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1 **Running head: Long-term hurricane impacts on tropical forests**

2

3 **Title: Long-term hurricane damage effects on tropical forest tree growth and mortality**

4

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15

16 **Abstract**

17 Hurricane winds can have large impacts on forest structure and dynamics. To date, most

18 evaluations of hurricane impacts have focused on short-term responses after a hurricane, often

19 lack pre-hurricane measurements, and miss responses occurring over longer time scales. Here we

20 use a long-term dataset (1974–2009, 35 years) of tree stems (> 3 cm in diameter at 1.3 m) in four

21 sites (0.35 ha in total) in montane rain forest (c.1600 m) in Jamaica to investigate the patterns of

22 crown damage in individual stems by Hurricane Gilbert in 1988, and how subsequent growth and

23 mortality were affected by hurricane damage, sprouting, and the incidence of multiple stems.

24 Topographical position on a mountain ridge was the best predictor of crown damage, followed
 25 by crown size and species identity. The average diameter growth rate of stems that survived the
 26 hurricane was greater than that pre-hurricane for the whole 21 year post-hurricane period.
 27 Growth of stems with damaged crowns increased less than those with undamaged crowns;
 28 differences in growth rate between damaged and undamaged trees disappeared after eleven
 29 years. Hurricane-damaged stems had 2 to 8 times higher mortality than undamaged stems for 19
 30 years post hurricane. Many stems sprouted shortly after the hurricane, but few sprouts managed
 31 to establish (grow to > 3 cm diameter at breast height). However, sprouting and multi-stemming
 32 were associated with reduced mortality rate, particularly in damaged trees. From an initial
 33 population of 1670 stems in 1974, 54% were still alive in 2009 (21 years after the hurricane). We
 34 conclude that despite the high frequency of hurricane damage to tree crowns and the subsequent
 35 increased mortality rate in this hurricane-prone tropical montane forest, many stems will be hit
 36 and recover from several hurricanes in their lifetime.

37
 38 Keywords: Bayesian; Caribbean; cyclone; defoliation; demography; disturbance; forest
 39 dynamics; forest structure; mortality; multiple-stems; sprouting; tree growth.

40
 41 **INTRODUCTION**

42
 43 Natural disturbances such as fires and hurricanes can have major impacts on forests' structure
 44 and dynamics despite their short duration (from hours to a few days) (Overpeck et al. 1990;
 45 Foster et al. 1998). Wind storms can damage large numbers of trees (Coultts and Grace 1995;
 46 Vandermeer et al. 2000) affecting subsequent tree demography, forest dynamics and ecosystem

47 processes (Foster and Boose 1995; Foster et al. 1998). The effects of tropical cyclones are
 48 particularly strong (Zimmerman et. al. 1996; Lugo 2008), and their intensity (wind speed and
 49 amount of rainfall) is expected to increase in the coming decades due to climate change (Field et
 50 al. 2012). Despite the importance of these effects, only a few studies have assessed the long-term
 51 (more than a decade) consequences of wind damage on the growth of individual trees (e.g.,
 52 Merrens and Peart 1992, Busby et al. 2008) and fewer still on tree mortality (e.g., Weaver 1986,
 53 Burslem et al. 2000). Most studies are done within a few years of the impact of a cyclone (called
 54 hurricanes in the Atlantic), and describe the form of damage and differences between species in
 55 damage and mortality (e.g., in Jamaica, Bellingham et al. 1995; in Puerto Rico, Ostertag et al.
 56 2005; see Everham and Brokaw 1996, Lugo 2008, for general reviews). These short-term studies
 57 may miss tree and forest responses occurring over longer time scales, and quite often lack pre-
 58 hurricane data to serve as a baseline for comparison of post-hurricane dynamics.

59 The scarcity of long-term studies results in high uncertainties regarding the magnitude and
 60 duration of hurricane impacts on tree mortality and growth. In lower montane rain forest in
 61 Puerto Rico, mortality rates increased and growth rates were lower in hurricane-damaged stems
 62 than in undamaged stems for about four years after a major hurricane (Uriarte et al. 2004, 2012).
 63 In Florida, over seven years after Hurricane Kate, growth and mortality rates were higher or
 64 lower than pre-hurricane rates depending on the tree species (Batista and Platt 2003). In the
 65 Solomon Islands, recruitment and mortality rates were still higher 24–28 year after cyclones
 66 struck (Burslem et al. 2000). In New Hampshire, tree growth was higher in a hurricane-damaged
 67 stand than in a comparatively undamaged stand, for two of four species for 44–48 years after a
 68 hurricane (Merrens and Peart 1992). In South Carolina, previously damaged trees were more
 69 likely to be damaged by a subsequent hurricane (Putz and Sharitz 1991). These studies establish

70 that hurricane effects on tree mortality and growth can be long-lasting, but also highly variable.
 71 The factors driving the apparent variation in the magnitude, species-specificity, and duration of
 72 hurricane impacts remain unclear.

