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Thermophilization – changes in community composition towards greater relative abundances of species associated with warmer environments – has been described for plants and animals in many locations around the world. Disturbances of various kinds have increased rates of thermophilization in temperate sites, and this has been proposed, but not demonstrated, for some tropical environments. In this study, we tested whether disturbance by a category 4 hurricane in 1988 (Hurricane Gilbert) increased thermophilization in a Jamaican montane forest by using pre- and post-hurricane data collected over four decades (1974–2014). We analysed tree species composition in permanent plots at ca 1580 m above sea level in Jamaica's Blue Mountains. There were 66 tree species with stem diameters ≥ 3 cm at breast height. We used published data on the altitudinal distribution of 62 species (94% of genetic individuals (genets)) to calculate the mean community altitude scores (MCAS) of the trees recorded in each census, as well as the MCAS of the survivors, recruits and dead trees after each decade. We found that thermophilization did occur (i.e. MCAS decreased significantly over time), and that this was due both to a decreasing MCAS of recruits through the four decades (significantly lower than expected in the last three decades) as well as a high MCAS of trees that died. Thermophilization was fastest in the post-hurricane decade, during which time there was marked and significant increase in the MCAS of dead trees; this change was above and beyond expectations of long-term successional dynamics. The rate of compositional change equates to an overall decrease in MCAS of 1.6 m yr^{-1} over the forty-year study period. We conclude that this Jamaican montane forest is undergoing thermophilization (likely due to rising temperature) and that the hurricane-caused disturbance accelerated thermophilization through differential mortality.

Keywords: altitude, climate change, cyclone, forest inventory plots, global warming, mortality, recruitment, species migration, trees, tropical

Introduction

Global warming is causing an upward altitudinal migration of many plant species, leading to local increases in the relative abundances of thermophilic (i.e. heat-loving) species (Lenoir et al. 2008, Fadrique et al. 2018, Feeley et al. 2020, Freeman et al. 2021). It has been hypothesized that disturbances may accelerate thermophilization ('species migrations from lower altitudes to summits'; Erschbamer et al. 2011), because disturbance can hasten the mortality of stressed individuals in suboptimal habitats and open up areas for recruitment (Williams et al. 2021). However, the role of disturbances in influencing the rates and patterns of thermophilization remain largely untested, especially in the tropics.

Previous studies have quantified rates of thermophilization for trees in neotropical forests (Feeley et al. 2011, 2013, Duque et al. 2015) that are in line with an upward shift in regional mean temperatures of 2.0 m yr⁻¹ (based on reported regional warming rates and an average adiabatic lapse rate of 5.5°C km⁻¹, Duque et al. 2015). However, given the short duration of these previous studies, as well as their focus on 'undisturbed' forests, they were not appropriate for determining how factors other than warming that could influence, or contribute to, the changes in relative abundance of species in tree communities observed in tropical montane forests. For example, long-term shifts in community composition could result from forest recovery, through the process of succession, from previous intense and large-scale anthropogenic or natural disturbance, as has been observed in lowland secondary forests in Puerto Rico (Zimmerman et al. 1995, Foster et al. 1999). Additionally, shorter-term impacts on tree community composition, which may punctuate longer-term directional trends (Burslem et al. 2000), could be caused by impacts of individual disturbance events that were not severe enough to initiate a new secondary succession (Bellingham et al. 1995). The influence of each of these factors on tree community composition will be mediated by their relative impacts on the key demographic processes (recruitment, growth and mortality) through the regeneration cycle of the individual tree species (Burslem et al. 2000, Condit et al. 2004), thus reflecting a component of their respective 'regeneration niches' (Grubb 1977b).

Addressing the potential drivers of thermophilization, in Colombian montane forests, Duque et al. (2015) suggested that disturbance by cattle may have facilitated the establishment of species from hotter ranges. In the Peruvian Andes, Lutz et al. (2013) suggested that landslides might facilitate the upward migration of forest species and treelines, and hence thermophilization. In the European Alps, Dainese et al. (2017) reported that roads were a key factor in rapid upward spread of plant species. In larch forest in Siberia, Wang et al. (2019) showed that fire caused upward movement of the tree line, potentially causing thermophilization. In a study of herbs in California, Stevens et al. (2015) concluded that thermophilization was reinforced by disturbance. It thus seems likely that many forms of disturbance, potentially including silvicultural activities, can accelerate thermophilization due to the increased opportunities they provide for recruitment of species from warmer areas (due to increased dispersal of propagules or greater availability of sites suitable for establishment), and perhaps increased mortality of species from cooler areas.

In this paper, we evaluate changes in tree species composition in tropical montane rain forests in Jamaica over a 40-year period, which included a major disturbance event, a category 4 tropical cyclone (Hurricane Gilbert), 14 years after the study began. Tree species alpha diversity (stems ≥ 3 cm dbh) increased after the hurricane, as did mortality and recruitment (Tanner and Bellingham 2006, Tanner et al. 2014); mortality of hurricane-damaged stems was higher than undamaged stems for up to 19 years post-hurricane (Tanner et al. 2014). Thus, there is reason to suspect that the effect of this hurricane on composition had the potential to influence the process of thermophilization, and that this might be evident for decades.

