

Review

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Review

Tropical Trees Will Need to Acclimate to Rising Temperatures. But Can They?

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Abstract: For tropical forests to survive anthropogenic climate change, the trees that comprise them will need to tolerate the newly emerging conditions through adaptation or acclimation, or they can avoid climate change through range shifts and “species migrations”. In this review, we show that the rapid pace and extreme severity of modern climate change makes it extremely unlikely that tropical tree species can adapt (with some possible exceptions). We also show that while many tropical tree species are shifting their distributions to higher, cooler elevations, the rate of these migrations are mostly insufficient to offset ongoing changes in temperatures, especially in lowland tropical rainforests where thermal gradients are shallow or nonexistent. We argue that the best hope for tropical tree species to avoid becoming “committed to extinction” is acclimation. While several new methods are being developed to test for acclimation, we unfortunately still do not know if tropical tree species can acclimate or what factors may prevent or facilitate acclimation. Until these questions are answered, our ability to predict the fate of tropical species and tropical forests – and the many services that they provide to humanity – remains critically impaired.

Keywords: adaptation; acclimation; species migrations; climate change; global warming; tropical forests; trees; biodiversity

1. Introduction

Despite covering a relatively small fraction of the Earth's surface [1], rainforests harbor myriad known and unknown species [2,3], and support many millions of humans directly through the production of food and other natural resources [4] and indirectly through a diverse range of important ecosystem services such as carbon sequestration and climate regulation [5–7]. Unfortunately, anthropogenic climate change threatens the persistence of many tropical tree species [8], and perhaps even the persistence of tropical rainforests as a whole [9,10].

It is widely recognized that species have a limited number of options for responding to climate change. Specifically, species can tolerate changes in climate through adaptation or acclimation, or they can avoid climate change through species migration. Any species that fail to adapt, acclimate, or migrate will experience decreased performance and may become “committed to extinction” [11]. Here we argue that in the case of tropical trees, the options may be even more limited, and the fate of tropical forests will depend most heavily on the ability of trees to acclimate.

2. Tropical trees are unlikely to be able to adapt to anthropogenic climate change

Evolutionary adaptation (hereafter referred to simply ‘adaptation’) requires heritable changes in a population's or species' genotype across multiple generations. Many rainforest tree species are long-lived, with average life spans of several hundred years [12,13] and some individuals reaching ages of more than 1,000 years old [14]. Furthermore, rainforest trees can take decades to reach reproductive maturity [15]. Since adaptation, even at its fastest, requires many generations, the extreme speed at which global warming is now occurring (>2 °C warming per century) relative to the long lifespans and generation times of most trees precludes adaptation as a response [16–18]. Indeed,

previous studies have shown that rates of thermal niche adaptation by plants (including even non-trees with shorter generation times) after the last glacial maximum were many orders of magnitude slower than required to keep up with subsequent warming [19] and that evolution of tolerance to high temperatures is particularly slow due to intrinsic physical constraints [20,21]. Indeed, tropical tree species and genera typically exhibit strong thermal niche conservatism with closely related taxa tending to occur at similar elevations or temperatures (even when comparing across hemispheres), suggesting that there are evolutionary constraints preventing their adaptation to new elevational/thermal niches, and that speciation occurs most often due to genetic isolation and/or adaptation to non-climatic factors [22–26]. Further bolstering this argument is the fact that many trees, including in the tropics, maintained high climate fidelity through past climate change episodes [27]. Taken together, these findings indicate that tropical tree species could not, or at least did not, respond to past climate change through adaptation. Given that the Earth is now hotter than it has been for >125,000 years [28] and that temperatures continue to rise at rates that are at least an order of magnitude faster than past post-glacial warming and are unprecedented for at least the past 50+ million years (and possibly 250+ million years)[29,30], we contend that adaptation and evolutionary rescue [31] are not viable responses for most tree species to modern anthropogenic climate change.