73 In Jamaica, our studies of forest dynamics in permanent plots in the Blue Mountains have
 74 already shown that mortality and growth increased shortly after a hurricane impact (Bellingham
 75 et al. 1995) and that species composition changed over the twenty year period 1984–2004 (with
 76 Hurricane Gilbert in 1988), with an increase in rarer species and recruitment of light-demanding
 77 species formerly absent from the plots (Tanner and Bellingham 2006). In the current paper we
 78 exploit this long-term (14 years pre-hurricane and 21 years post-hurricane) tropical forest dataset
 79 to address the following questions: 1. What factors were associated with hurricane damage to
 80 tree crowns? 2. What was the magnitude and duration of hurricane-caused damage on stem
 81 growth and mortality? 3. Was tree sprouting after the hurricane and possession of multiple stems
 82 associated with long-term survival of trees post-hurricane?

83
 84 **METHODS**

85
 86 We report analyses of data from before and after Hurricane Gilbert, the eye of which
 87 passed less than 10 km South of our study sites on 12 September 1988. Hurricane Gilbert had the
 88 lowest atmospheric pressure yet recorded for a North Atlantic cyclone: its wind speeds were up
 89 to 194 km h⁻¹ as it crossed Jamaica (Lawrence and Gross 1989). In the subsequent 21 years of
 90 our study, no hurricane eye passed over (eastern) Jamaica although there were several near
 91 misses in the period 2004–2009. These near misses did not have strong effects on the natural
 92 forest as judged by the fact that no stems of the very light-demanding but short-lived species

93 *Bocconia frutescens* were observed in the forest in the vicinity of the study sites in 2009,
 94 whereas for at least five years after Hurricane Gilbert in 1988 stems of this small tree were
 95 widespread. In the 37 years between Hurricanes Charlie in 1951 and Gilbert in 1988, no other
 96 hurricane eye passed within 50 km from the study sites. We conclude that the effects we are
 97 studying are predominantly attributable to Hurricane Gilbert in 1988 and not those of earlier or
 98 more recent but more distant hurricanes.

99 Our study sites are in forests that are on and near the main ridge of the Blue Mountains of
 100 Jamaica (18° 05'N; 76° 39'W, 1500–1650 m altitude). We had four sites (named 'Col' 0.09 ha,
 101 'Mor' 0.06 ha, 'Mull' 0.1 ha and 'Slope' 0.1 ha); each site was composed of 6–10 contiguous 10
 102 × 10 m plots (Appendix A; further details in Tanner 1977, Tanner and Bellingham 2006). The
 103 Mull, Col and Mor sites are on the crest of an undulating steep-sided main ridge that runs
 104 approximately SE to NW. The slope to the NE of the Mull site is 42° and to the SW of it 33°.
 105 The main ridge rises by 60 m over a horizontal distance of 150 m from the SE to the Mull site
 106 and then falls by about 15 m to the NW into a 'gap' in the main ridge where the Col site is
 107 situated; it then rises by about 30 m to a knoll where the Mor site is situated (Appendix A). The
 108 Slope site is 15–50 m down the northern side of the main ridge. The hurricane came in from the
 109 SE and the eye passed overland to the south of the main ridge. Thus the Mull site was most
 110 exposed, the Mor next most exposed, the Col was relatively protected by the 15 m decrease in
 111 altitude from the Mull to the Col (and the 30 m rise in altitude from the Col to the Mor) and its
 112 position ~ 150 m back from the top of the slope leading up to the Mull. The Slope site was the
 113 least exposed because of its position on the northern slopes, which were relatively protected from
 114 the eye of Hurricane Gilbert (Bellingham 1991).

115 The stems were measured in 1974, 1984, 1989, 1991, 1994, 2004 and 2009. At each
 116 census, all stems with diameter at breast height (dbh, 1.3 m) > 3 cm were scored as live or dead,
 117 identified to species, and measured on a painted band (see Appendix B for descriptive statistics
 118 of the number of stems, species and stem size for each site). Stems part of multi-stemmed
 119 individuals were recorded as separate stems and their connection recorded. In the first re-
 120 enumeration after Hurricane Gilbert (1989) crowns of living trees were scored for damage using
 121 a four-point qualitative scale: 1) crown-detached (crowns broken off but with epicormic sprouts
 122 developing), 2) crown bare (no leaves, i.e., completely defoliated), 3) crown sparse (few leaves),
 123 or 4) crown undamaged; herein we amalgamated the three categories 1, 2, and 3 into a category
 124 of ‘damaged’ to be compared with ‘undamaged’. For 703 stems with smaller diameter crowns
 125 (mean stem dbh 7.2 cm, SE 0.1 cm) the crowns were scored as a whole; for 622 stems with
 126 larger diameter crowns (mean stem dbh 15.6 cm, SE 0.3 cm) the crowns were divided into upper
 127 and lower portions, which were scored separately; we used only data from the upper portion.
 128 Species names follow Adams (1972), updated and with other authorities from
 129 <http://www.theplantlist.org/> (Appendix C).