Our primary research objective was to answer the questions 'are tropical montane forests in Jamaica experiencing thermophilization?' and if so, 'what processes and factors have influenced the rate of thermophilization in these forests that are subject to severe hurricane impact?' To address this, we first calculated the mean community altitude score (MCAS) for the trees in a set of permanent forest plots in five censuses (1974, 1984, 1994, 2004 and 2014) and tested for changes in the MCAS through time in the overall tree community as well as separately for recruits and dying trees in each decade. These analyses revealed that MCAS was decreasing through time and that this was due both to a decreasing MCAS of recruits through the four decades as well as a high MCAS of trees that died. We then assessed the variation in rate of thermophilization amongst the four decades and between ecological species groups in order to determine what factors might be driving thermophilization rates, including the potential roles of warming, long-term succession and the disturbance impact of a major hurricane.

Methods

The study plots, the climate and the hurricane

This study was conducted using data from four closely-located plots (called 'sites' in previous papers) spanning a narrow altitudinal range at ca 1580 m, but differing in topographic position, forest structure and species composition. The four plots were in the Blue and John Crow Mountains National Park, Jamaica (18°5′N, 76°39′W, 1543–1610 m elevation; maps in Tanner 1977, Chai et al. 2012); the Blue Mountains have forest cover from ca 500 to 2256 m. Each study plot was 0.06–0.10 ha in area: Col forest (Gap forest of Tanner 1977, 0.09 ha sampled); Wet Slope forest (0.1 ha); Mull Ridge forest (0.1 ha) and Mor Ridge forest (0.06 ha); hereafter abbreviated to Col, Slope, Mull and Mor. The Col, Mull and Mor plots are on the ridge top, at 1580, 1580 and 1620 m respectively, the Slope plot is on the north side of

the ridge at ca 1560 m. Across all years for stems ≥ 3 cm dbh there were 2332 genets containing 2981 ramets; comprising 66 tree species in total; 38 in the Col, 53 in the Slope, 46 in the Mull and 17 in the Mor plot. The forest at the plot sites is evergreen tropical upper montane rain forest (sensu Grubb 1977a), it is not a 'mossy' forest (photos in Grubb and Tanner 1976). The plots were selected in 1974 as being representative of the most common forest types in the western Blue Mountains for a study of nutrient cycling; subsequently, they became valuable as permanent plots to study forest dynamics. The forest in the Mull and perhaps the Col plots is probably old secondary, dating from the mid-1800s when coffee plantations in the area were abandoned (Chai and Tanner 2011). The soils are more than one metre deep on the ridge crest (Col, Mull and Mor) but in the Slope they are shallower, up to 30 cm, and of variable depth. Soils were well-drained, surface water was seen only once in many years, in the Col, after heavy rains; there was no gleying (due to waterlogging) in any of the soil profiles.

The mean annual temperature above the canopy in a shielded weather station on nearby Bellevue Peak (1822 m) was 15.9°C in 1995 (Hafkenscheid 2000). The long-term mean annual rainfall at Cinchona Botanic Garden was 2275 mm (located ca 4 km SSE of the plots at about 1480 m altitude, ca 100 m lower than our site, and in a partial rainfall shadow of the main ridge of the Blue Mountains). Rainfall above the plot sites was measured in three separate years: 1974–1975, 1977–1978 and 1980–1981, in those three years it was on average 8% higher than that at Cinchona. There are occasional dry periods at Cinchona – months with less than 60 mm rainfall (potential evapotranspiration was 800 mm per year, Kapos and Tanner 1985). Rainfall data for 1974–2014 from nine locations (all at lower altitudes than the plots) in the adjacent Parish of Portland (Portland extends from the crest of the Blue Mountains to the north coast, the study plots are on its south-western boundary) show that on average there was less than one month per year between 1974 and 2014 with less than 60 mm of rainfall and that 2005 had the largest mean (1.6) of consecutive months with < 60 mm of rainfall (Supporting information); we conclude that there were no major droughts in our site between 1974 and 2014 and therefore dismiss drought as a potential cause of variation in thermophilization rate during the study period. The annual mean relative humidity was 85% in 1995, the monthly mean relative humidity was above 80% for every month; net radiation was 53% of potential radiation due to persistent cloud; cloudy conditions persisted even in drier periods (Hafkenscheid 2000). There is very little fog-drip from intercepted cloud water under the tree canopy; a shielded and covered fog gauge on the crest of the range (Bellevue Peak; 1822 m) recorded fog input of only 7% of precipitation in 1995 (Hafkenscheid 2000).

Hurricanes have repeatedly affected the forests in the plot sites (McLaren et al. 2019). The hurricanes that might have had a strong effect were: Gilbert in 1988 (4 on Saffir–Simpson scale), Charlie in 1951 (3 on S–S) and unnamed storms in 1912 and 1903 (both 3 on S–S). Other hurricanes between 1852 and 2014 were more distant from Jamaica and/or of lower strength, and would have had minimal effects on the plots. Hurricane Charlie in 1951 had a ca 30% lower windspeed than Gilbert (McLaren et al. 2019). Effects on mortality of the hurricanes before Gilbert would have become non-significant by 1974. However, changes in species composition due to these previous hurricanes would still be evident during the study period; indeed, the forest will likely always be in some stage of change due to previous hurricanes (McLaren et al. 2019).