There are some possible exceptions that are worth highlighting. If, as has been previously posited, plants do not have segregated germlines, then flowers on different branches of long-lived trees would be separated by many generations of cell divisions and therefore may accumulate different somatic mutations [32]. This could potentially increase the genetic variability of a single tree's offspring and thereby allow for accelerated evolutionary adaptation. Contrary to this idea, newer studies have found that many plants do in fact have 'functional germlines' [33–35]. This means that the reproductive cells in a tree are separated by fewer cell divisions, which protects them from accumulating somatic mutations and decreases intra-individual genetic variability (i.e., the unit of reproduction in plants is in fact the individual and not the branch or individual flower). However, additional research is clearly needed to understand germline segregation in plants and its effects on adaptability.

A second potential mechanism for accelerated adaptation in trees is that even if the trees themselves are slow to evolve, their microbial symbionts may be able to evolve much faster and help their partner trees "adapt" to changing conditions [36–38]. Studies have found that the tolerances of some plants to environmental stressors such as heat, drought, and salt, can be determined at least in part through interactions with endophytic and/or mycorrhizal fungal symbionts [39–43], and potentially even the interactions of the fungi with their viruses [44]. Since these fungal symbionts have much shorter generation times, they may be able to quickly adapt and consequently confer greater tolerances to their partner plants. Alternatively, the plants may shift their interactions to favor symbiotic species that incur increased tolerances [45]. Inoculation experiments have demonstrated the potential for altered mycorrhizal fungi communities to strongly enhance stress tolerances of herbaceous crop plants [46] and temperate trees [45], but at this point, it remains unclear what role fungal symbionts play in determining the environmental tolerances of tropical trees, much less the potential for symbionts to enable tropical tree species to better adapt to rising temperatures [47].

3. Many tropical tree species are shifting their geographic distributions in response to modern climate change, but not fast enough to offset warming

It has been previously said of plants that "it is easier to move than to evolve" [48,49]. Indeed a growing body of research provides strong evidence that modern climate change is forcing many tropical tree species to shift their geographic ranges, or "migrate", out of the areas that are becoming "too hot" and into areas that were previously "too cold" (e.g., to higher elevations), with important effects on community composition and ecosystem dynamics [50–55]. During past climate change episodes, tropical trees were able to migrate fast enough to maintain climate fidelity. However, it appears that species are no longer able to "keep up" and that the current migration rates are markedly slower than what is required for tropical tree species to remain at equilibrium with modern anthropogenic warming [53,56]. For example, Fadrique et al. (2018) documented widespread changes

in the functional composition of Andean tree communities consistent with upward species migrations. Specifically, they found that in the Andean plots with repeat censuses, the relative abundances of lowland heat-tolerant (i.e., “thermophilic”) species had increased through time while the abundance of highland species had decreased (a pattern referred to as “community thermophilization”). The rates of compositional change observed in the Andes corresponded to an average species thermal migration rate of just 0.003 or 0.007 °C per year (equivalent to approximately 0.5 or 1.3 m elevation per year) depending on the methods and plots used, which was markedly less than the concurrent regional warming rate of 0.06 °C per year. Similar studies from other forests suggest that tree species migrations and compositional changes may be even slower in lowland tropical areas [57] where climatic gradients are shallow or nonexistent [58–60] and thus distances between climate analogs are greatest [61] and climate change velocities are fastest [62].

The slow rates of species migration in the tropics, even in montane systems with steep temperature gradients, may be due to the natural dispersal limitations of the tree species (exacerbated by defaunation and the loss of dispersers [63]) as well as the inherent stability of the systems, which hinders migrations and compositional changes. For example, species migrations may be impeded at ecotonal boundaries where factors other than temperatures limit species distributions [64,65]. Indeed, in many parts of the high tropical Andes, the upper elevational limit of tree growth (i.e., the treeline) has remained remarkably stable over the past several decades despite rapidly rising temperatures [66]. In the case of treeline, the stability may be due to the effects of UV radiation, cold nighttime temperatures, cold snaps, or species interactions preventing the expansion or shift of the forest species’ ranges into higher elevations [67,68]. As a visually dramatic ecotone, the treeline has been the focus of numerous studies; other ecotones, such as those occurring at cloudbase or where soil conditions change [69–71], may be equally important in setting current and future species’ distributions [64,65] but have received considerably less attention.