130 We used hierarchical Bayesian modeling to estimate the effects of spatial location (site,
 131 plot) and individual characteristics (species, crown size – large or small – and previous diameter
 132 growth rate – an indicator of tree vitality) on the probability of crown damage (‘damaged’ cf.
 133 ‘undamaged’) by the hurricane (n = 1259 stems from 48 species, excluding dead trees and tree
 134 ferns). Specifically, for every individual stem i of species j growing in plot l at site k , the
 135 probability of being damaged (φ_{ijkl}) was modeled as

136
$$\text{logit}(\varphi_{ijkl}) = \alpha_k + \gamma_l + \delta_j + \beta_1 * \text{crown size}_i + \beta_2 * \text{growth rate}_i$$

137 where crown size was a binary variable (either large or small) and growth rate represents the
 138 average stem growth rate during the period 1974–1984 (pre-hurricane). We used relatively non-
 139 informative priors for all parameters. Parameters β_1 and β_2 had Normal priors with mean 0 and
 140 large standard deviation (1000). In this and all subsequent analyses, site effects (α_k , $k = 1, \dots, 4$)
 141 were modelled as fixed effects $\alpha_k \sim Normal(0, 1000)$, while plot (γ_l) and species (δ_j) effects
 142 were modelled hierarchically as $\gamma_l \sim Normal(0, \sigma_{plot})$ and $\delta_j \sim Normal(0, \sigma_{species})$. Both standard
 143 deviations σ_{plot} and $\sigma_{species}$ had flat priors *Uniform*(0, 10).

144 Stem diameter growth rates over time were modeled as a function of location (site, plot),
 145 species, individual and damage score. For this analysis we only included stems surviving the
 146 whole study period ($n = 915$ stems from 41 species). Specifically, the average diameter growth
 147 rate G of a stem i of species j growing in plot l at site k during census t ($t = 1, 2, \dots, 6$) was
 148 modeled as

$$149 \quad G_{ijklt} \sim Normal(g_{ijklt}, \sigma_G) \text{ where } g_{ijklt} = \alpha_k + \gamma_l + \delta_j + \theta_i + \beta_t + \omega_t * Damage_i.$$

150 Damage is a binary variable separating hurricane-damaged from undamaged trees. ω_t was given
 151 a standard non-informative prior, $\omega_t \sim Normal(0, 1000)$. Site (α_k), plot (γ_l) and species (δ_j)
 152 effects were modeled as above. We accounted for individual variation in growth rates by
 153 including random individual effects $\theta_i \sim Normal(0, \sigma_i)$, with inter-individual standard deviation
 154 σ_i having flat prior *Uniform*(0, 10), as well as the residual standard deviation σ_G .

155 We modeled stem mortality as a Bernoulli process, accounting for the different duration
 156 of census intervals (Ogle et al. 2006). The probability of mortality of any stem during census t
 157 (τ_{it}) was equal to $1 - (1 - M_{it})^{Y_t}$, where M_{it} is the annual probability of mortality of stem i during
 158 census t , and Y_t is the number of years spanning the census (Lines et al. 2010). The annual

159 probability of mortality of any stem was subsequently modeled for each census taking into
 160 account its location, species identity and damage status:

161
$$\text{logit}(M_{ijkl}) = \alpha_k + \gamma_l + \delta_j + \beta_D * \text{Damage}_i.$$

162 We modeled site, plot and species effects ($\alpha_k + \gamma_l + \delta_j$ respectively) as above, and the effects of
 163 damage on mortality were given a standard non-informative prior: $\beta_D \sim \text{Normal}(0, 1000)$.

164 Many stems sprouted in response to hurricane damage. We analyzed the variation in
 165 sprouting frequency among stems, plots and species, and the subsequent effects of sprouting on
 166 post-hurricane mortality. In the 1989 census, one year after the hurricane, we recorded the stems
 167 that had sprouted from the crown base (above 2.5 m high). The probability of sprouting was then
 168 modeled as a function of stem location (site, plot), species, damage score (damaged or not) and
 169 crown size (large or small) using the logit link. Subsequently, we assessed whether crown
 170 sprouting and being multi-stemmed had any influence on overall post-hurricane mortality (1989–
 171 2009) by repeating the mortality analysis above for individual trees ($n = 1390$), this time
 172 including parameters accounting for sprouting, multi-stemming and their interaction.

173 As we aim to explain tree responses to hurricane damage in these particular sites rather
 174 than extrapolating to other forests, we report finite-population standard deviations throughout
 175 (Gelman and Hill 2007). All analyses were run in R 3.0 (R Development Core Team 2013) and
 176 JAGS 3.3.0 (Plummer 2003) by means of the R2jags package (Su and Yajima 2012).