Hurricane Gilbert struck Jamaica in September 1988. It 'immediately' killed about 2% of stems in the study forests, and 13% of stems over the subsequent 16-year period (Tanner and Bellingham 2006). The hurricane uprooted 5% of stems, broke crowns from 4% of stems and completely defoliated 19% of stems, thus increasing light availability at the forest floor for up to 33 months after the hurricane (Bellingham et al. 1995, 1996).

Mortality, recruitment, hurricane damage, community altitudes and thermophilization rates

In each of the four plots, all stems ≥ 3 cm diameter at breast height (dbh) were measured, labelled, marked with a paint ring and identified to species in 1974, 1984, 1994, 2004 and 2014; dead stems were located and tallied. Taxonomic nomenclature follows Adams (1972) and Proctor (1985), except where other authorities are listed. Stems (ramets) were grouped into genetic individuals (genets) for calculations of recruitment, mortality and thermophilization rates (see below; previous papers using earlier parts of the same data set have used ramet data). We focused on mortality and recruitment of genets because multi-stemmed genets are common in Jamaican montane forests (e.g. 16% of genets were multi-stemmed across widespread plots; Bellingham and Sparrow 2009). Mortality of stems on multi-stemmed genets is often offset by recruitment of stems on the same genet so that these genets persist, with mortality rates more than 5 times lower than that of single-stemmed genets (Bellingham and Sparrow 2009). As such, genet-based analyses are more indicative, than ramet based analyses, of fundamental changes in community composition, with longer-term significance. Mortality and recruitment rates in each plot were calculated over four decadal census intervals from 1974 to 2014 using the following formulae. Mortality (% yr^{-1}) is: $100 \times (1 - [1 - (N_0 - N_1)/N0]^{1/t})$, where N_0 = number of genets at the beginning of a period, N_1 = number of survivors at the end of a period and t = time in years. Recruitment (% yr^{-1}) is: $100 \times (1 - (1 - N_r/N_t)^{1/t})$, where N_r = number of recruits during a period and N_t is the number of genets at the end of the period. Diameter growth rates (mm yr^{-1}) were calculated using stem (ramet) data. Hurricane damage was assessed in 1989: stems were recorded as dead or alive, and separately as uprooted, broken or defoliated; stem heights were estimated in 1991.

Mean altitude values, for Jamaica, were calculated for 62 of the 66 tree species (94% of genets) as the midpoint of the

species' ranges as reported in Adams (1972), Proctor (1985), Adams (2014) and Mill (2015). The vast majority of the altitude data come from Adams (1972), who was careful to include only data based on herbarium specimens or trusted authorities (pers. comm. 1974). As a check, inclusion of later, somewhat higher, altitude records from Bellingham et al. (1995) did not affect the overall patterns we describe. An overall mean community altitude score (MCAS) was then calculated for each census based on the mean species altitude values weighted by the number of genets per species. Next, the thermophilization rate (TR, m yr^{-1}) over each 10-year census period was calculated for all four plots combined as the annualized differences in MCAS. To test if the observed TRs differed from expectations due to random changes in composition, we compared the observed TR (TR$_{observed}$) over each decadal census period to a distribution of null values generated through permutation-based simulations. For the simulations, the species altitude values were randomly swapped between individuals within each of the four plots and a TR$_{null}$ was then calculated for each the four subsequent census intervals. This process was reiterated 50 000 times to generate a distribution of TR$_{null}$ values for each interval. By swapping species altitude values between the individual genets, each individual's overall timeline of recruitment and mortality was preserved, as well as the number of individuals, species diversity, mortality rate and recruitment rate in each plot in each period. In other words, the permutation algorithm maintains the observed forest structure and dynamics, but breaks any association between changes in composition and the species altitude values. An interval's TR$_{observed}$ was considered significantly different from random if it fell outside the 95% quantiles of the corresponding TR$_{null}$ values.

We also calculated the MCAS of just the genets that recruited or died over each census interval. Under upward species migrations and thermophilization, we predicted that the MCAS of recruits would be lower than expected by random chance and that the MCAS of dying trees would be higher than expected by chance leading to the lower-altitude species increasing in relative abundance and the higher-altitude species decreasing in relative abundance in the plots. As with TR, the observed MCAS values were compared to null expectations based on the repeated swapping of the species altitude values between the genets within each plot. We also assessed the MCAS and TR of each of the four plots separately (Supporting information).

In order to investigate the alternative mechanism of possible long-term succession, rather than warming, causing the detected changes in tree community composition, we assessed changes in the MCAS of genets within groups of species differing in their regeneration ecology. Bellingham et al. (1994) and McDonald et al. (2003) classified 35 of the species in the plots into 11 groups which we amalgamated into four ecological groups: pioneers (9 species, 399 genets in 2014); gap-favoured (14 species, 414 genets in 2014); shade-tolerant (6 species, 252 genets in 2014) and species that rarely had seedlings (6 species, 44 genets in 2014); these 35 species represented 80% of genets present in 2014. For the pioneers,

gap-favoured and shade-tolerant species, we calculated the MCAS in each census and the TR over each decadal period due to differential recruitment and mortality.