Another natural factor that may slow or prevent tree migrations is priority effects [72]. For a species to migrate and expand its range into new areas it will have to compete with the established incumbent species. Incumbent species may be at an inherent advantage and thus may be able to persist and prevent incursions by new species, even as the climate becomes increasingly unsuitable for them. For example, while elevated temperatures in an area may slow the growth of an incumbent tree species and/or prevent it from reproducing, any surviving adults may still prevent more-thermophilic tree species from immigrating and establishing by casting deep shade, producing allelopathic chemicals, or simply by occupying space. If this is the case, then disturbances that hasten the mortality of established trees and thereby reduce priority effects may accelerate species migrations and compositional changes [73]. This will be especially true if the mortality caused by the disturbance is non-random and disproportionately affects the species that are already stressed by the changing climate. An example of this phenomenon comes from Jamaica, where the rate of thermophilization in montane forest communities was greatly accelerated in the years after a strong hurricane that elevated the mortality of highland tree species and subsequently allowed for increased recruitment of the more-thermophilic lowland species [74].

Beyond these natural limitations to species migrations, humans are creating many additional barriers. In the Amazon, deforestation and habitat modification/degradation is reducing the amount of suitable habitat available for species to migrate to and is also increasing the distances that species need to migrate to remain at equilibrium with climate [75,76]. Indeed, it is predicated that for large parts of the Amazon, deforestation will soon sever all connections between analog climates, making it extremely unlikely that any resident tree species will be able to escape rising temperatures through migrations [75].

4. We do not know (yet) if tropical trees can acclimate to climate change

Given their long lifespans, many trees alive today have already experienced >1 °C warming and may live to see an additional 1-2 °C global warming. The rapid pace of climate change relative to trees’ lifespans necessitates that individuals acclimate to changes in climate (i.e., change their

behavior, physiology, metabolism, and/or structure through phenotypic plasticity) to maintain consistent performance and fitness.

Previous studies have attempted to test for the acclimation of plants to climate change by examining how performance and/or functional traits vary over natural environmental gradients (e.g., across latitude or elevation), which serve as “space-for-time” proxies for future climate scenarios [77,78]. For example, if there are differences between the traits of individual plants growing in hot places compared to the traits of conspecific plants growing in colder places, this could suggest that the species is capable of acclimating in response to rising temperatures. For example, looking at leaf traits of conspecific trees growing across a temperature and moisture gradient in southern Brazil, Souza et al. (2018) found that variation in morphological and functional traits (and plasticity of traits) was associated with differences in the temperature, aridity, and light availability [79]. As another example, Slot et al. (2021) measured the photosynthetic heat tolerances of leaves from seven tree species growing at different elevations and temperatures in Panama and found that heat tolerances and critical temperatures decrease with elevation and increase with temperature in just over half the species [80]. An important caveat to any studies using large-scale gradients is that they typically include many confounding variables such as spatially patterned changes in precipitation, seasonality, soil type, co-occurring species, etc. [81]. Perhaps even more importantly, any observed differences in traits across large-scale gradients may reflect genetic differentiation and local adaptation of allopatric populations, rather than just the acclimation of individuals [82,83]. Indeed, most studies on tropical gradients focus on *interspecific* variation and only a much smaller number even attempt to assess *intraspecific* variation.