177

178 **RESULTS**

179

180 **Crown damage**

181 Hurricane Gilbert caused extensive crown damage: 5–8 months after the hurricane of the 622
 182 stems with larger crowns scored for damage, 38% were undamaged, 28% sparsely foliated, 18%
 183 bare and 16% crown-detached.; of the 703 stems with smaller crowns 66% were undamaged,
 184 22% sparsely foliated, 5% bare and 7% crown-detached. The best predictor of whether a crown
 185 was damaged was topographical position. Trees in the most affected (Mull) site, on a convex
 186 ridge top, had a 37% greater probability of crown damage on average than trees in the least
 187 affected, north-facing, Slope site (Table 1, Fig. 1). The next most important predictors were
 188 crown size and species; having a large crown increased damage probabilities by 26% (calculated
 189 from values in Table 1); and belonging to the most susceptible species (*Solanum punctulatum*)
 190 increased the probability of damage by 47% compared with the least susceptible species
 191 (*Podocarpus urbanii*) (Appendix C). However, we did not detect strong differences in
 192 susceptibility to damage amongst most species: only three species had estimated susceptibility
 193 significantly different from zero and mean effect size lay between + and – 0.5 for 38 out of 48
 194 species, including some that were relatively abundant (Appendix C). Finally, pre-hurricane
 195 growth rates only had a small effect on the likelihood that a stem was damaged, as a 1 mm yr⁻¹
 196 higher growth rate (a big difference given that the average growth rate of all stems alive
 197 throughout the study period was 0.6 ± 0.02 mm yr⁻¹) translated into only an 8% decrease in the
 198 overall probability of damage (Table 1, Fig. 1).

199

200 **Stem growth and mortality**

201 The average stem diameter growth rate of surviving stems over the full 21-year post-
 202 hurricane period was greater than that pre-hurricane (Fig. 2, Appendix D). Whereas growth rates
 203 of damaged stems were quite stable over the whole post-hurricane period, undamaged stems

204 showed a four-fold increase immediately after the hurricane, declining to the same level as
 205 damaged trees by 11 years after the hurricane (Fig. 2). Average diameter growth rates of
 206 damaged and undamaged stems 1–3 years after the hurricane (1989–1991) were 77% and 160%
 207 higher, respectively, than before the hurricane (1974–1984). The diameter growth rate of
 208 damaged stems was significantly lower than that of undamaged stems for up to six years post-
 209 hurricane (1989–1991 and 1991–1994; Fig. 2). There was also substantial variation among
 210 species and individuals within species (Appendix D): although surviving trees of all species
 211 responded positively to the hurricane in terms of subsequent growth rate, the increase was much
 212 greater in some species (e.g., *Alchornea latifolia*) than others (*Lyonia octandra*) (Appendix E).
 213 Overall stem mortality rates (damaged and undamaged stems together) were higher in the six
 214 years after the hurricane and slowly returned to pre-hurricane rates 6–21 years post-hurricane
 215 (Fig. 3). The increase was entirely attributable to the significantly greater mortality rates of stems
 216 with hurricane-damaged crowns ($3.4\% \text{ yr}^{-1}$, 1989–1994) versus stems with undamaged crowns
 217 ($0.45\% \text{ yr}^{-1}$, 1989–1994). During the same six-year period, the probability of mortality of stems
 218 with undamaged crowns was less than half that of the pre-hurricane years. Hurricane effects on
 219 mortality were long-lasting: stems with damaged crowns had significantly greater mortality than
 220 undamaged stems for between 16 and 21 years post-hurricane (Fig. 3). At the time of the last
 221 census (2009), mortality rates of stems with damaged and undamaged-crowns had still not fully
 222 converged. Hurricane damage thus had longer term effects on mortality than on growth;
 223 differences in stem diameter growth between damaged and undamaged trees mostly disappeared
 224 between six and 16 years after the hurricane (Fig. 2).

225

226 **Sprouting**

227 Sprouts above 2.5 m on a stem were present on 38% of stems in 1989, a year after the
 228 hurricane. The presence of sprouts was very species-dependent, including frequent sprouters
 229 (e.g., *Eugenia biflora*, *Lyonia octandra*, *Chaetocarpus globosus*, and *Sideroxylon montanum*)
 230 and non-sprouters (*Clusia havetioides* and *Schefflera sciodaphyllum*). On average, large-crowned
 231 undamaged trees showed the highest probability of sprouting (33%; Table 2). Damaged stems
 232 showed slightly lower sprouting (~25%) regardless of their crown size. Despite the intense post-
 233 hurricane sprouting (both above and below 2.5 m on a stem), the percentage of multiple-
 234 stemmed individuals hardly changed throughout the 35 year period, from 13.0% in 1974 to
 235 13.5% in 1989, 14.1% in 1994, 14.6% in 2004 and 13.9% in 2009. Sprouting and having
 236 multiple stems (which were correlated) were associated with lower long-term (1989–2009)
 237 mortality in damaged trees (average mortality rate around 2.3% per year compared to 3.5% for
 238 damaged single-stem, non-sprouted trees). Sprouting and multi-stemming effects on mortality
 239 were apparently much weaker for undamaged trees; the significant effect for ‘undamaged
 240 sprouted multi-stems’ (Table 3) has a wide credible interval and is based on only 23 stems. There
 241 were 365 recruits to the plots in years one to six after the hurricane (1989–1994); 34% of these
 242 were part of a multi-stemmed individual, not significantly different from the 30% of 121 stems
 243 recruited between 1984 and 1989 (four years before and first year immediately after the
 244 hurricane in 1988). Thus, stem recruitment after the hurricane derived mostly from sexual
 245 regeneration (i.e., seeds or seedling bank) rather than basal sprouting of older individuals.