Results

Changes in forest structure and community composition over 40 years

The number of living genets in the plots was 1.5% lower in 2014 than in 1974; 42% of the genets alive in 1974 had died by 2014 and 41% of the genets alive in 2014 were recruited after 1974. The changes in total basal area were smaller – total basal area was 0.5% lower in 2014 than in 1974; stems comprising 11% of the basal area alive in 1974 had died by 2014 and 10% of the total basal area in 2014 was accounted for by stems recruited after 1974. The species composition changed somewhat over the 40 years; the Bray–Curtis similarity of genets in 1974 and 2014 was 75% (Supporting information). Some ecological groups changed more than others. Eight of the nine pioneer species showed decreases in their number of genets between 1974 and 2014, five of the 14 gap-favoured species decreased (one was unchanged and eight increased) and the seven shade-tolerators mostly increased or showed no change in abundance. These decreases in abundance of pioneer species and increases in shade-tolerators suggest that slow succession was occurring in these plots, notwithstanding the major impact of Hurricane Gilbert 14 years after the initial census, which did not cause marked changes in the trends in the post-hurricane decade (Supporting information).

Mortality and recruitment of genets in the four sites before and after the hurricane in 1988

The combined-site mortality rates over the four decadal census intervals were 1.25, 2.07, 1.17 and 1.40% yr^{-1} (Fig. 1). The highest mortality rate (66% higher than the pre-hurricane rate) was in the decade including Hurricane Gilbert (1984–1994); rates in the following two decades were similar to that in the pre-hurricane decade. Recruitment rates of genets were 1.53, 2.55, 1.61 and 1.16% yr^{-1} (Fig. 1), with the rate in the decade including Hurricane Gilbert (2.55% yr^{-1}) being 67% higher than the rate in the pre-hurricane decade. Recruitment decreased in the post-hurricane decade to close to the pre-hurricane rate, and then decreased further during the final decade.

Changes over time in mean community altitude

There were no significant differences amongst the four plots in their mean community altitude scores (MCAS) across the four decades of the study period (Supporting information); therefore, they were combined for subsequent analyses. The MCAS of genets (all four plots combined) decreased by nearly 60 m over the 40-year study period, from 1335 m in 1974 to 1276 m in 2014 (Fig. 2A) with the fastest

Figure 1. Rates (% yr^{-1}) of genet mortality and recruitment over decadal census intervals between 1974 and 2014 (for four sites combined). Mortality rates are indicated by black lines and recruitment rates are indicated by gray lines. The vertical dashed line indicates Hurricane Gilbert in September 1988.

change occurring 1994–2004. Thermophilization rates (TR) averaged 1.6 m yr^{-1} over the four decades. Observed TR were significantly faster than expected to occur under random composition changes in all of the census decades except 1984–1994 (Fig. 2B). These directional changes in composition (increasing relative abundances of species from lower altitudes) were the result of both greater genet recruitment of species with lower mean altitude values and greater genet mortality of species with higher mean altitude values (Fig. 3). The MCAS of the recruits was lower than expected in all four decades, significantly so in the last three decades 1984–2014 (Fig. 3B). The MCAS of the dying genets was always higher than that of the recruiting genets and was significantly higher than expected by chance during 1994–2004 (Fig. 3A). Thus, the accelerated thermophilization that occurred in the post-hurricane decade (1994–2004) was due to the much larger MCAS of dying genets during that decade and the smaller, but still significantly, lower MCAS of recruits, which continued during 1984–2014.

When species were grouped according to their regeneration ecologies, we found that there were significant decreases in MCAS through time within both the shade-tolerant and gap-favoured species groups, but not within the pioneer group (Fig. 4). For the shade-tolerant species, TR was significantly faster than expected in the 1974–1984 and 1984–1994 census periods, and for the gap-favoured species, TR was faster than expected in the 1984–1994 and 1994–2004 periods. The thermophilization of the gap-favoured and shade-tolerant species was due to the lower MCAS of recruiting individuals rather than dying individuals; this difference was most striking for gap-favoured species in the post-hurricane period of 1994–2004 when the MCAS of dying individuals was markedly higher than expected (Supporting information).
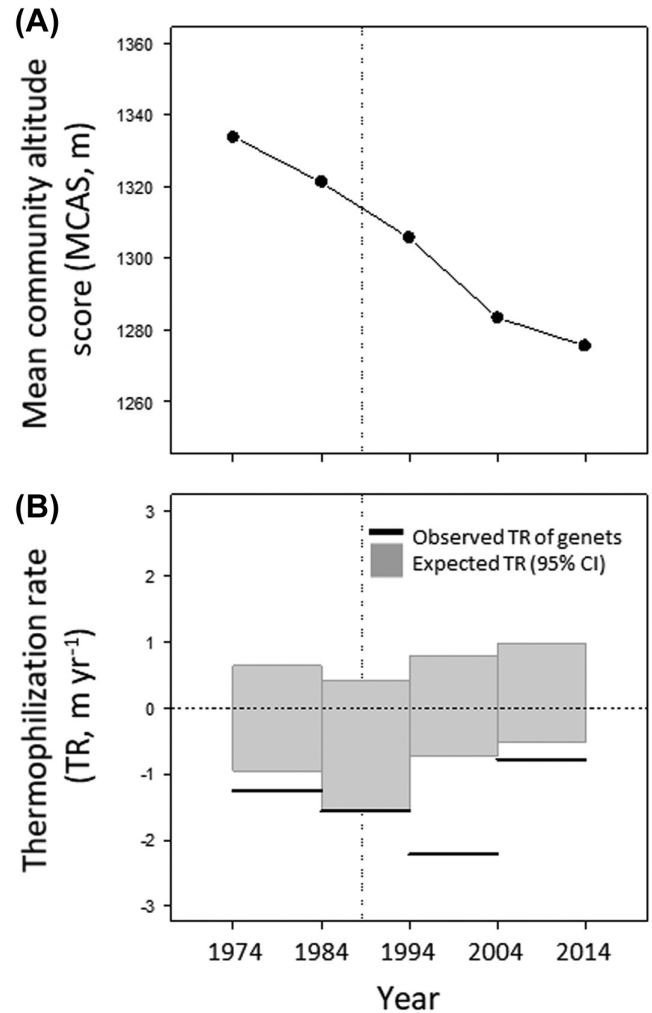

