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Tanner, Edmund V. J.; Bellingham, Peter J; Healey, John; Feeley, Kenneth J

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TITLE

Hurricane disturbance accelerated the thermophilization of a Jamaican montane forest

AUTHORS and affiliations

Edmund V. J. Tanner, Department of Plant Sciences, University of Cambridge, UK

& Smithsonian Tropical Research Institute, Panama, Republic of Panama

Peter, J. Bellingham, Manaaki Whenua – Landcare Research, Lincoln, NZ and School of

Biological Sciences, University of Auckland, NZ

John R. Healey, School of Natural Sciences, Bangor University, Gwynedd, UK

Kenneth J. Feeley, Department of Biology, University of Miami, Coral Gables, FL, USA

Correspondence

Edmund V. J. Tanner, Department of Plant Sciences, University of Cambridge, Attenborough Building, Pembroke Street, Cambridge, CB2 3QZ, UK. Email evt1@cam.ac.uk

RUNNING HEAD Thermophilization and hurricane disturbance

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

38 *Key words:* Tropical; altitude; recruitment; mortality; trees; climate change; cyclone; forest
39 inventory plots; global warming; species migration.

40 INTRODUCTION

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

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

67 Addressing the potential drivers of thermophilization, in Colombian montane forests,
68 Duque et al. (2015) suggested that disturbance by cattle may have facilitated the establishment
69 of species from hotter ranges. In the Peruvian Andes, Lutz et al. (2013) suggested that

70 landslides might facilitate the upward migration of forest species and treelines, and hence
71 thermophilization. In the European Alps, Dainese et al. (2017) reported that roads were a key
72 factor in rapid upward spread of plant species. In larch forest in Siberia, Wang et al. (2019)
73 showed that fire caused upward movement of the tree line, potentially causing
74 thermophilization. In a study of herbs in California, Stevens et al. (2015) concluded that
75 thermophilization was reinforced by disturbance. It thus seems likely that many forms of
76 disturbance, potentially including silvicultural activities, can accelerate thermophilization due to
77 the increased opportunity they provide for recruitment of species from warmer areas (due to
78 increased dispersal of propagules or greater availability of sites suitable for establishment), and
79 perhaps increased mortality of species from cooler areas.

80 In this paper, we evaluate changes in tree species composition in tropical montane rain
81 forests in Jamaica over a 40-year period, which included a major disturbance event, a Category
82 4 tropical cyclone (Hurricane Gilbert), 14 years after the study began. Tree species alpha
83 diversity (stems ≥ 3 cm dbh) increased after the hurricane, as did mortality and recruitment
84 (Tanner and Bellingham 2006, Tanner et al. 2014); mortality of hurricane-damaged stems was
85 higher than undamaged stems for up to 19 years post-hurricane (Tanner et al. 2014). Thus, there
86 is reason to suspect that the effect of this hurricane on composition had the potential to
87 influence the process of thermophilization, and that this might be evident for decades.

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

100

101 **METHODS**

102 *The study plots, the climate and the hurricane*

103 This study was conducted using data from four closely-located plots (called ‘sites’ in previous
104 papers) spanning a narrow altitudinal range at c. 1580 m, but differing in topographic position,
105 forest structure and species composition. The four plots were in the Blue and John Crow
106 Mountains National Park, Jamaica (18° 5′N, 76° 39′W, 1543–1610 m elevation; maps in Tanner
107 1977, Chai et al. 2012); the Blue Mountains have forest cover from c. 500 m to 2,256 m. Each
108 study plot was 0.06 to 0.1 ha in area: Col forest (Gap forest of Tanner 1977, 0.09 ha sampled);
109 Wet Slope forest (0.1 ha); Mull Ridge forest (0.1 ha) and Mor Ridge forest (0.06 ha); hereafter
110 abbreviated to Col, Slope, Mull and Mor. The Col, Mull and Mor plots are on the ridge top, at
111 1580 m, 1580 m, and 1620 m respectively, the Slope plot is on the north side of the ridge at c.
112 1560 m. Across all years for stems ≥ 3 cm dbh there were 2332 genets containing 2981 ramets;
113 comprising 66 tree species in total; 38 in the Col, 53 in the Slope, 46 in the Mull, and 17 in the
114 Mor plot. The forest at the plot sites is evergreen tropical upper montane rain forest (sensu Grubb
115 1977a), it is not a ‘mossy’ forest (photos in Grubb and Tanner 1976). The plots were selected in
116 1974 as being representative of the most common forest types in the western Blue Mountains for
117 a study of nutrient cycling; subsequently, they became valuable as permanent plots to study
118 forest dynamics. The forest in the Mull and perhaps the Col plots is probably old secondary,
119 dating from the mid-1800s when coffee plantations in the area were abandoned (Chai and Tanner
120 2011). The soils are more than one metre deep on the ridge crest (Col, Mull, and Mor) but in the
121 Slope they are shallower, up to 30 cm, and of variable depth. Soils were well-drained, surface
122 water was seen only once in many years, in the Col, after heavy rains; there was no gleying (due
123 to waterlogging) in any of the soil profiles.

124 The mean annual temperature above the canopy in a shielded weather station on nearby
125 Bellevue Peak (1822 m) was 15.9 °C in 1995 (Hafkenschied 2000). The long-term mean annual
126 rainfall at Cinchona Botanic Garden was 2275 mm (located c. 4 km SSE of the plots at about
127 1480 m altitude, c. 100 m lower than our site, and in a partial rainfall shadow of the main ridge
128 of the Blue Mountains). Rainfall above the plot sites was measured in three separate years:
129 1974–1975, 1977–1978 and 1980–1981, in those three years it was on average 8% higher than

130 that at Cinchona. There are occasional dry periods at Cinchona – months with less than 60 mm
131 rainfall (potential evapotranspiration was 800 mm per year, Kapos and Tanner 1985). Rainfall
132 data for 1974–2014 from nine locations (all at lower altitudes than the plots) in the adjacent
133 Parish of Portland (Portland extends from the crest of the Blue Mountains to the north coast, the
134 study plots are on its south-western boundary) show that on average there was less than one
135 month per year between 1974 and 2014 with less than 60 mm of rainfall and that 2005 had the
136 largest mean (1.6) of consecutive months with < 60 mm of rainfall (Appendix S1); we conclude
137 that there were no major droughts in our site between 1974 and 2014 and therefore dismiss
138 drought as a potential cause of variation in thermophilization rate during the study period. The
139 annual mean relative humidity was 85% in 1995, the monthly mean relative humidity was
140 above 80% for every month; net radiation was 53% of potential radiation due to persistent
141 cloud; cloudy conditions persisted even in drier periods (Hafkenscheid 2000). There is very
142 little fog-drip from intercepted cloud water under the tree canopy; a shielded and covered fog
143 gauge on the crest of the range (Bellevue Peak; 1822 m) recorded fog input of only 7% of
144 precipitation in 1995 (Hafkenscheid 2000).