246

247

248 **DISCUSSION**

249

250 **Hurricane damage: its correlates and its effects on stem growth and mortality**

251 Crown damage caused by Hurricane Gilbert was related to topographic position, crown size
 252 and species identity. Our results show that topographic position and the degree of exposure to
 253 strong winds are important predictors of damage in sites along a mountain ridge (see also Boose
 254 et al. 1994, 2004) and can override other factors (e.g., tree size, species identity) that are often
 255 emphasized in the literature on hurricane impacts (Everham and Brokaw 1996). In highly
 256 exposed stands, most trees will experience greater damage regardless of their individual
 257 characteristics, and vice versa: protected stands will act as ‘refugia’ where both less susceptible
 258 and more susceptible trees will be more likely to escape hurricane damage. Topographical
 259 effects, when investigated, have sometimes given apparently contradictory results. For example,
 260 after different hurricanes affected forests in the Luquillo Mountains in Puerto Rico, Ostertag et
 261 al. (2005) reported that trees growing on ridges and valleys were more affected than those on
 262 slopes, whereas Scatena and Lugo (1995) found that trees on slopes were more affected than
 263 those on ridges; possibly because the root-grafted *Dacryodes excelsa* was particularly abundant
 264 on ridges in that area (Lugo 2008). Another study in a 16 ha plot in the Luquillo Mountains
 265 found that topographical effects were of lesser importance than tree size and species identity in
 266 determining crown damage caused by Hurricane Hugo (Canham et al. 2010). Therefore, the
 267 probability of hurricane damage seems to be determined by the interplay of landscape position
 268 and individual tree characteristics (e.g. large trees were more affected). These interactions
 269 between intrinsic (individual) and extrinsic (landscape) factors should be considered more
 270 thoroughly in future studies assessing patterns of hurricane damage in forests.

271 The average stem diameter growth rate (all stems damaged and undamaged) was greater for
 272 the full 21-year post-hurricane period than in the pre-hurricane period. The growth of stems with
 273 hurricane-damaged crowns increased less than those with undamaged crowns; this difference
 274 persisted for eleven years after the hurricane hit. The increased stem growth rate after the
 275 hurricane was probably due to increased light reaching the middle and lower levels of the canopy
 276 (Bellingham et al. 1996, Tanner and Bellingham 2006) and reduced below-ground competition,
 277 caused by the severe damage to many large crowns; similar patterns have been found elsewhere
 278 (Lugo 2008). In Puerto Rican rain forests affected by Hurricane Hugo, the diameter growth of
 279 undamaged stems exceeded that of damaged for six of twelve dominant tree species for four
 280 years post-hurricane (Uriarte et al. 2004), in a general context of increased forest growth rates
 281 (e.g., net primary productivity in nearby forests tripled after two hurricanes, Lugo 2008). Other
 282 studies found longer-lasting increases of tree growth post-hurricane, e.g. at least 7 years in
 283 Florida (Batista and Platt 2003), a decade in the Dominican Republic (Sherman et al 2012) and
 284 >40 years in New Hampshire (Merrens and Peart 1992). Hence, even though increased growth
 285 of surviving trees after a hurricane – especially those less damaged- seems to be a general
 286 phenomenon, there is considerable variation in the duration and magnitude of growth stimulation
 287 among species and forest types. These could be explained by differences in forest structure,
 288 damage intensity, species resilience and post-disturbance recovery strategies, and speed of
 289 canopy closure after the hurricane (Lugo 2008). Our results confirm that, even within the same
 290 forest, post-hurricane growth rates will vary substantially between species and trees within
 291 species depending on the amount of damage (Fig. 2, Appendices D and E). Hence studies based
 292 on short-term time series (e.g. lacking evaluation of damage immediately after the hurricane, or
 293 pre-hurricane growth data) and focused on stand rather than individual scales (e.g. analyzing

294 changes in total basal area rather than individual stems' demography) may miss more subtle yet
 295 important long-term consequences of hurricane disturbances on forest dynamics.

