TREE MORTALITY

Changing forests under climate change

Changes in climate, including increases in the frequency of lightning, will differentially affect the fitness and mortality of tropical tree species. Variation in the sensitivity of species to climate change will in turn lead to shifts in the composition of tropical forests and the services that they provide.

Kenneth J. Feeley and Daniel Zuleta

A basic tenet of ecology is that species must be adapted to local climate and environmental conditions in order for them to prosper at a given location. This explains why you find different sets of species with different functional traits in different ecosystems with different climates. For example, in parts of the tropics that experience seasonal droughts, you often find dry forests comprised of dense-wooded, drought-tolerant tree species, while in wetter parts of the tropics you find rainforests including many larger, lighter-wooded species that would perish under dryer conditions. Because of these different functional compositions, different plant communities have distinct structure and dynamics, provide different ecosystem services and are sensitive to different aspects of climate change.

This matching of community composition to conditions underlies the observation that global change is driving shifts in ecosystems worldwide via changes in species survival, growth and reproduction[1]. As temperatures rise, heat-tolerant species are more likely to benefit, while cold-adapted species are more likely to suffer, leading to the directional shifts in community composition referred to as thermophilization. In some cases, thermophilization can lead to abrupt changes in the distributions of entire ecosystems, as is occurring in high-latitude and high-altitude systems, where rising temperatures allow for greater abundances and sizes of woody plants, resulting in 'greening' — the transformation of tundra or alpine grasslands into shrublands or forests[2,3]. Likewise, dryer conditions, due either to regional changes in precipitation patterns or to changes in exposure resulting from deforestation and habitat fragmentation, can lead to xerophilization. On the flipside, in the places that are getting wetter, we may see decreasing abundances of drought-adapted species and community mesophilization.

Beyond climate change, altered biotic interactions — due to either the introduction of species or local extinctions and defaunation — can have marked impacts on the composition of plant communities and hence the services that these communities provide. For example, the loss of large vertebrate seed dispersers from tropical forests due to hunting is hypothesized to favour tree species with smaller seeds, which also tend to have lighter wood. As lighter-wooded species prosper and denser-wooded species decline in abundance, the amount of carbon stored in these 'empty forests' will decrease[4]. In another example, a 100-fold increase in the population of crop-raiding native wild boar in Malaysia, triggered by the bounty of oil palm plantations, resulted in a dramatic reduction in the abundance of small trees used by the pigs to construct their nests in nearby forests, thereby reducing tree diversity and altering the composition of future forests[5].

Just as chronic drivers (also known as 'presses'; for example, sustained changes in temperature, precipitation and vapour pressure deficit) can impact tree species differently[6] and induce compositional changes, so can changes in the frequency and/or intensity of acute events (also known as 'pulses') such as wildfires, droughts, heat waves, cold snaps, windthrows and biotic attacks[7]. These transient disturbances particularly manifest through differential changes in tree mortality, because changes due to tree death, which occur more abruptly than changes due to growth or recruitment, are mainly responsible for spatial variation in forest carbon stocks[8]. In other words, the 'sudden' death of just a few large trees will cause large and immediate impacts in forest community structure and function, while changes in recruitment patterns can take many years to emerge as measurable changes in structure or function.

In this issue, Richards et al.[9] provide evidence for a surprising way that climate can selectively affect the mortality of tree species and hence tropical forest community composition: through lightning. Lightning is an underappreciated source of mortality in tropical forests, responsible for 40–50% of large tree deaths, reducing the average lifespans of large trees by nearly 40 years, and accounting for >15% of tree biomass turnover in the only tropical forest where it has been systematically studied[10,11]. Being struck by lightning is commonly cited as the epitome of randomness, and one could reasonably expect that the extreme power and heat discharged by lightning would immediately kill any tree that is struck. Yet, by following the fates of nearly 100 mapped lightning strikes on Barro Colorado Island, Panama, Richards et al. show that there are actually large discrepancies between tree species in their susceptibility to being struck by lightning, as well as in their ability to survive lightning strikes. Indeed, three species — *Dipteryx oleifera* (Fabaceae), *Hura crepitans* (Euphorbiaceae) and *Pouteria reticulata* (Sapotaceae) — survived 100% of lightning strikes, while other species (especially palms (Arecaceae)) were almost certain to die when struck. Interestingly, those tree species that were most likely to be struck had the lowest risk of mortality, suggesting a potential trade-off between lightning susceptibility and tolerance. Given the importance of lightning-induced mortality, the newly revealed differences in susceptibility and tolerances between tree species can be expected to have important fitness consequences; thus, differences in lightning frequencies across space or through time should lead to differing taxonomic and functional compositions[9].

By examining the relationships between lightning-induced mortality rates and various species-level functional traits, Richards et al. hoped to uncover what adaptations allow for tolerance. Surprisingly, the only trait associated with lightning tolerance was wood density. Wood density is sometimes referred to as a 'master trait' because of its strong association with life history. Dense-wooded tree species tend to be more conservative, meaning that they are generally slower growing and longer lived[12]. It might be thought that dense-wooded species would have higher electrical resistivity and should thus be more sensitive to lightning strikes[13], but Richards et al. actually found that dense-wooded tree species had greater tolerances to lightning, based on their analysis accounting for differences in the historical background mortality rates of the species. This counterintuitive result might reflect the fact that electrical resistivity is an emergent property of various anatomical and physiological characteristics and is poorly predicted by any single trait such as wood density (for example, *D. oleifera* has extremely dense wood, yet its resistivity is similar to, or lower than, that of many lighter-wooded species). The positive relationship between lightning tolerance and wood density might also be due to the influence of other factors associated with the slow–fast life history continuum that are not directly connected to lightning. For example, trees with low wood density may have died not directly by lightning but by the secondary indirect effects of the strikes (for example, subsequent damage by falling trees or limbs, or biotic attacks). In other words, although the direct effect of a lightning strike should depend on a tree's electrical properties, there are many other complex interacting mechanisms involved in mortality that, when integrated, may result in the higher tolerance of dense-wooded tree species. The relative role of these comorbidity factors can only be assessed by recording data for a broad suite of variables on living trees and monitoring them over long periods of time[14].

Climate change is driving up global temperatures. Higher temperatures increase the amount of atmospheric energy, leading to stronger and more electrically active storms. If lightning increases in the tropics by 25–50%, mortality rates for large tropical trees are predicted to increase by approximately 10–20%[10]. Given the negative correlation between wood density and lightning-induced mortality, increases in lightning could conceivably reduce the abundance of large trees while at the same time driving an increase in the abundance of dense-wooded species. These changes in forest structure and functional composition could in turn have cascading effects that alter dynamics and sensitivity to other climatic factors (for example, wood density is often associated with drought tolerance[15]). In addition, lightning-induced changes in forest structure and dynamics will affect critical ecosystem services such as carbon cycling and storage.

As highlighted by the results of Richards et al.[9], there are myriad ways that global change can differentially affect the fitness and mortality of tree species, potentially driving complex, and sometimes unexpected, shifts in ecosystem composition, structure and function[6]. These changes can affect ecosystem services and must be accounted for in climate and carbon cycle models. It is critical that we support and expand both on-the-ground and remote efforts to monitor natural ecosystem responses to climate so that we can better predict their responses to future climate change. ❐

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Competing interests

The authors declare no competing interests.