Figure 2.(A) Mean community altitude scores (MCAS, m) of tree genets recorded in plot censuses from 1974 to 2014, and (B) thermophilization rates (TR, m yr^{-1}; TR is calculated as the annualized change in MCAS – i.e. the line slopes from panel A) over the decadal census intervals. In B, the gray bars indicate the 95% confidence intervals of TR$_{null}$ values in each census interval, and the black lines indicate the observed TR (see text). Negative TR values indicate a decrease in MCAS, which is indicative of increasing relative abundances of lower-altitude tree species. The vertical dashed line indicates Hurricane Gilbert in September 1988.

Discussion

Changes in tree species composition over time in Jamaican montane forest

A powerful category 4 hurricane in September 1988 (Hurricane Gilbert) caused increased mortality and recruitment in Jamaica's montane forests (Fig. 1). The increased mortality, especially among damaged stems, continued for nearly two decades after the hurricane (Tanner et al. 2014). This major disturbance appears to have accelerated ongoing processes of compositional change and thermophilization. The recruits in each decade between 1974 and 2014 included a greater
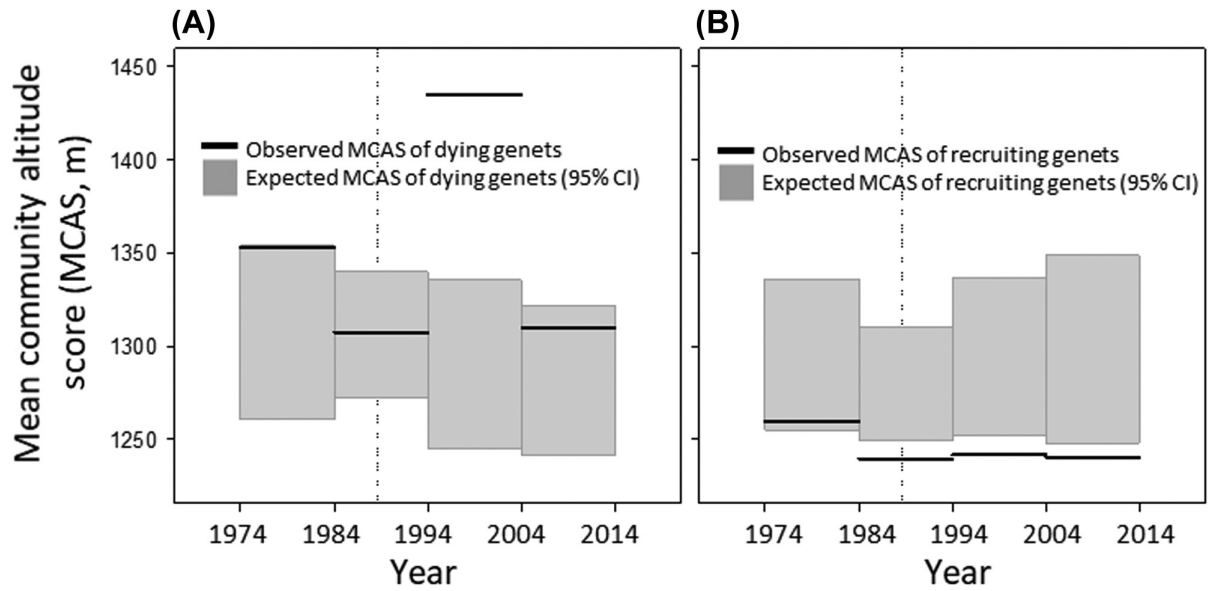
Figure 3. The mean community altitude scores (MCAS, m) of tree genets (A) dying and (B) recruiting over the decadal census intervals between 1974 and 2014. The gray bars indicate the 95% confidence intervals of expected MCAS values and black lines indicate observed values. The vertical dashed line indicates Hurricane Gilbert in September 1988.
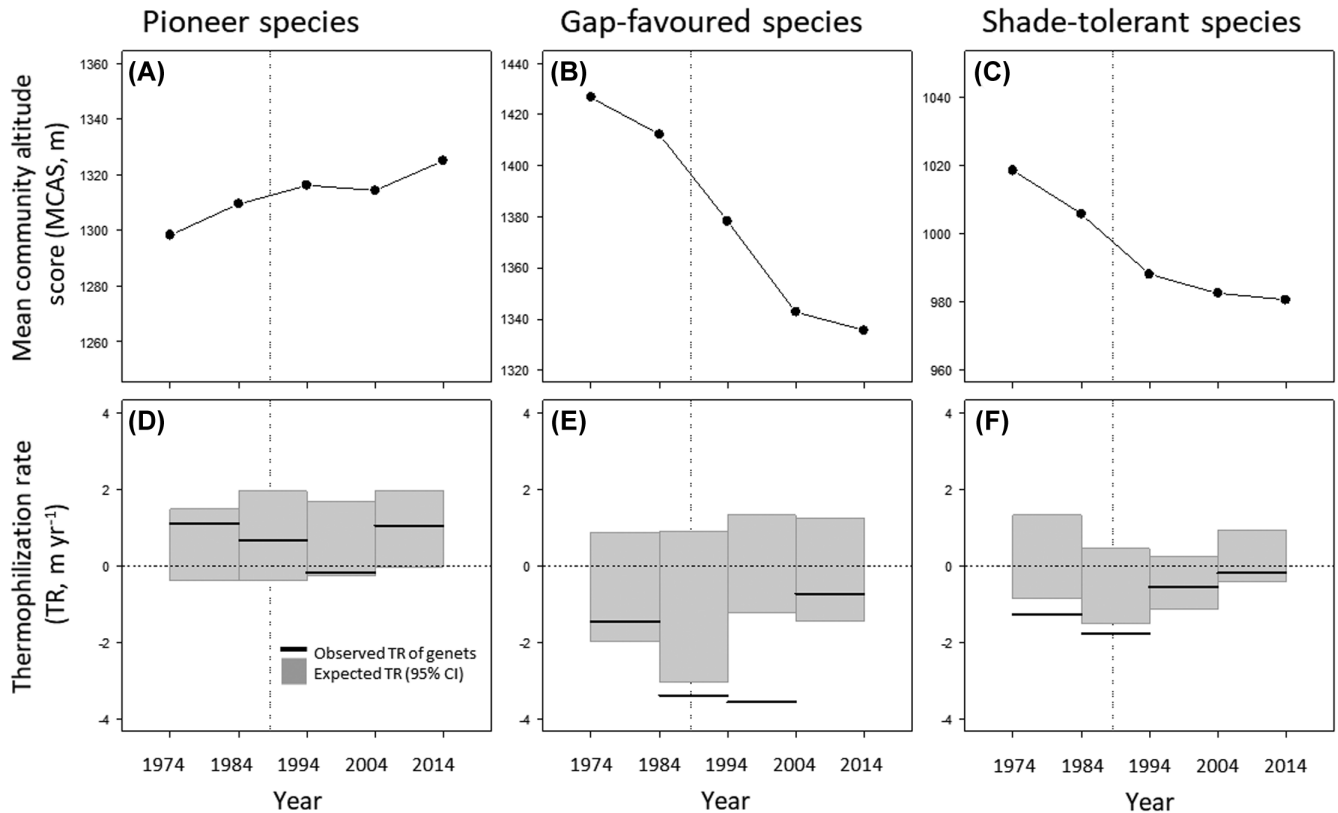