By combining gradient-based studies with common gardens or transplant experiments, it may be possible to decouple the roles of adaptation vs. acclimation in determining intraspecific trait variation [e.g., 84–86]. Likewise, *in situ* experimental warming experiments can be used to test for acclimatory responses to rising temperatures [87]. For example, in the Rwanda TREE project, individuals of 20 different tree species have been experimentally transplanted into three montane locations spanning elevations corresponding to a ~6 °C gradient in mean annual temperature (coupled with water and nutrient availability treatments). So far, results from these transplants show mixed evidence for acclimation to higher temperatures. Studies testing for the acclimation of leaf functional traits and photosynthetic parameters in 18 of the species found differences in the responses of species to warming, as well as between successional groups. Specifically, leaf area decreased with warming for early successional but not later successional species, while decreases in leaf mass per area and increases in leaf width-to-length ratio were common in both species groups [88]. Net photosynthesis strongly decreased with warming in both sets of species under dry conditions, but only decreased in later successional species under wet conditions [89]. In another study of three species with different water use strategies and leaf morphologies, all of the species exhibited acclimation of photosynthetic heat tolerances linked to the saturation level of thylakoid membrane lipids when grown at higher temperatures. However, this acclimation was insufficient to offset the higher leaf and air temperatures, leading to narrower thermal safety margins [90]. Finally, a study using two of the same species as above did not find evidence of acclimation in the species' thermal optima of photosynthesis or other photosynthetic parameters, but did find acclimatory decreases in photosynthetic capacity and leaf respiration in trees grown at the warmer sites [91]. In an analogous transplant study in the Colombian Andes (Montane-acclim), individuals of 15 tree species with different thermal affinities (i.e., 11 cold-affiliated and 4 warm-affiliated species) have been planted into three common-garden sites spanning a 2000-m elevation gradient corresponding to a ~12 °C gradient in mean annual temperatures. Five months after planting, measures of leaf photosynthesis and respiration showed that all tree species continued to perform best at the temperatures closest to their natural distributions but also showed some evidence of acclimation in photosynthetic and respiratory parameters (with patterns suggesting greater plasticity of photosynthetic capacity in the cold-affiliated vs. warm-affiliated species)[92].

In situ warming experiments have likewise produced mixed evidence for acclimation of tropical trees to rising temperatures. The TRACE project applies a 4 °C warming treatment to understory

plants in a wet Puerto Rican rainforest using infrared heaters. Studies of the two most common species (both small understory shrubs) have shown contrasting results between species. One species responded to warming through an increase in the temperature at which photosynthesis is optimized but did not show any evidence of acclimation of respiration. The second species did not show any evidence of acclimation of respiration and actually exhibited decreased photosynthetic yields, possibly due to lower stomatal conductances under elevated temperatures [93].

The TRACE, Rwanda TREE, and Montane-acclim projects are all ongoing (along with several other transplant studies and field experiments to test the effects of changing water availability - [e.g., 94,95]). Unfortunately, these sorts of experimental studies are generally not logistically or financially feasible for most tropical forests, are limited to small scales and thus cannot include many species or species interactions (for example, the TRACE warming experiment includes three warming plots and three control plots, each of which are just 12 m²), can usually only test for relatively short-term responses in smaller growth forms or early life stages (since it is logistically infeasible to transplant adult trees, wait for planted seeds to grow into adult trees, or manipulate the climate around large trees - for example, in the TRACE warming experiment, the heaters are <3 m above the ground meaning that only smaller understory plants are included), and apply instantaneous or unrealistically fast warming rates [96,97]. These problems are further compounded in laboratory or chamber-based warming experiments, which can provide precise data on physiological responses to temperature and climate [e.g., 98–100] but only for small numbers of isolated and small-statured individuals growing in artificial *ex situ* conditions.

A potential way to overcome some of the intrinsic limitations of these experimental studies and to test for long-term acclimation in adult trees is through longitudinal studies [83]. In longitudinal studies, traits of interest are measured repeatedly through time on individual trees as the climate changes concurrently. However, due to the relative recency of functional trait studies, the individual-level data required for long-term longitudinal studies are non-existent for tropical trees. Indeed, to look at how functional traits have changed on individual trees due to climate change over the past decades, we would need to go back in time to measure functional traits on the trees that are alive today; fortunately, there are at least two approaches that may allow us to do just this – tree rings and herbarium samples.

