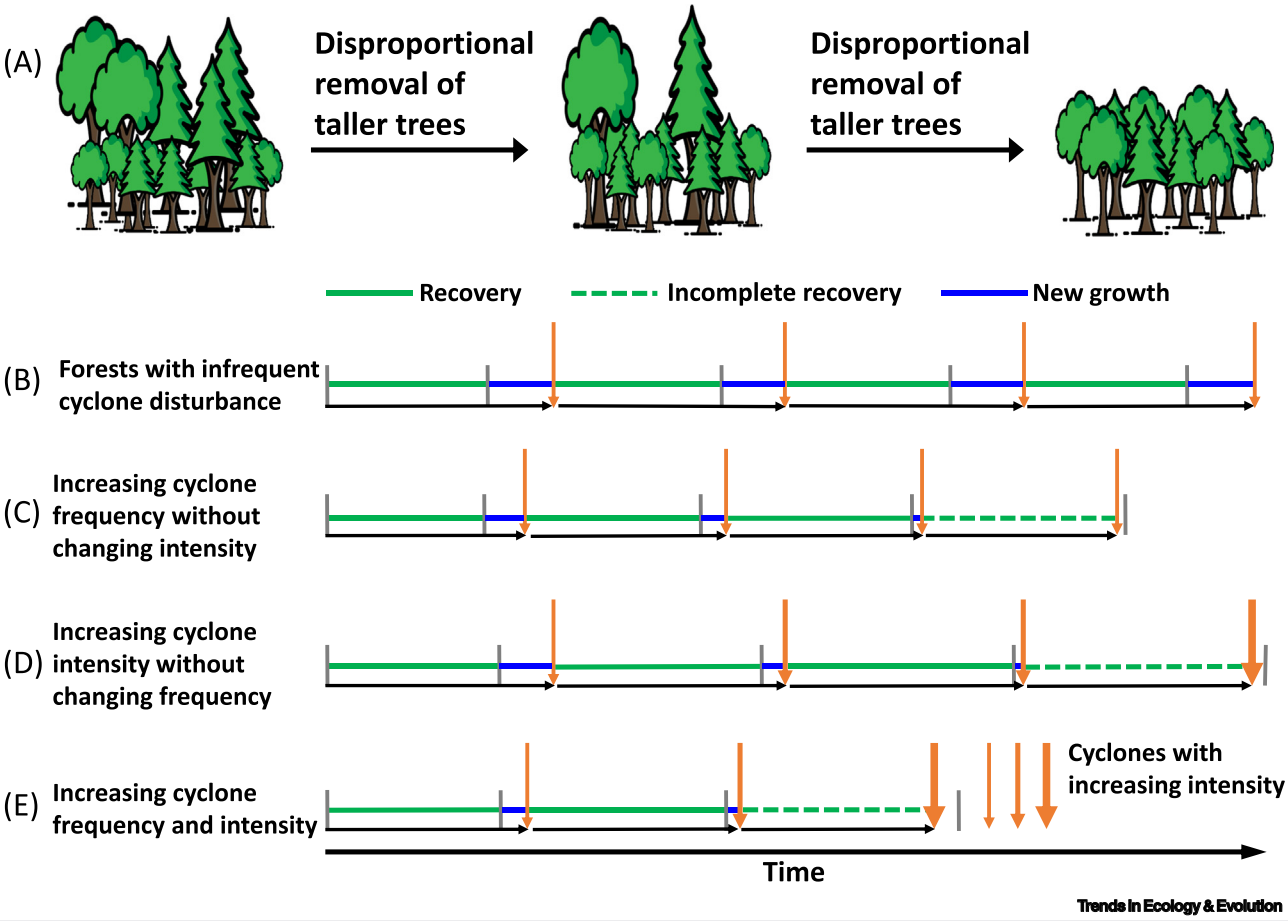

Figure I. Forest Dwarfing Caused by Increases in Cyclone Frequency.

USA, southern Japan, or northeastern Australia, where forests may gradually lose their largest trees. A study in northern Florida reported that a main canopy-dominant species (*Magnolia grandifolia*) showed high hurricane damage but minimal understory recruitment [65]. Additionally, in an old-growth forest in southwestern Japan, cyclone-induced tree mortality was particularly high for trees with diameter at breast height >150 cm, most of which are upper canopy trees [66]. The affected old-growth forests may be still old if the cyclones are not stand-replacing

Box 2. Ecological Significance of Cyclone-Induced Defoliation

Defoliation is perhaps the most common cyclonic storm-related damage to trees (Figure I). Tree leaf loss affects the forests on multiple scales, but its role in forest ecology is underappreciated.