Figure 4. (A–C) Mean community altitude scores (MCAS, m) of tree genets recorded in plot censuses from 1974 to 2014 within pioneer, gap-favoured and shade-tolerant ecological groups, and (D–F) thermophilization rates (TR, m yr^{-1}) over the decadal census intervals for each ecological group (the gray bars indicate the 95% confidence intervals of TR$_{null}$ values in each census interval, and the black lines indicate the observed TR). Negative TR values indicate a decrease in MCAS, which is indicative of increasing relative abundances of lower-altitude tree species. The vertical dashed line indicates Hurricane Gilbert in September 1988. Pioneer species (n = 9), gap-favoured species (n = 14) and shade-tolerant species (n = 6) accounted for 399, 414 and 252 genets in 2014, respectively. Note that the y-axes differ between panels in the top row.

proportion of lower-altitude species, and the genets dying included a greater proportion of higher-altitude species; both compared with the existing community. These non-random patterns of mortality and recruitment combined to drive directional changes in composition – thermophilization – as reflected in the greater decrease in MCAS than expected by chance. Thermophilization was especially pronounced in the 1994–2004 decade, when there was a marked and significant spike in the average species altitude values of dying trees (note that an elevated loss of high-altitude species leads to a decrease in MCAS). While we hypothesize that this elevated thermophilization rate reflects a hurricane effect, this interpretation must be conditional as we have no data from a control forest, which was not struck by a hurricane, over the same period.