5. Tropical dendroecology

Annual tree rings are undoubtedly less distinct and less widespread in the tropics than in the temperate and boreal zones, but an increasing number of studies have demonstrated that many tropical tree species (i.e., >230 species; [101,102]) do in fact exhibit visible annual growth rings (including in the wettest perhumid tropical forests [103]). Even in the absence of visible annual rings, it is possible to date wood samples and create chronosequences based on high-resolution isotopic measurements and/or radiocarbon dating [104,105]. Dated wood samples allow for records of individual tree growth rates, wood functional traits (e.g., conduit size and density, cell wall thickness and tissue percentage [106]), and isotopic compositions that can extend back many decades or even centuries. These measurements can be used to test whether or not trees are acclimating to changes in their surrounding environments.

In one study using tree ring measurements to assess patterns of long-term growth in tropical trees, van der Sleen et al. (2015) looked at changes in growth rates and water use efficiency in 12 tropical tree species sampled from three lowland rainforest sites (Bolivia, Thailand, and Cameroon). In accord with the “carbon fertilization” hypothesis, they found significant increases in intrinsic water use efficiency (the rate of moisture loss per unit of carbon gain) in almost all of the species over the past 150 years. They did not, however, find consistent significant changes in site-level tree growth rates [107]. These results are mirrored by findings of dendrochronology studies of other tropical species in other sites [108–110], which show that water use efficiency is increasing in many of the tropical sites and species examined to date (with faster increases at drier vs. wetter sites; [111]), while tree growth rates show nonsignificant or inconsistent changes [110,112]. One interpretation of these results is that tropical trees are acclimating their water use efficiency (potentially through changes in

stomatal traits and stomatal conductances in response to higher CO₂), which reduces the effects of climate change on growth rates.

A more-recent study by Zuidema et al. (2022) collated tree growth measurements from a new tropical tree-ring network and found that annual tree growth rates increased primarily with dry-season precipitation and decreased with dry-season maximum temperature, and that dry-season climate responses were amplified in regions that are drier, hotter, and more climatically variable [113]. Likewise, another recent tree ring study showed that the longevity of trees in the lowland tropics decreases markedly at high temperatures, including temperatures likely to soon be experienced in most lowland tropical forests [102]. Shorter-term plot-based studies also show intraspecific declines in (multi-annual) tropical tree growth and productivity associated with higher temperatures and changes in vapor pressure deficit or water availability [114–117]. These patterns all suggest that many tropical trees may not be able to acclimate their growth rates to new climates and that global warming could lead to widespread declines in productivity and increases in tree mortality. More work is needed to assess long-term patterns of growth, water use efficiency, and mortality in more tropical sites and more tropical species.

6. Historical collections

Another way that we can look back in time and test for long-term acclimation in individual tropical trees is through the use of herbaria and other historical biological collections [16]. To perform a longitudinal study using herbarium specimens, we would need to measure traits on preserved herbarium specimens and then compare these measurements to measurements of the same traits on new samples collected from the same individual source tree from which the herbarium specimen came [118]. Unfortunately, this is rarely possible since botanical collectors do not typically map or mark their individual source trees. However, during the installation of some permanent tropical forest plots, collections were made of the mapped trees to aid with species identifications, and many of the resulting herbarium specimens include the unique tag number of their original source trees. Therefore, by cross-referencing these tag numbers with the most recent plot census data, it should be possible to identify the source trees that are still alive, relocate these source trees within the plots, and then measure a select suite of functional traits on both the historical and modern samples from these trees to test for changes in the traits of individuals through time in relation to local climate change patterns. We are not aware of any such study from the tropics, but this approach was successfully used by Miller Rushing et al. (2009) to test for acclimation of stomatal traits in individual temperate trees growing in the Arnold Arboretum (Boston, MA, USA). As predicted under carbon fertilization, stomatal densities decreased through time. However, there were also concurrent increases in stomatal guard cell lengths and thus no net changes in water use efficiency [118]. An important caveat is that the trees included in this study were growing in a managed arboretum and thus they may have been buffered from many abiotic and biotic stressors. While not at the individual level, a study from the African tropics used historical herbarium samples to show decreases in species' average stomatal densities but decreasing water use efficiency over the last 80 years [119]. Other analyses of herbarium samples (again not at the individual level) have shown leaf size, and specifically leaf width, to decrease through time in some tree species in response to global warming [120,121].