145 Hurricanes have repeatedly affected the forests in the plot sites (McLaren et al. 2019).
146 The hurricanes that might have had a strong effect were: Gilbert in 1988 (4 on Saffir–Simpson
147 scale), Charlie in 1951 (3 on S–S), and unnamed storms in 1912 and 1903 (both 3 on S–S).
148 Other hurricanes between 1852 and 2014 were more distant from Jamaica and/or of lower
149 strength, and would have had minimal effects on the plots. Hurricane Charlie in 1951 had a c.
150 30% lower windspeed than Gilbert (McLaren et al. 2019). Effects on mortality of the hurricanes
151 before Gilbert would have become non-significant by 1974. However, changes in species
152 composition due to these previous hurricanes would still be evident during the study period;
153 indeed, the forest will likely always be in some stage of change due to previous hurricanes
154 (McLaren et al. 2019).

155 Hurricane Gilbert struck Jamaica in September 1988. It ‘immediately’ killed about 2%
156 of stems in the study forests, and 13% of stems over the subsequent 16-year period (Tanner and
157 Bellingham 2006). The hurricane uprooted 5% of stems, broke crowns from 4% of stems and
158 completely defoliated 19% of stems, thus increasing light availability at the forest floor for up to
159 33 months after the hurricane (Bellingham et al. 1995, 1996).

160

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

162 In each of the four plots, all stems ≥ 3 cm diameter at breast height (dbh) were measured,
163 labelled, marked with a paint ring and identified to species in 1974, 1984, 1994, 2004, and
164 2014; dead stems were located and tallied. Taxonomic nomenclature follows Adams (1972) and
165 Proctor (1985), except where other authorities are listed. Stems (ramets) were grouped into
166 genetic individuals (genets) for calculations of recruitment, mortality and thermophilization
167 rates (see below; previous papers using earlier parts of the same data set have used ramet data).
168 We focused on mortality and recruitment of genets because multi-stemmed genets are common
169 in Jamaican montane forests (e.g., 16% of genets were multi-stemmed across widespread plots;
170 Bellingham and Sparrow 2009). Mortality of stems on multi-stemmed genets is often offset by
171 recruitment of stems on the same genet so that these genets persist, with mortality rates more
172 than 5 times lower than that of single-stemmed genets (Bellingham and Sparrow 2009). As
173 such, genet-based analyses are more indicative of fundamental changes in community
174 composition, with longer-term significance, than ramet-based analyses. Mortality and
175 recruitment rates in each plot were calculated over four decadal census intervals from 1974 to
176 2014 using the following formulae. Mortality (% yr⁻¹) is: $100 \times (1 - [1 - (N_0 - N_1)/N_0]^{1/t})$, where
177 N_0 = number of genets at the beginning of a period, N_1 = number of survivors at the end of a
178 period, and t = time in years. Recruitment (% yr⁻¹) is: $100 \times (1 - (1 - N_r/N_t)^{1/t})$, where N_r =
179 number of recruits during a period and N_t is the number of genets at the end of the period.
180 Diameter growth rates (mm yr⁻¹) were calculated using stem (ramet) data. Hurricane damage
181 was assessed in 1989: stems were recorded as dead or alive, and separately as uprooted, broken
182 or defoliated; stem heights were estimated in 1991.

183 Mean altitude values, for Jamaica, were calculated for 62 of the 66 tree species (94% of
184 genets) as the midpoint of the species' ranges as reported in Adams (1972), Proctor (1985),
185 Adams (2014), and Mill (2015). The vast majority of the altitude data come from Adams
186 (1972), who was careful to include only data based on herbarium specimens or trusted
187 authorities (pers. comm. 1974). As a check, inclusion of later, somewhat higher, altitude records
188 from Bellingham et al. (1995) did not affect the overall patterns we describe. An overall Mean
189 Community Altitude Score (MCAS) was then calculated for each census based on the mean

190 species altitude values weighted by the number of genets per species. Next, the
191 thermophilization rate (TR , $m\ yr^{-1}$) over each 10-year census period was calculated for all four
192 plots combined as the annualized differences in MCAS. To test if the observed TR s differed
193 from expectations due to random changes in composition, we compared the observed TR
194 ($TR_{observed}$) over each decadal census period to a distribution of null values generated through
195 permutation-based simulations. For the simulations, the species altitude values were randomly
196 swapped between individuals within each of the four plots and a TR_{null} was then calculated for
197 each the four subsequent census intervals. This process was reiterated 50,000 times to generate
198 a distribution of TR_{null} values for each interval. By swapping species altitude values between the
199 individual genets, each individual's overall timeline of recruitment and mortality was preserved,
200 as well as the number of individuals, species diversity, mortality rate and recruitment rate in
201 each plot in each period. In other words, the permutation algorithm maintains the observed
202 forest structure and dynamics, but breaks any association between changes in composition and
203 the species altitude values. An interval's $TR_{observed}$ was considered significantly different from
204 random if it fell outside the 95% quantiles of the corresponding TR_{null} values.

205 We also calculated the MCAS of just the genets that recruited or died over each census
206 interval. Under upward species migrations and thermophilization, we predicted that the MCAS
207 of recruits would be lower than expected by random chance and that the MCAS of dying trees
208 would be higher than expected by chance leading to the lower altitude species increasing in
209 relative abundance and the higher altitude species decreasing in relative abundance in the plots.
210 As with TR , the observed MCAS values were compared to null expectations based on the
211 repeated swapping of the species altitude values between the genets within each plot. We also
212 assessed the MCAS and TR of each of the four plots separately (Appendices S2-S3).