296 Higher tree mortality rates after hurricanes have often been documented (Everham and
 297 Brokaw 1996), though the duration of that increase is rarely reported. In the Jamaican forest in
 298 this study, mortality of damaged stems was higher for about 19 years after a severe hurricane. In
 299 forests of the Luquillo Mountains in Puerto Rico, Hurricane Hugo caused increased tree
 300 mortality over about four years (Uriarte et al. 2004) but this effect was not evident by a third
 301 census 11–12 years after the hurricane (Uriarte et al. 2012). Despite the increased mortality
 302 post-hurricane, many trees are likely to survive several hurricanes; in Jamaica, 54% of the initial
 303 population of 1670 stems in 1974, 71% of all stems present in 1984 (before Hurricane Gilbert),
 304 and 59% of those damaged by the hurricane were still alive by 2009. Average annual mortality
 305 rates in the 21 years post-hurricane were 0.5% higher (1.6%) than pre-hurricane baselines
 306 (1.1%). Thus, although return times of hurricanes to the Jamaican Blue Mountains are very
 307 irregular, given that the average is ~ 25 years (five hurricanes eyes passed within 20 km of the
 308 Blue Mountains between 1870 and 2010), most stems will experience more than one hurricane in
 309 their lifetime. This seems to be true in other forests, too; in Puerto Rico, 26% of stems >4.1 cm
 310 dbh survived from 1946 to 2000 (Weaver 2002), a period that included hurricanes in 1956, 1989
 311 and 1998, .

312

313 **Role of sprouting in post-hurricane recovery**

314 After a hurricane, epicormic sprouting on tree trunks is obvious (Yih et al. 1991 in
 315 Nicaragua; Bellingham et al. 1994 in Jamaica ; Zimmermann et al. 1994 in Puerto Rico).
 316 Sprouting is an efficient means of mobilizing stored reserves to regain lost biomass and leaf area

317 (Sakai and Sakai 1998). Hurricanes often cause widespread defoliation and sprouts may help
 318 maintain photosynthesis in the years immediately after the hurricane while the stems regrow
 319 their main canopy. In Puerto Rican rain forests affected by Hurricane Hugo, Walker (1991)
 320 asserted that widespread sprouting and minimal breakage of large branches would result in tree
 321 recovery despite that fact that 56% of trees were defoliated, and Boucher (1990) made similar
 322 predictions about Nicaraguan rain forests affected by Hurricane Joan. In our study sprouting was
 323 positively related to survivorship: stems with hurricane-damaged crowns that sprouted above 2.5
 324 m height had much lower mortality (2.3% per year over the 21-year post-hurricane period) than
 325 non-sprouted stems (3.5%). Some sprouts from below 1.3 m survived and grew large enough to
 326 be included in stem censuses (≥ 3.0 cm dbh), but two-thirds of the newly recruited stems five
 327 years after the hurricane originated from seedlings, not sprouts from existing tree stems. The
 328 importance of sprouting for post-disturbance recovery is however strongly species-specific
 329 (Table 2; Dietze and Clark 2008; Uriarte et al. 2012). Beyond new stem recruitment, basal
 330 sprouts contribute to multi-stemmed individuals having a greater chance of survival than single-
 331 stemmed individuals, in Jamaica (Bellingham & Sparrow 2009) Samoa (Webb et al 2014) and
 332 probably Puerto Rico (Uriarte et al. 2012). However, experimental removal of basal sprouts will
 333 be necessary to establish if sprouting causes increased survival or if it is simply that more
 334 vigorous individuals have both more sprouts and higher survival.

335

336 **Long-term effects of hurricanes at the stand level**

337 In Jamaica, stems with 32% of the total basal area present in 1974 had died by 2004
 338 (Tanner and Bellingham 2006). However, total basal area per plot remained very similar due to
 339 the increased growth of survivors (Fig. 2) and the increased post-hurricane recruitment (Tanner

340 and Bellingham 2006) that compensated for the basal area mortality. Results from several other
 341 countries also show that the total stand basal area can remain quite stable or recover quickly after
 342 major wind damage (Lugo 2008), though there are often other changes such as shifts in species
 343 composition (Bellingham et al. 1995) or stand structure including shifts to more, smaller, stems
 344 (Bellingham et al. 1995; Merrens and Peart 1992). Such changes can happen slowly, even in the
 345 course of several centuries (Foster et al. 1998; Lugo 2008). The disturbance regime is likely to
 346 govern responses. We have shown that in Jamaica, where the average return interval for
 347 hurricanes is 25 years, a single hurricane increased overall growth for the whole 21 year post-
 348 hurricane period and hurricane damaged stems had reduced growth for eleven years and
 349 increased mortality for 19 years. However, some forests are subject to several powerful cyclonic
 350 storms within a decade; for example, in northeastern Australia (Webb 1958), Taiwan (Lin et al.
 351 2011), and the northeastern USA (Papaik and Canham 2006). The consequences of damage to
 352 individual stems in these “hyper-disturbed” forests have not been determined. The species
 353 composition of forests and the traits of individual species, including their susceptibility to
 354 pathogens, are likely to determine responses to repeated disturbances. In species-rich forests,
 355 differential damage among species (Canham et al. 2010) can result in long-term differences in
 356 growth among species (Appendix E). This in turn can lead to compositional shifts along a
 357 continuum of resilient to resistant species (Bellingham et al. 1995, Batista and Platt 2003; see
 358 also Wonkka et al. 2013), which is likely to be related to time since disturbance (Holling 1973).
 359 Finally the high variability in frequency of hurricane impacts at any location (Healey 1990,
 360 Sherman et al. 2012) will further complicate these effects. Thus, the interaction of disturbance
 361 regimes and species differential responses generate complex and varied patterns of forest
 362 dynamics (Papaik & Canham 2006).