While promising, there are clearly many limitations to both the use of tree rings and herbarium samples. Both of these methods are severely limited by a lack of appropriate species, the small number of samples available per species, and the small number of traits that can be measured on each sample (i.e., most leaf traits require fresh leaf material and thus cannot be measured on preserved specimens). In addition, these methods can be biased by factors that are hard to control for such as the effects of ontogeny (age and size) and changing local abiotic and biotic site conditions on leaf and wood traits. Both methods can also suffer from survivorship bias and the overrepresentation of the individuals and species that can acclimate and tolerate new conditions [122–129]. Despite these and other limitations, tree rings and herbarium samples may be our best tools for assessing the long-term acclimation responses of individual trees to past anthropogenic climate change. In the future, we should also be able to conduct repeat trait censuses of the forests and trees that we are studying now

to test for any acclimation that is currently underway (towards this aim, we encourage researchers to record sufficient metadata to allow for individual-level resurveys and to make their data and metadata publicly available).

Until we can determine if tropical trees can acclimate or not, our ability to predict the fate of tropical forests is greatly limited [130]. For example, Feeley et al. (2012) modeled the potential changes of local tree diversity in Amazonian ecoregions under various scenarios of climate change and deforestation and with different assumptions about 1) the ability of tree species to migrate, 2) the effects of rising CO₂ on water use efficiency, and 3) the ability of species to tolerate higher temperatures through acclimation [131]. By far, the greatest source of uncertainty in the predicted effects of climate change on diversity was the ability of tree species to acclimate or not. If Amazonian trees acclimate to tolerate higher temperatures, then median rates of local tree diversity loss were predicted to be <30% even under the most severe warming and deforestation scenarios. This rate was not dramatically impacted by the ability of species to migrate or by their responses to CO₂. If, on the other hand, tropical tree species cannot adequately acclimate to rising temperatures, the median species loss was predicted to exceed 75% even under the most sanguine scenarios of climate change and deforestation (under the most severe warming and deforestation scenarios, median species losses without acclimation were 100%). As before, changing the presumed ability of species to migrate and their response to CO₂ had essentially no effects on the results [131].

Beyond improving our ability to predict the effects of climate change, understanding how tropical trees acclimate or not will also help to improve our predictions of climate change itself. Many of the Earth System Models that are used to predict changes in temperature and precipitation incorporate information about vegetation and plant traits [132–136]. To improve accuracy of these models it is important to know how traits vary spatially and temporally due to acclimation. Likewise, it is increasingly recognized that better information about thermal acclimation in tropical trees is needed to properly parameterize Dynamic Global Vegetation Models [137–139].

7. Conclusions

Extensive and healthy tropical forests are critical to the future of nature and humanity. Unfortunately, it is not yet clear how the many thousands of tree species that comprise tropical forests are responding to climate change, especially in the face of other anthropogenic disturbances such as habitat loss and defaunation [140]. Given the rapid pace and extreme severity of modern climate change, it is unlikely that tropical tree species can adapt (with the caveat that a small number of species may be able to ‘adapt’ by taking advantage of their mutualistic fungal symbionts’ quicker generation times and adaptability, or by switching mutualistic partners). Many tropical tree species are ‘migrating’; while migrations were sufficient to offset past climate change, they appear insufficient to keep up with current changes in temperatures and precipitation (especially in the context of other anthropogenic disturbances). We argue that the last and best hope for tropical tree species to avoid declines in performance and population densities is acclimation. New methods are being developed to test for acclimation, but at this point we still do not know if tropical tree species can acclimate or what factors may facilitate or prohibit acclimation. As such the future of tropical trees – and thus tropical forests – remains uncertain.

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