213 In order to investigate the alternative mechanism of possible long-term succession,
214 rather than warming, causing the detected changes in tree community composition, we assessed
215 changes in the MCAS of genets within groups of species differing in their regeneration ecology.
216 Bellingham et al. (1994) and McDonald et al. (2003) classified 35 of the species in the plots into
217 11 groups which we amalgamated into four ecological groups: pioneers (9 species, 399 genets
218 in 2014); gap-favoured (14 species, 414 genets in 2014); shade-tolerant (6 species, 252 genets in
219 2014) and species that rarely had seedlings (6 species, 44 genets in 2014); these 35 species

220 represented 80% of genets present in 2014. For the pioneers, gap-favoured, and shade-tolerant
221 species, we calculated the MCAS in each census and the TR over each decadal period due to
222 differential recruitment and mortality.

223

224

225 RESULTS

226 *Changes in forest structure and community composition over 40 years*

227 The number of living genets in the plots was 1.5% lower in 2014 than in 1974; 42% of
228 the genets alive in 1974 had died by 2014, and 41% of the genets alive in 2014 were recruited
229 after 1974. The changes in total basal area were smaller – total basal area was 0.5% lower in
230 2014 than in 1974; stems comprising 11% of the basal area alive in 1974 had died by 2014 and
231 10% of the total basal area in 2014 was accounted for by stems recruited after 1974. The species
232 composition changed somewhat over the 40 years; the Bray–Curtis similarity of genets in 1974
233 and 2014 was 75% (Appendix S4). Some ecological groups changed more than others. Eight of
234 the nine pioneer species showed decreases in their number of genets between 1974 and 2014,
235 five of the 14 gap-favoured species decreased (one was unchanged and eight increased) and the
236 seven shade-tolerators mostly increased or showed no change in abundance. These decreases in
237 abundance of pioneer species and increases in shade-tolerators suggest that slow succession was
238 occurring in these plots, notwithstanding the major impact of Hurricane Gilbert 14 years after
239 the initial census, which did not cause marked changes in the trends in the post-hurricane
240 decade (Appendix S4).

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

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

250

251



252

253 Fig. 1. Rates (% yr⁻¹) of genet mortality and recruitment over decadal census intervals between
254 1974 and 2014 (for four sites combined). Mortality rates are indicated by black lines and
255 recruitment rates are indicated by gray lines. The vertical dashed line indicates Hurricane
256 Gilbert in September 1988.

257

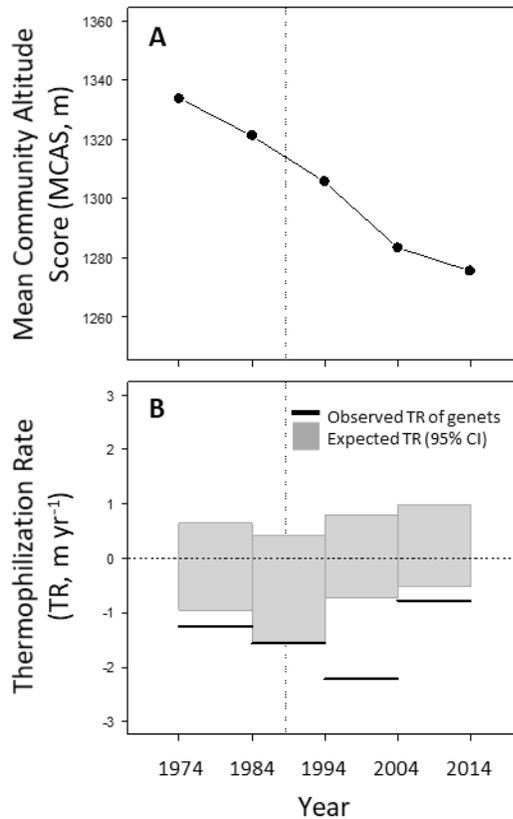
258

259 *Changes over time in mean community altitude*

260 There were no significant differences amongst the four plots in their Mean Community
261 Altitude Scores (MCAS) across the four decades of the study period (Appendix S2); therefore,
262 they were combined for subsequent analyses. The MCAS of genets (all four plots combined)
263 decreased by nearly 60 m over the 40-year study period, from 1335 m in 1974 to 1276 m in
264 2014 (Fig. 2A) with the fastest change occurring 1994–2004. Thermophilization rates (TR)
265 averaged 1.6 m yr⁻¹ over the four decades. Observed TR were significantly faster than expected
266 to occur under random composition changes in all of the census decades except 1984–1994
267 (Fig. 2B). These directional changes in composition (increasing relative abundances of species
268 from lower latitudes) were the result of both greater genet recruitment of species with lower
269 mean altitude values and greater genet mortality of species with higher mean altitude values
270 (Fig. 3). The MCAS of the recruits was lower than expected in all four decades, significantly so
271 in the last three decades 1984–2014 (Fig. 3B). The MCAS of the dying genets was always
272 higher than that of the recruiting genets and was significantly higher than expected by chance
273 during 1994–2004 (Fig. 3A). Thus, the accelerated thermophilization that occurred in the post-
274 hurricane decade (1994–2004) was due to the much larger MCAS of dying genets during that
275 decade and the smaller, but still significantly, lower MCAS of recruits, which continued during
276 1984–2014.

277 When species were grouped according to their regeneration ecology, we found that there
278 were significant decreases in MCAS through time within both the shade-tolerant and gap-
279 favoured species groups, but not within the pioneer group (Fig. 4). For the shade-tolerant species,
280 TR was significantly faster than expected in the 1974–1984 and 1984–1994 census periods, and
281 for the gap-favoured species, TR was faster than expected in the 1984–1994 and 1994–2004
282 periods. The thermophilization of the gap-favoured and shade-tolerant species was due to the
283 lower MCAS of recruiting individuals than dying individuals; this difference was most striking
284 for gap-favoured species in the post-hurricane period of 1994–2004 when the MCAS of dying
285 individuals was markedly higher than expected (Appendix S5).