Defoliation directly reduces photosynthesis and the net primary production of the forest community [67,68], which may take many years to recover. The recovery (refoliation) from a 66% reduction of forest foliage following multiple typhoons without major tree mortality (<2%) [22] took nearly a decade at the Fushan Experimental Forest (northeastern Taiwan) [69]. Defoliation also reduces wind resistance of individuals and the entire forest community and, therefore, reduces the risk of further damage (e.g., individual stem breakage) and mortality. Defoliation allows greater light penetration to the forest floor [56,70,71], enhancing the establishment and growth of understory plants, especially shade-intolerant pioneer species. However, because canopy defoliation is patchy, understory light increases are spatially variable, allowing plants with different light requirements to coexist, which may maintain understory plant diversity in tropical forests [71]. At the ecosystem level, defoliation represents the transfer of carbon from a living pool (i.e., tree biomass) to a nonliving pool (i.e., necromass). Heavy typhoon-induced rainfall may further leach carbon and other nutrients from defoliated litter into river systems, thereby altering forest nutrient cycling [72].

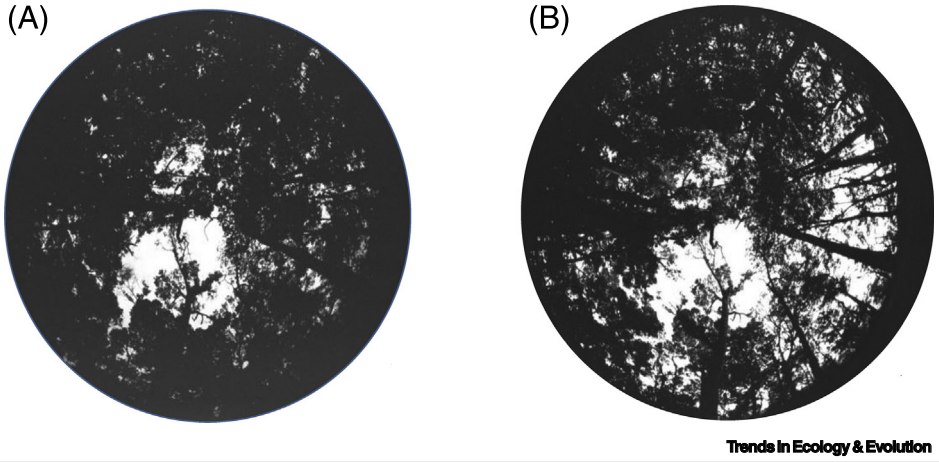

Figure I. Fish-Eye Lens, Hemispherical Canopy Images Taken from the Same Location before (A) and after (B) Category 3 Typhoon Herb (1996) at the Fushan Experimental Forest of Northeastern Taiwan. The proportion of canopy gap area increased 25% as a result of defoliation, but all trees in the pretyphoon image survived the typhoon.

disturbances (i.e., do not initiate secondary succession, as is the case in Taiwan), but the forests will likely lose many large tall trees. In other words, increases in the frequency of cyclone disturbance of these old-growth forests may lead to the development of old-growth forests that do not look old, and they may act as another threat to the large trees of the world.

Ecosystem-Level Effects

Cyclone disturbance effects acting on the community level are coupled to the ecosystem-level responses to cyclone disturbance to varying degrees. If cyclone-induced tree mortality is high, large amounts of carbon and other elements can be lost from the ecosystem [73,74], leading to reduced nutrient uptake by tree roots, and altered rates of **nutrient cycling** at the ecosystem level. For example, levels of stream-exported nitrate were elevated for 18 months in the Luquillo Experimental Forest after Hurricane Hugo in 1989 [75]. Tree damage is a major control of ecosystem nitrate export in stream water following cyclone disturbance, but postcyclone tree leaf production and regrowth control the return of stream nitrate to precyclone levels [76].

If tree leaf loss and mortality are low, most trees can continue to cycle nutrients, so that stream nutrient concentrations may return to the precyclone level within weeks. The forests in Taiwan

illustrate a scenario in which the high structural **resistance** at the community level (i.e., low tree mortality) contributes to the functional **resilience** at the ecosystem level (i.e., rapid recovery of nutrient cycling) [21,77]. In other words, forests that are structurally resistant are also inherently resilient to cyclone disturbance functionally, suggesting that resistance and resilience are not necessary negatively related, as previously suggested [78], and instead one facilitates the other [68]. Notably, although cyclone effects on nutrient cycling could be important for long-term ecosystem structure and functioning, studies on this aspect lag far behind those focusing on vegetation dynamics (Figure 1) across all cyclone regions.