While the continuing decrease of MCAS fits with the predicted effects of rising temperature, these observed changes in composition may have also been driven at least in part by slow vegetation succession initiated by the series of intensive hurricane impacts in the early 20th century followed by an exceptionally long period with little hurricane disturbance until Hurricane Charlie (category 3) in 1951 and Hurricane Gilbert (category 4) in 1988 (McLaren et al. 2019) and/ or the human disturbance to the forests in the area of the study sites prior to the abandonment of coffee plantations ca 150 years ago (Chai and Tanner 2011). It was suspected that long-term succession may have contributed to the observed thermophilization of the sites in Jamaica because the species we classified as 'shade-tolerant', which increased over the 40-year study, had a lower mean altitude score (977 m) than the pioneer species (1219 m), which decreased in abundance. However, our analyses indicate that the decreased abundance of pioneer species from 1994 to 2004 did not affect the observed pattern of thermophilization. In fact, when changes of composition were assessed within the separate ecological groups, we found that both the gap-favoured and shade-tolerant species groups exhibited steady thermophilization over the 4-decade study period, and that thermophilization was particularly strong for gap-favoured species in the decades including and after Hurricane Gilbert (Fig. 4) due particularly to the death of high-elevation individuals. The increased MCAS of mortality in the post-hurricane decade was not a result of the death of trees recruited post-hurricane (1989–1994) – only 17% of the mean MCAS of mortality during 1994–2004 was due to such recruits. Thus, the changes in composition after the hurricane are in addition to any ongoing long-term thermophilization due to succession. We conclude that the observed thermophilization over the 40-year period was most likely to be due to rising temperatures favouring a steady recruitment of lower-altitude species (which were already present in the plots) and that it was accelerated in the post-hurricane decade by increased mortality of higher-altitude species, especially within the gap-favoured ecological group.

Rates of thermophilization have previously been quantified for neotropical montane tree communities in Peru, Colombia and Costa Rica (Feeley et al. 2011, Feeley et al. 2013, Duque et al. 2015). The 1.6 m yr⁻¹ decrease in mean community altitude score in Jamaica is very similar to the rates observed in Colombia (2.0 m yr⁻¹, 95% confidence interval 0.4–4.0 m yr⁻¹, Duque et al. 2015), Peru (1.1 m yr⁻¹, 95% confidence interval 0.4–1.9 m yr⁻¹, Feeley et al. 2011) and Costa Rica (1.2 m yr⁻¹, 95% confidence interval 0.1–2.4 m yr⁻¹, Feeley et al. 2013) (note that the original studies have variably reported positive or negative rates to indicate thermophilization, but in all cases – including in Jamaica – there have been increases in the relative abundance of lower-altitude, thermophilic, species through time). Comparing our new results with these previous studies shows that the different approaches (decadal measurements at one altitude in Jamaica versus shorter-term measurement in plots at a range of altitudes on mainland tropical mountains) result in similar findings – increases in the relative abundances of lower-altitude species and decreases in the relative abundances of higher-altitude species through time. In Costa Rica and Colombia, it was the mortality of species with higher-altitude distributions that was the main cause of thermophilization (Feeley et al. 2013, Duque et al. 2015); in Jamaica, both the recruitment of lower-altitude species and the mortality of higher-altitude species were important. Unique amongst these studies, thermophilization in Jamaica was markedly accelerated by a severe disturbance event, a category 4 hurricane, which caused significantly increased mortality of higher-altitude species in the post-hurricane decade.

Characteristics associated with tree mortality and recruitment, and their contribution to thermophilization, in Jamaica

We investigated whether there were characteristics of individuals or species that were correlated with mortality and recruitment, irrespective of species ecological group, partly because some of these characteristics were not well-correlated with successional status in this forest. An example of this lack of expected correlation was in wood density, which was higher in shade-tolerant species, but was not significantly different between 'pioneer' and 'gap-favoured' species. This lack of difference is because some of the 'pioneers' are slow-growing species (with high wood density) that colonise the mineral soil of landslides (Dalling 1994).

Factors affecting tree mortality are likely to be different from those affecting recruitment, and each can affect the other. Mortality can have many causes: windthrow, shading, drought, pests and diseases; recruitment, on the other hand, is determined by seed sources, germination, persistence and growth of seedlings below the canopy. Mortality and recruitment are linked because disturbance increases mortality, which in turn increases opportunities for recruitment, and increased recruitment results in a greater subsequent mortality of small trees.

Mortality in our plots in the post-hurricane decade was highly non-random, such that genets of higher-altitude species tended to be lost faster than expected. Species-level measures of pre-hurricane diameter growth, stem height

and key traits such as leaf nitrogen and wood density (Tanner 1977, Bellingham et al. 1995) were not correlated with mortality (Supporting information). Thus we could not find any characteristics or traits of the higher-altitude species (besides mean altitude) that predicted their higher mortality compared with the lower-altitude species in the post-hurricane decade. More specific information about the 'neighbourhood' around each genet might provide future post-hurricane studies with a better understanding of the causes of such mortality.