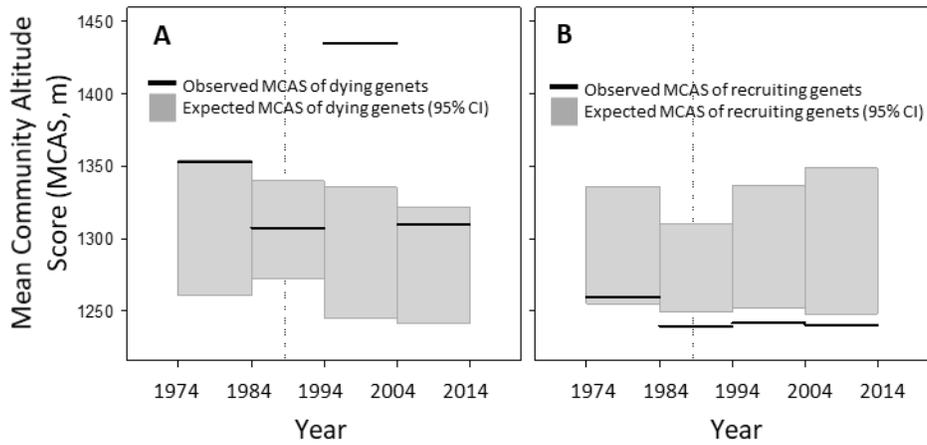
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287

288 Fig. 2. (A) Mean Community Altitude Scores (MCAS, m) of tree genets recorded in plot
 289 censuses from 1974 to 2014, and (B) Thermophilization Rates (TR, m yr⁻¹; TR is calculated as
 290 the annualized change in MCAS – i.e., the line slopes from panel A) over the decadal census
 291 intervals. In B, the gray bars indicate the 95% Confidence Intervals of TR_{null} values in each
 292 census interval, and the black lines indicate the observed TR (see text). Negative TR values
 293 indicate a decrease in MCAS, which is indicative of increasing relative abundances of lower
 294 altitude tree species. The vertical dashed line indicates Hurricane Gilbert in September 1988.

295



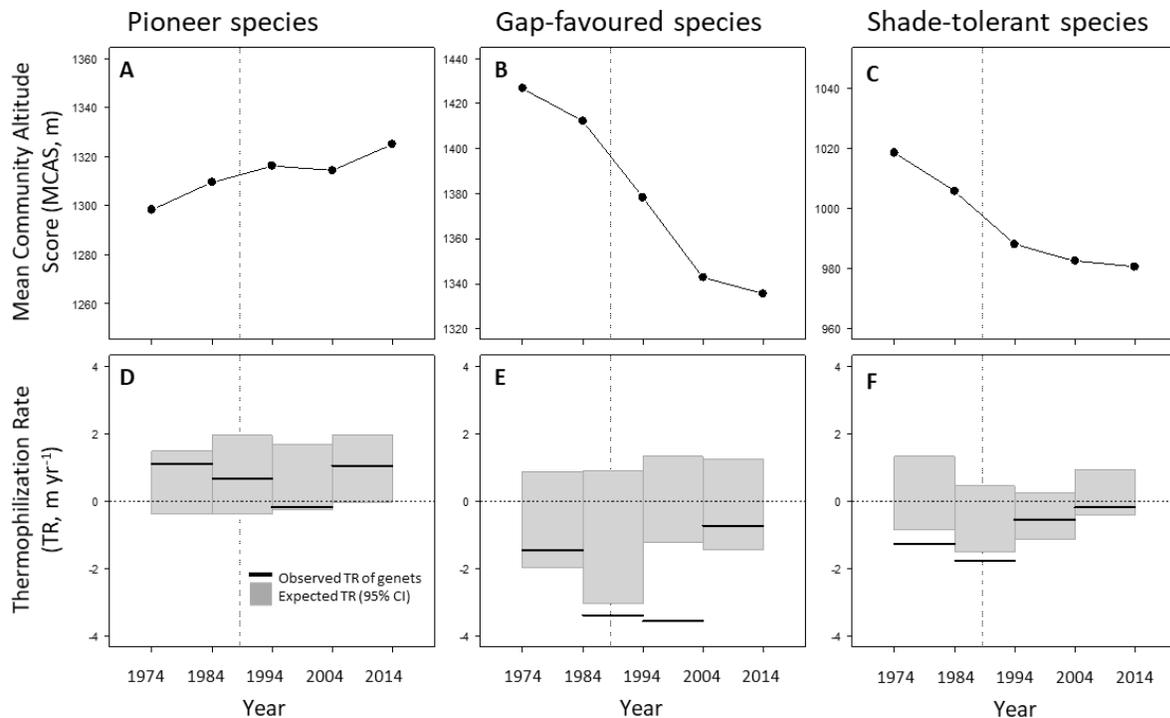
297

298 Fig. 3. The Mean Community Altitude Scores (MCAS, m) of tree genets (A) dying and (B)
 299 recruiting over the decadal census intervals between 1974 and 2014. The gray bars indicate the
 300 95% Confidence Intervals of expected MCAS values and black lines indicate observed values.
 301 The vertical dashed line indicates Hurricane Gilbert in September 1988.

302

303

304



305

306 Fig. 4. (A-C) Mean Community Altitude Scores (MCAS, m) of tree genets recorded in plot
307 censuses from 1974 to 2014 within pioneer, gap-favoured, and shade-tolerant ecological groups,
308 and (D-F) Thermophilization Rates (TR, m yr⁻¹) over the decadal census intervals for each
309 ecological group (the gray bars indicate the 95% Confidence Intervals of TR_{null} values in each
310 census interval, and the black lines indicate the observed TR). Negative TR values indicate a
311 decrease in MCAS, which is indicative of increasing relative abundances of lower altitude tree
312 species. The vertical dashed line indicates Hurricane Gilbert in September 1988. Pioneer species
313 (n = 9), gap-favoured species (n = 14), and shade-tolerant species (n = 6) accounted for 399,
314 414, and 252 genets in 2014, respectively. Note that the y-axes differ between panels in the top
315 row.