363 **Conclusion**

364 Long-term monitoring of forest plots can provide important insights on the effects of
 365 hurricanes and other natural disturbances on tree demography and forest stand dynamics. The
 366 availability of pre-hurricane data enabled us, for instance, to detect a significant overall increase
 367 of stem growth rates following the hurricane. In the absence of pre-hurricane baseline data,
 368 hurricane-induced changes in tree demography would remain undetected or, even worse,
 369 misinterpreted. Furthermore, the demographic impacts of hurricane damage can be long-lasting –
 370 in Jamaica, 19 years for mortality and 11 for growth. In forests where there is a lot of
 371 topographic diversity (as in Jamaica), position in the landscape is a strong determinant of
 372 hurricane damage; after which crown size and tree species are the next most important correlates.
 373 Recovery from damage was higher in multiple stemmed trees and stems with sprouts above 2.5
 374 m. Some basic aspects of forest structure are often not greatly affected by hurricanes – for
 375 example, total basal area. Other aspects of structure, like canopy height and crown diameters, are
 376 likely to be more affected by hurricanes but are rarely recorded before hurricanes (a notable
 377 exception is the study of Wunderle et al. 1992).

378 Despite the high frequency of damage to tree crowns and associated increased mortality
 379 rate, most stems survived long after the hurricane. Given the high frequency of hurricanes and
 380 windstorms in many tropical areas, it is likely that many canopy trees will be damaged and
 381 recover from several severe disturbances in their lifetime.

382

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384

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526

527 Supplemental material

528 Appendix A. Map of the location of the four study sites.

529 Appendix B. Forest site characteristics in 1984.

530 Appendix C. Species' relative susceptibility to hurricane damage as recorded in 1989.

531 Appendix D. Hurricane damage effects on stem growth rates over time.

532 Appendix E. Hurricane damage effects on tree growth rates for the most abundant species.

533

534

535

536 **Table 1.** Estimated effects of location (site and plot), species identity, crown size and pre-
 537 hurricane growth rate (1974-1984) on the probability of damage by the hurricane (recorded in
 538 1989), for 1259 stems of 48 species (tree ferns were excluded) that were alive in 1974, 1984 and
 539 1989. Mean effect size, standard error and 2.5% and 97.5% credible intervals are shown (logit
 540 scale); positive mean values indicate higher probability of damage compared to small-crowned
 541 stems with zero net growth pre-hurricane, which were used as the baseline.

542

543

	mean	se	2.5%	97.5%
Site Col	-1.10	0.30	-1.70	-0.52
Site Mor	-0.25	0.30	-0.83	0.37
Site Mull	0.45	0.26	-0.06	0.95
Site Slope	-1.43	0.27	-1.99	-0.91
Large crown	1.28	0.15	1.00	1.57
Pre-hurricane growth rate (cm yr ⁻¹)	-4.12	0.97	-6.02	-2.26
Random effects (standard deviations)				
Species	0.68	0.12	0.47	0.93
Plot	0.46	0.09	0.29	0.65

544

545 **Table 2.** Effects of stem location (site and plot), species, crown size and damage status on the
 546 probability of sprouting after the hurricane (n = 1670 stems from 63 species). Mean effect size,
 547 standard error and 2.5% and 97.5% credible intervals are shown (logit scale); positive mean
 548 values indicate more sprouting compared to undamaged, small-crowned stems used as baseline.
 549

	mean	se	2.5%	97.5%
Site Col	-1.99	0.39	-2.77	-1.25
Site Mor	-0.64	0.40	-1.43	0.14
Site Mull	-1.47	0.35	-2.16	-0.81
Site Slope	-1.89	0.36	-2.60	-1.19
Undamaged and large crown	0.78	0.20	0.39	1.17
Damaged and small crown	0.43	0.18	0.07	0.79
Damaged and large crown	0.40	0.18	0.05	0.74
Random effects (standard deviations)				
Species	1.48	0.23	1.11	2.00
Plot	0.62	0.11	0.43	0.85

550

551 **Table 3.** Effects of tree location (site and plot), species, hurricane damage, sprouting and multi-
 552 stemming on the long-term probability of mortality of individual trees (1989-2009; n = 1390).
 553 Mean effect size, standard error and 2.5% and 97.5% credible intervals are shown (logit scale);
 554 positive mean values indicate higher probability of mortality compared to undamaged, single,
 555 non-sprouted stems used as baseline.

	mean	se	2.5%	97.5%
Site Col	-4.28	0.22	-4.72	-3.84
Site Mor	-4.52	0.27	-5.05	-4.00
Site Mull	-4.32	0.22	-4.74	-3.89
Site Slope	-4.83	0.22	-5.27	-4.39
Undamaged sprouted (single stem)	-0.32	0.23	-0.78	0.13
Undamaged multistem (not sprouted)	-0.20	0.46	-1.17	0.60
Undamaged sprouted multistem	-2.14	1.29	-5.29	-0.24
Damaged (single stem, not sprouted)	1.17	0.15	0.87	1.47
Damaged sprouted (single stem)	0.72	0.20	0.34	1.11
Damaged multistem (not sprouted)	0.74	0.28	0.16	1.28
Damaged sprouted multistem	0.10	0.29	-0.49	0.62
Random effects (standard deviations)				
Species	0.90	0.12	0.67	1.15
Plot	0.17	0.09	0.01	0.34