Cyclone disturbance may also cause ecosystem state shifts in nutrient cycling. For example, Taiwanese forests shifted from nitrogen conservative during regular periods, to nitrogen leaking during cyclone storm periods [77,79]. With the projected increases in cyclone intensity, state shifts in ecosystem nutrient cycling may become more common. The potential for ecosystems to reach tipping points for key ecosystem processes, such as nutrient cycling, beyond which the shifted state does not return to the original state [80–82], increases with greater disturbance frequency and magnitude [83]. Changes in nutrient availability have been shown to affect interspecific competition [84,85] and, thus, ecosystem-level alterations in functioning due to cyclone disturbance likely feedback to affect lower levels of ecosystem organization (e.g., community and population dynamics). There is a need to better understand how nutrient availability and the movement of nutrients within the ecosystem drive or respond to community and species-level dynamics. For example, one study illustrated how added nitrogen increased hurricane damage and prolonged the recovery time of scrub mangrove trees in the Indian River Lagoon of Florida, USA [86]. A second study showed that the formation of multistemmed trees in cyclone-disturbed Jamaican forests was related to low levels of soil phosphorus, and that turnover rates of multistemmed individuals were 60% lower than for single-stemmed trees [87]. To our knowledge, however, no studies have explored the effects of cyclonic storms on forest species composition in relation to the strength of interspecific competition because of disturbance-driven altered nutrient availability.

Notably, the effects of cyclones on nutrient cycling are more related to total rainfall than to the wind intensity of cyclones and the two are not always positively correlated. For example, the category 1 Hurricane Danny (1997) brought 900–1000 mm of rain over Mobile Bay, Alabama, USA [88] and the category 2 Typhoon Meari (2004) brought extreme rainfall, with a peak rain intensity of >100 mm h^{-1}, in the mountainous Kii Peninsula of Japan [89]. An analysis of 14 typhoons affecting central Taiwan indicated no significant relationship between rainfall quantity and typhoon intensity [77]. Thus, the disproportional representation of the most intense cyclones in the literature (Figure S2 in the supplemental information online) may overlook the effects of less intense cyclones on nutrient cycling. The effects of small cyclones, or storms in general, with high rainfall intensity on nutrient transport has long been recognized in hydrochemistry [90,91] and should be included in studies of cyclone effects on nutrient cycling.

Concluding Remarks and Future Perspectives

Effects of cyclones at the community and ecosystem levels are mediated by the effects at the individual and species levels. The accumulation of short-term cyclone effects contributes to the long-term formation of observed ecosystem structure and function. For example, the gradual removal of tall trees by individual cyclone events leads to dwarfed forests with low biomass and carbon sequestration in regions with frequent cyclone disturbance. Thus, a scale perspective is critical for a mechanistic understanding of storm ecology.

Reliable assessments of present-day storm impacts are imperative to forecasting the effect of cyclone disturbance on forests as cyclones increase in their importance as a disturbance

Outstanding Questions

Does the decrease in cyclone frequency from low to high latitude and the decrease in cyclone intensity from the coast to inland contribute to characterizing latitudinal and coastal–inland vegetation patterns (e.g., vegetation height and species composition)? Exploring the role of cyclone disturbance on large-scale vegetation patterns could aid in the prediction of future changes in global vegetation.

Which morphological and physiological traits are most relevant to plant adaptation to cyclone disturbance? In addition to wood density, leaf size, crown size, and branching pattern, additional plant characteristics, such as leaf morphologies (e.g., lamina length and width or petiole length), wood anatomy (e.g., vessel structure, wood tissue physical structure, and chemical composition), branching and rooting patterns, and the presence of buttresses, are likely to affect the vulnerability of plants to wind damage. Further work examining the importance of these traits in explaining interspecific differences in susceptibility to cyclone effects will enable predictions of how changes in cyclone disturbance regime will affect forest species composition.

Can the rates of change in forest species composition toward species that are more adaptive to cyclone disturbance keep pace with the changes in cyclone intensity, frequency, seasonality, and size, or will we see landscape-scale shifts in vegetation structure and species composition?

Can our current understanding of the effects of cyclone disturbances on forest ecosystems help to predict future forest responses to cyclones under altered disturbance regimes because of climate change? The answer to this important question must be empirically evaluated though cross-ecosystem comparisons that span the global variation forest structure and function and the global range in cyclone disturbance regimes.

agent. Ideally, measurements should be taken shortly before and after a storm to limit the influence of other confounding factors. Nevertheless, acquiring precyclone information in regions with infrequent cyclone disturbance is challenging. Given the relatively recent improvements in storm forecasting and meteorological model development in relation to cyclones, taking surveys shortly before a cyclone is increasingly feasible. Interested ecologists should monitor forecasts to decide whether collecting last-minute prestorm data is worthwhile. In addition, ecologists should leverage large networks to study gradients in cyclone disturbance intensity and frequency, such as the International Long-Term Ecological Research (ILTER) Network, or the Smithsonian's Forest Global Earth Observatory. Surveys could be synchronized at multiple sites that are likely to be affected by the same cyclone but with different intensities, in terms of wind speed and rainfall, to reveal nuances in the responses of individuals, populations, communities, and ecosystems, and their underlying causes. Some scientists have urged for the organizing of a global collaboration to advance cyclone ecology [92]; we believe such efforts in combination with the existing networks provide the most exciting opportunity to address some of the fundamental issues in cyclone disturbance ecology (see Outstanding Questions).

Acknowledgments

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Supplemental Information

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