316 **DISCUSSION**

317 *Changes in tree species composition over time in Jamaican montane forest*

318 A powerful Category 4 hurricane in September 1988 (Hurricane Gilbert) caused
319 increased mortality and recruitment in Jamaica's montane forests (Fig. 1). The increased
320 mortality, especially among damaged stems, continued for nearly two decades after the
321 hurricane (Tanner et al. 2014). This major disturbance appears to have accelerated ongoing
322 processes of compositional change and thermophilization. The recruits in each decade between
323 1974 and 2014 included a greater proportion of lower altitude species, and the genets dying
324 included a greater proportion of higher-altitude species; both compared with the existing
325 community. These non-random patterns of mortality and recruitment combined to drive
326 directional changes in composition – thermophilization – as reflected in the greater decrease in
327 MCAS than expected by chance. Thermophilization was especially pronounced in the 1994–
328 2004 decade, when there was a marked and significant spike in the average species altitude
329 values of dying trees (note that an elevated loss of high-altitude species leads to a decrease in
330 MCAS). While we hypothesize that this elevated thermophilization rate reflects a hurricane
331 effect, this interpretation must be conditional as we have no data from a control forest, which
332 was not struck by a hurricane, over the same period.

333 While the continuing decrease of MCAS fits with the predicted effects of rising
334 temperature, these observed changes in composition may have also been driven at least in part
335 by slow vegetation succession initiated by the series of intensive hurricane impacts in the early
336 20th century followed by an exceptionally long period with little hurricane disturbance until
337 Hurricane Charlie (category 3) in 1951 and Hurricane Gilbert (category 4) in 1988 (McLaren et
338 al. 2019) and/or the human disturbance to the forests in the area of the study sites prior to the
339 abandonment of coffee plantations c. 150 years ago (Chai and Tanner 2011). It was suspected
340 that long-term succession may have contributed to the observed thermophilization of the sites in
341 Jamaica because the species we classified as 'shade-tolerant', which increased over the 40-year
342 study, had a lower mean altitude score (977 m) than the pioneer species (1219 m), which
343 decreased in abundance. However, our analyses indicate that the decreased abundance of
344 pioneer species from 1994 to 2004 did not affect the observed pattern of thermophilization. In
345 fact, when changes of composition were assessed within the separate ecological groups, we

346 found that both the gap-favoured and shade-tolerant species groups exhibited steady
347 thermophilization over the 4-decade study period, and that thermophilization was particularly
348 strong for gap-favoured species in the decades including and after Hurricane Gilbert (Fig. 4)
349 due particularly to the death of high-elevation individuals. The increased MCAS of mortality in
350 the post-hurricane decade was not a result of the death of trees recruited post-hurricane (1989–
351 1994) – only 17% of the mean MCAS of mortality during 1994–2004 was due to such recruits.
352 Thus, the changes in composition after the hurricane are in addition to any ongoing long-term
353 thermophilization due to succession. We conclude that the observed thermophilization over the
354 40-year period was most likely to be due to rising temperatures favouring a steady recruitment
355 of lower altitude species (which were already present in the plots) and that it was accelerated in
356 the post-hurricane decade by increased mortality of higher altitude species, especially within the
357 gap-favoured ecological group.

358 Rates of thermophilization have previously been quantified for neotropical montane tree
359 communities in Peru, Colombia and Costa Rica (Duque et al. 2015, Feeley et al. 2011, Feeley et
360 al. 2013). The 1.6 m yr^{-1} decrease in mean community altitude score in Jamaica is very similar
361 to the rates observed in Colombia (2.0 m yr^{-1} , 95% confidence interval $0.4 - 4.0 \text{ m yr}^{-1}$, Duque
362 et al. 2015), Peru (1.1 m yr^{-1} , 95% confidence interval $0.4 - 1.9 \text{ m yr}^{-1}$, Feeley et al. 2011), and
363 Costa Rica (1.2 m yr^{-1} , 95% confidence interval $0.1 - 2.4 \text{ m yr}^{-1}$, Feeley et al. 2013) (note that
364 the original studies have variably reported positive or negative rates to indicate
365 thermophilization, but in all cases – including in Jamaica – there have been increases in the
366 relative abundance of lower altitude, thermophilic, species through time). Comparing our new
367 results with these previous studies shows that the different approaches (decadal measurements
368 at one altitude in Jamaica versus shorter-term measurement in plots at a range of altitudes on
369 mainland tropical mountains) result in similar findings – increases in the relative abundances of
370 lower altitude species and decreases in the relative abundances of higher altitude species
371 through time. In Costa Rica and Colombia, it was the mortality of species with higher altitude
372 distributions that was the main cause of thermophilization (Duque et al. 2015, Feeley et al.
373 2013); in Jamaica, both the recruitment of lower-altitude species and the mortality of higher-
374 altitude species were important. Unique amongst these studies, thermophilization in Jamaica
375 was markedly accelerated by a severe disturbance event, a Category 4 hurricane, which caused
376 significantly increased mortality of higher-altitude species in the post-hurricane decade.

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

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

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

393 Mortality in our plots in the post-hurricane decade was highly non-random, such that
394 genets of higher-altitude species tended to be lost faster than expected. Species-level measures
395 of pre-hurricane diameter growth, stem height, and key traits such as leaf nitrogen and wood
396 density (Tanner 1977, Bellingham et al. 1995) were not correlated with mortality (Appendix
397 S6). Thus we could not find any characteristics or traits of the higher altitude species (besides
398 mean altitude) that predicted their higher mortality compared with the lower altitude species in
399 the post-hurricane decade. More specific information about the ‘neighbourhood’ around each
400 genet might provide future post-hurricane studies with a better understanding of the causes of
401 such mortality.

402 Recruitment (into the ≥ 3 cm dbh tree community) of genets came consistently from
403 species with a lower mean altitude than expected by chance. When forests are compared across
404 large altitudinal ranges on tropical mountains, those at lower altitude generally have higher leaf
405 nitrogen concentrations (Grubb 1977a) and higher wood density but, in the Jamaican forests,

406 species' leaf nitrogen and wood density were not correlated with the number of recruits per
407 species. Future studies of thermal physiology may help to determine the factors leading to
408 differential recruitment under rising temperatures.

409 The changes in the tree community in the plots in Jamaica are overwhelmingly due to
410 changes in relative abundance within the existing set of species within both the shade-tolerant
411 and gap-favoured ecological groups. Although species diversity increased somewhat after the
412 hurricane, that increase was due to a few rare species recruiting into the plots from the
413 surrounding forests at the same altitude, not from lower altitudes (Tanner and Bellingham
414 2006).