Recruitment (into the ≥ 3 cm dbh tree community) of genets came consistently from species with a lower mean altitude than expected by chance. When forests are compared across large altitudinal ranges on tropical mountains, those at lower-altitude generally have higher leaf nitrogen concentrations (Grubb 1977a) and higher wood density but, in the Jamaican forests, species' leaf nitrogen and wood density were not correlated with the number of recruits per species. Future studies of thermal physiology may help to determine the factors leading to differential recruitment under rising temperatures.

The changes in the tree community in the plots in Jamaica are overwhelmingly due to changes in relative abundance within the existing set of species within both the shade-tolerant and gap-favoured ecological groups. Although species diversity increased somewhat after the hurricane, that increase was due to a few rare species recruiting into the plots from the surrounding forests at the same altitude, not from lower altitudes (Tanner and Bellingham 2006).

When we assessed the plots separately (Supporting information), changes in species composition were smallest in the Mor plot. Compared with the Mull, Slope and Col plot sites, the Mor site had a higher altitude and a distinct physiognomy of shorter, usually leaning, trees, with smaller leaves (Grubb and Tanner 1976). The Mor site soil had a surface organic layer of mor humus about 50 cm thick with a pH about 3, which would likely have deterred deforestation of this site since its soil is unsuitable for coffee and other crops. The tree community of the Mor site also had a higher mean altitude and lower rate of thermophilization (Supporting information). This accords with the finding in Colombia where the three plots with negative thermal migration rates (i.e. with increasing relative abundances of highland species) were all at higher altitudes than the plots with positive thermophilization rates (Duque et al. 2015). Not all montane forests show evidence of upward range shifts and thermophilization. For example, in subtropical montane forests in Taiwan, which are often disturbed by typhoons, 56% of tree species were found to have juveniles occurring at lower altitudes than conspecific adults – suggesting the potential for future downward range shifts (versus 35% of species with juveniles occurring at higher altitudes than conspecific adults; O'Sullivan et al. 2020). Likewise, in temperate montane systems, downward range shifts have been observed as a result of changing disturbance regimes (Zhang et al. 2019) or changes in water balance (Crimmins et al. 2011). Taken together, these findings suggest that, in many cases, higher-altitude sites with environmental conditions that are tolerated by only a subset of tree species will show lower rates of thermophilization (or even negative thermophilization) compared with lower-altitude sites on the same mountain ranges (Mamantov et al. 2021).

Climate change in the Jamaican Mountains

There are no recent, continuous long-term climate records from the upper elevations of mountains in Jamaica. Data for Kingston airport at sea level show a warming of 0.027°C yr^{-1} (Climate Studies Group 2012) and according to Berkeley Earth's extrapolated curated climate station database, the mean annual temperature for all of Jamaica increased by 0.015 ± 0.003°C yr^{-1} since the 1960s (<http://berkeleyearth.lbl.gov/regions/jamaica>). Assuming a typical moist air lapse rate of 5.5°C km^{-1}, warming of 0.015–0.027°C yr^{-1} equates to an increase in altitude of ca 2.7–4.9 m yr^{-1}. Thus, the rate of change in the MCAS of trees in Jamaica (1.6 m yr^{-1}) is much slower than the likely rate of simultaneous warming, as may be expected because of the time lag for the ecological processes (Jump and Peñuelas 2005) and the potential for some species to avoid range shifts through acclimation and/or adaptation. The 'slow' thermophilization rates further suggest that there is capacity for much more climate-driven compositional changes in these forests. Temperature changes seem to be the predominant climate change in the Jamaican mountains, since annual rainfall has not changed consistently during 1971–2015, according to records from the Parish of Portland or the Chelsa climatologies (<https://chelsa-climate.org/>). That said, even in the absence of changes in precipitation, rising temperatures may lead to greater vapour pressure deficit and evapotranspiration, which could contribute to a differential influence on recruitment and mortality (Esquivel-Muelbert et al. 2019).

Conclusion

In summary, thermophilization in Jamaican mountains was observed to occur throughout our 40-year study period, significantly so for at least the last 30 years, and notably faster from 1994 to 2004 following the severe disturbance caused by a major hurricane in 1988. The accelerated thermophilization in the post-hurricane decade was due to the greater mortality of higher-altitude species and, to a lesser extent, the greater recruitment of lower-altitude species, the vast majority of which were already growing in the sites. However, we could not identify the proximate causes of higher mortality of higher-altitude species in the post-hurricane decade. Many more detailed studies of the thermal physiology of species, coupled with observations of individual stems, their neighbouring trees (competition effects), the patchiness of disturbance and the environmental conditions (soil etc.) in their immediate surroundings, and how these conditions are affected by disturbances, will be necessary to identify the causes of the higher mortality of higher-altitude species and recruitment of lower-altitude species that is driving thermophilization.

Author contributions

Edmund V. J. Tanner: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Writing – original draft (lead); Writing – review and editing (equal). **Peter Bellingham**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Writing – review and editing (equal). **John Healey**: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Project administration (equal); Resources (equal); Writing – review and editing (equal). **Kenneth Feeley**: Conceptualization (lead); Formal analysis (equal); Methodology (lead); Software (lead); Writing – review and editing (equal).

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Data availability statement

Data and R codes are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.s4mw6m989> (Tanner et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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