415 When we assessed the plots separately (Appendices S2 and S3), changes in species
416 composition were smallest in the Mor plot. Compared with the Mull, Slope and Col plot sites,
417 the Mor site had a higher altitude and a distinct physiognomy of shorter, usually leaning, trees,
418 with smaller leaves (Grubb and Tanner 1976). The Mor site soil had a surface organic layer of
419 mor humus about 50 cm thick with a pH about 3, which would likely have deterred
420 deforestation of this site since its soil is unsuitable for coffee and other crops. The tree
421 community of the Mor site also had a higher mean altitude and lower rate of thermophilization
422 (Appendix S2). This accords with the finding in Colombia where the three plots with negative
423 thermal migration rates (i.e., with increasing relative abundances of highland species) were all
424 at higher altitudes than the plots with positive thermophilization rates (Duque et al. 2015). Not
425 all montane forests show evidence of upward range shifts and thermophilization. For example,
426 in subtropical montane forests in Taiwan, which are often disturbed by typhoons, 56% of tree
427 species were found to have juveniles occurring at lower altitudes than conspecific adults -
428 suggesting the potential for future downward range shifts (vs. 35% of species with juveniles
429 occurring at higher altitudes than conspecific adults; O'Sullivan et al. 2020). Likewise, in
430 temperate montane systems, downward range shifts have been observed as a result of changing
431 disturbance regimes (Zhang et al. 2019) or changes in water balance (Crimmins et al. 2011).
432 Taken together, these findings suggest that, in many cases, higher altitude sites with
433 environmental conditions that are tolerated by only a subset of tree species will show lower
434 rates of thermophilization (or even negative thermophilization) compared with lower altitude
435 sites on the same mountain ranges (Mamatov et al. 2021).

436 *Climate change in the Jamaican Mountains*

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

454

455 **CONCLUSION**

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

466 how these conditions are affected by disturbances, will be necessary to identify the causes of the
467 higher mortality of higher altitude species and recruitment of lower altitude species that is
468 driving thermophilization.

469

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494 **Author contributions**

495 **Edmund Tanner:** Conceptualisation (equal); Data collection (lead); Writing – original draft
496 (lead); Writing review and editing (lead); Resources (equal). **Peter Bellingham:**
497 Conceptualisation (equal); Data collection (lead); Writing review and editing (equal); Resources
498 (equal). **John Healey:** Conceptualisation (equal); Data collection (equal); Writing review and
499 editing (equal); Resources (equal). **Kenneth Feeley:** Conceptualisation (lead); Formal analysis
500 (lead); Writing review and editing (equal).

501

502 **DATA AVAILABILITY STATEMENT**

503 Data and R codes are included as supplemental documents.

504

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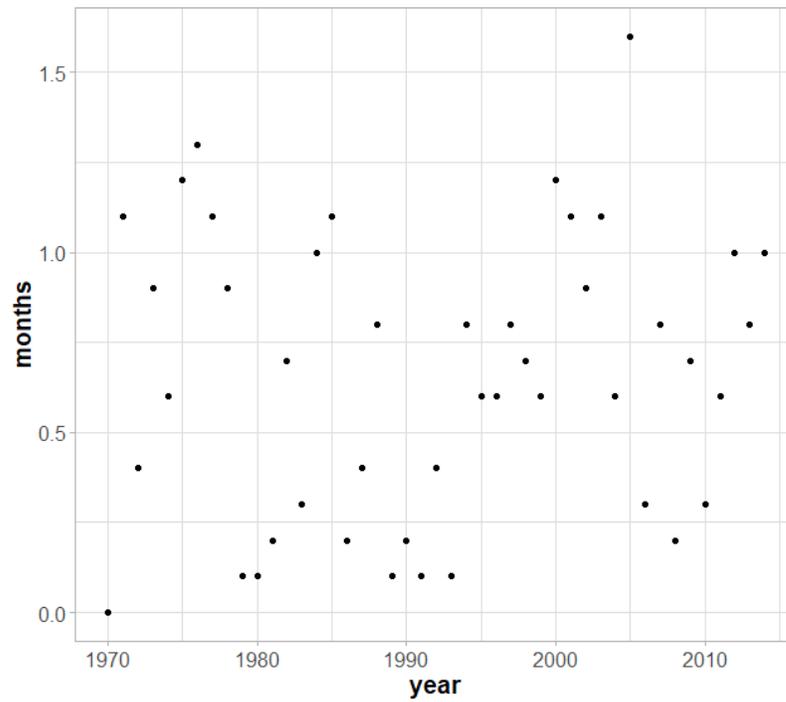
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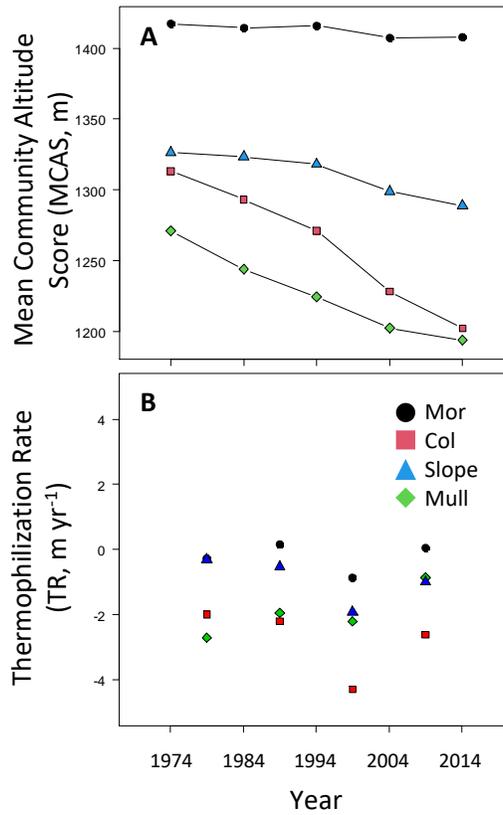
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605 Appendix S1. Mean number (of nine stations in the Parish of Portland, Jamaica) of consecutive
606 months in each year with < 60 mm rainfall. (e.g. of calculation, the mean for 2005 is from nine
607 stations whose number of consecutive months with < 60 mm rainfall was 2, 2, 2, 2, 2, 2, 1, 1, 0).

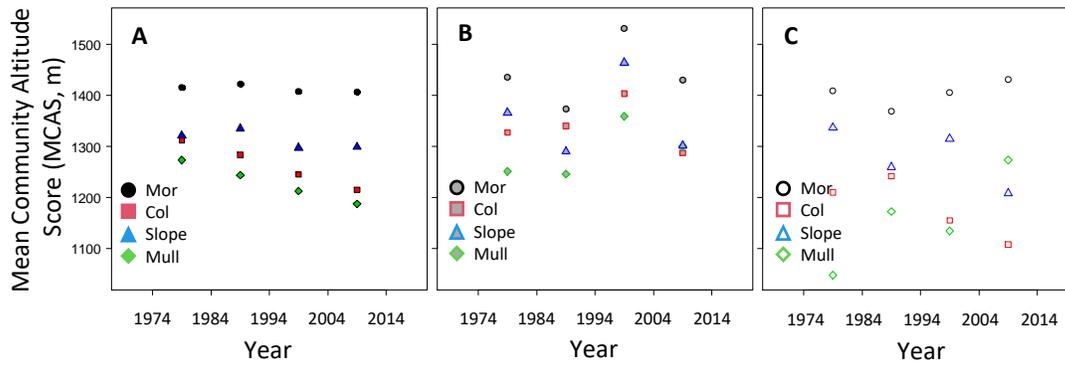


608

609 Appendix S2. The (A) Mean Community Altitude Scores (MCAS, m) of tree genets recorded in
 610 the four individual study sites in plot censuses from 1974 to 2014, and (B) Thermophilization
 611 Rates (TR, m yr⁻¹) for each site over the decadal census intervals. In B, points indicate the
 612 average TR over each of the corresponding intervals. Differences between the sites in MCAS
 613 and thermophilization rates were not significant.

614

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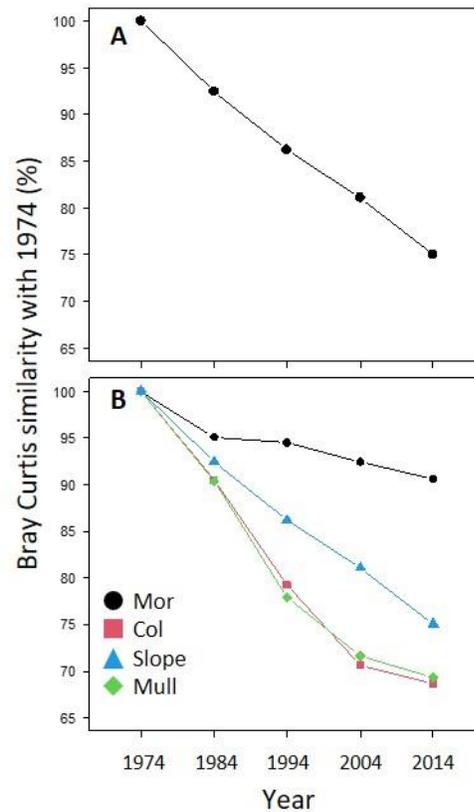


616

617 Appendix S3. The Mean Community Altitude Scores (MCAS, m) of tree genets (A) surviving,
618 (B) dying, and (C) recruiting in each of the four study sites over the decadal census intervals
619 from 1974 to 2014. Points indicate the average rates over each of the corresponding intervals.

620

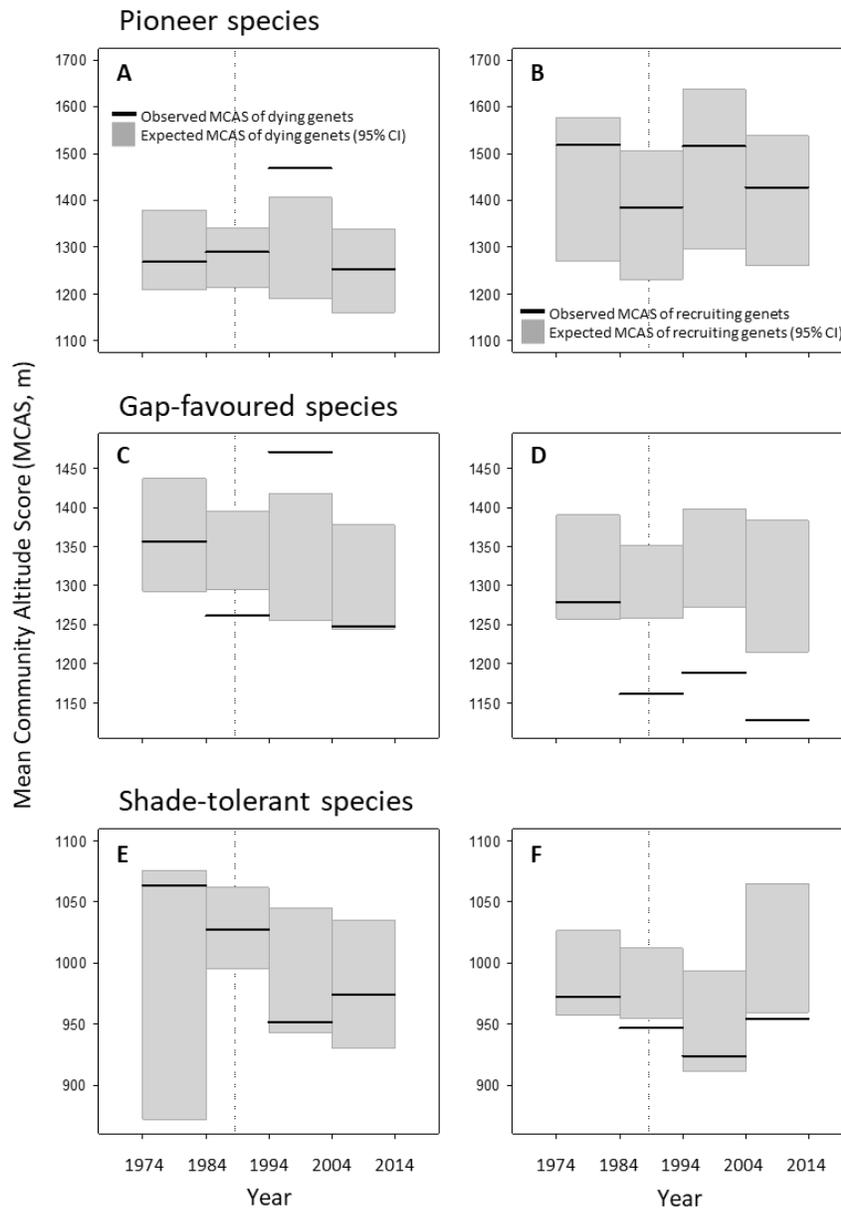
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622

623 Appendix S4. The Bray-Curtis similarity (%) of the tree communities relative to the initial
624 census in 1974 recorded in (A) all sites combined and (B) each individual site.

625



627

628 Appendix S5. The Mean Community Altitude Scores (MCAS, m) of tree genets (A, C, E) dying
 629 and (B, D, F) recruiting over the decadal census intervals between 1974 and 2014 within the
 630 Pioneer, Gap-favoured, and Shade-tolerant species ecological groups. The gray bars indicate the
 631 95% Confidence Intervals of expected MCAS values and black lines indicate observed values.
 632 The vertical dashed line indicates Hurricane Gilbert in September 1988. Note that the y-axes
 633 differ between rows.

634 Appendix S6. Tree species in Jamaican montane rain forests where $n \geq 19$ genets per species listed in descending order of abundance, with
635 annualised mortality rates in the post-hurricane (1994–2004) decade, mean elevation, and species traits (wood density, foliar N
636 concentration, diameter growth rates in the pre-hurricane (1974–1984) decade, and height. Pearson correlation coefficients and associated
637 P values between traits of individual species and annualised mortality rates in the post-hurricane (1994–2004) decade and mean elevation
638 of the same species. n denotes the number of species with available trait data from a total of ≥ 19 genets per species, and for the number of
639 species with traits for correlations.

Species	Family	n	Annual mortality (94–04) (%/yr)	Mean elevation (m)	Wood density (g/ml)	Foliar N (%)	Diameter growth (74–84) (cm/yr)	Height (m)
<i>Hedyosmum arborescens</i>	Chloranthaceae	303	0.009	1125.0	0.64	1.71	0.83	6.50
<i>Podocarpus urbanii</i>	Podocarpaceae	191	0.015	1708.0	0.62	0.77	0.54	8.50
<i>Clethra occidentalis</i>	Clethraceae	190	0.005	1095.0	0.60	1.14	0.30	10.00
<i>Lyonia octandra</i>	Ericaceae	151	0.008	1822.5	0.97	0.93	0.16	5.10
<i>Eugenia biflora</i>	Myrtaceae	108	0.006	1237.5	1.04	1.57	0.38	7.00
<i>Guarea glabra</i>	Meliaceae	88	0.003	915.0	0.67	1.88	0.63	10.50
<i>Urbananthus critoniformis</i>	Asteraceae	84	0.067	1575.0		2.30	0.63	5.00
<i>Cyrilla racemiflora</i>	Cyrillaceae	76	0.009	1245.0	1.02	0.97	0.11	16.50
<i>Cyathea pubescens</i>	Cyatheaceae	65	0.017	1663.5				12.00
<i>Clusia havetioides</i>	Clusiaceae	60	0.017	1065.0		0.68	0.21	6.00
<i>Dendropanax pendulus</i>	Araliaceae	58	0.012	1050.0			0.00	7.50
<i>Vaccinium meridionale</i>	Ericaceae	58	0.017	1560.0	0.73	0.95	0.20	7.75
<i>Alchornea latifolia</i>	Euphorbiaceae	57	0.000	877.5	0.51	1.60	0.53	11.00
<i>Meriania purpurea</i>	Melastomataceae	57	0.022	1575.0		1.91	0.37	8.00
<i>Chaetocarpus globosus</i>	Euphorbiaceae	56	0.000	1050.0	0.66	0.99	0.42	7.00
<i>Ilex macfadyenii</i>	Aquifoliaceae	44	0.018	1560.0	0.73	1.00	0.18	5.38

<i>Cyathea furfuracea</i>	Cyatheaceae	38	0.027	1663.5				4.00
<i>Sideroxylon montanum</i>	Sapotaceae	29	0.015	1330.0		1.09	0.35	9.00
<i>Schefflera sciadophyllum</i>	Araliaceae	28	0.007	1042.5		1.12	0.52	4.50
<i>Psychotria corymbosa</i>	Rubiaceae	26	0.020	1635.0	0.53		0.35	4.00
<i>Gordonia haematoxylon</i>	Theaceae	24	0.013	1005.0		1.16	0.25	10.50
<i>Ilex harrisii</i>	Aquifoliaceae	23	0.000	1365.0			0.31	6.50
<i>Ilex obcordata</i>	Aquifoliaceae	23	0.014	1710.0		0.92	-0.19	6.25
<i>Solanum punctulatum</i>	Solanaceae	20	0.006	1635.0	0.62	3.37	0.27	11.50
<i>Haenianthus incrassatus</i>	Oleaceae	19	0.000	1410.0		1.21	0.66	15.00
<hr/>								
<i>n</i>					13	20	23	25
Pearson correlation with annual mortality (<i>r</i> value)					-0.0155	0.206	0.0516	-0.377
<i>P</i>					0.960	0.384	0.815	0.0633
Pearson correlation with mean elevation (<i>r</i> value)					0.180	0.0760	-0.267	-0.222
<i>P</i>					0.557	0.750	0.219	0.285

640

641 Wood density values from Bellingham *et al.* (1995).

642 Foliar N concentrations computed per species averaged across four sites in Tanner (1977) and two sites in Wardle *et al.* (2015).

643 Species-specific growth rates (1974–1984) exclude those of two tree ferns (*Cyathea furfuracea* and *C. pubescens*) that do not exhibit radial
644 growth.

645 Mean heights from Adams (1972), Proctor (1985), and Mill (2015).

646 Annualised mortality rates calculated from Kohyama *et al.* (2018).

647 MCAS from Adams (1972), Proctor (1985), Iremonger (2002), and Mill (2015).

648

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