557
 558

559 **Figure legends**

560

561 **Figure 1.** Probability of hurricane damage according to stem location (four sites: Col, Mor, Mull
 562 and Slope), crown size and pre-hurricane (1974–1984) diameter growth rate (n = 1259 stems).
 563 Shaded areas represent 95% credible intervals. Dots represent observed growth rates for
 564 damaged and undamaged trees.

565

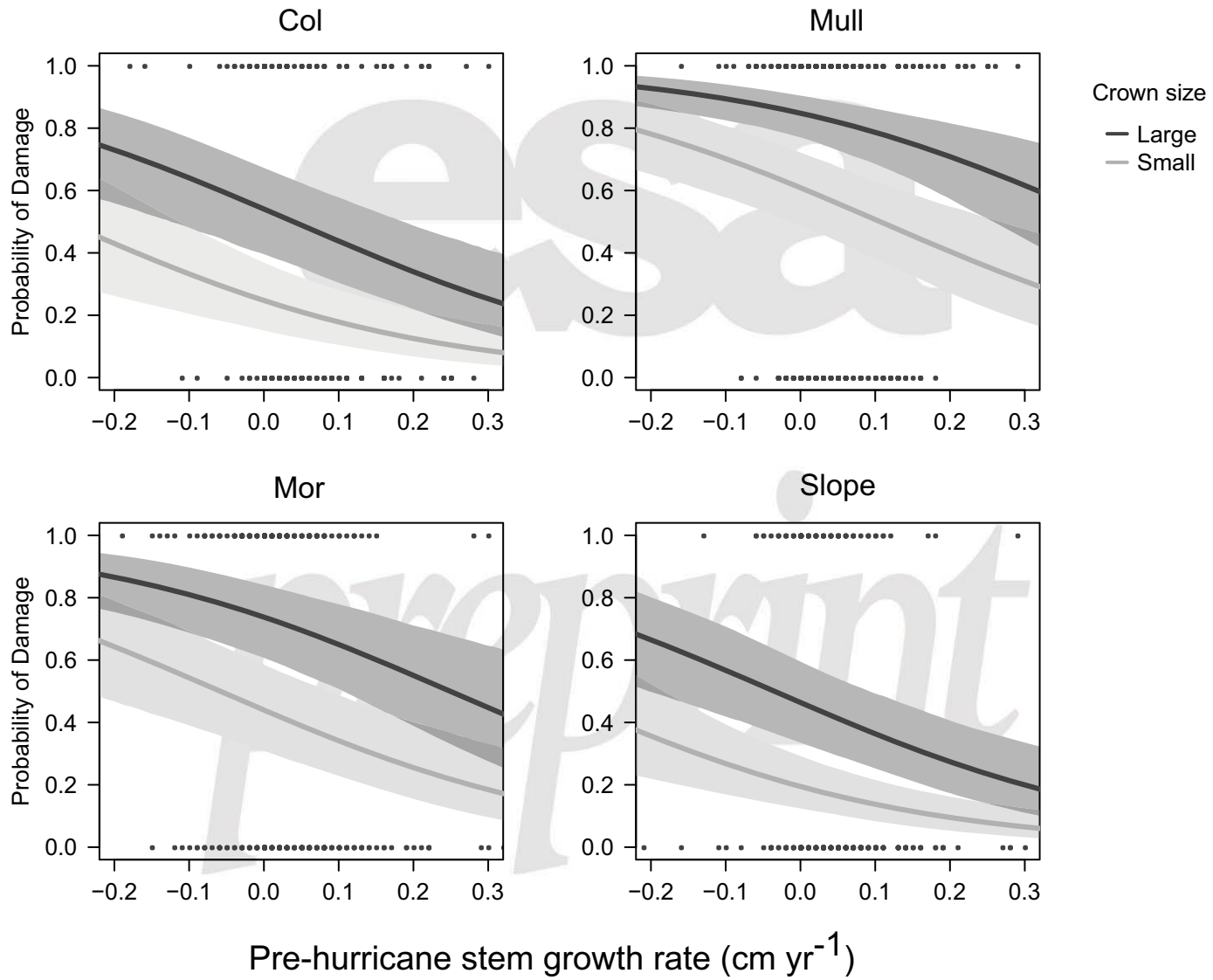
566 **Figure 2.** Stem diameter growth rates (mean \pm SE) prior to and following Hurricane Gilbert for
 567 crown-damaged and crown-undamaged stems. The dashed line marks the year of the hurricane
 568 (1988), data are plotted in the middle of the census period and staggered for clarity. Only stems
 569 surviving the whole period (1974–2009) were included in this analysis (n = 915 stems).

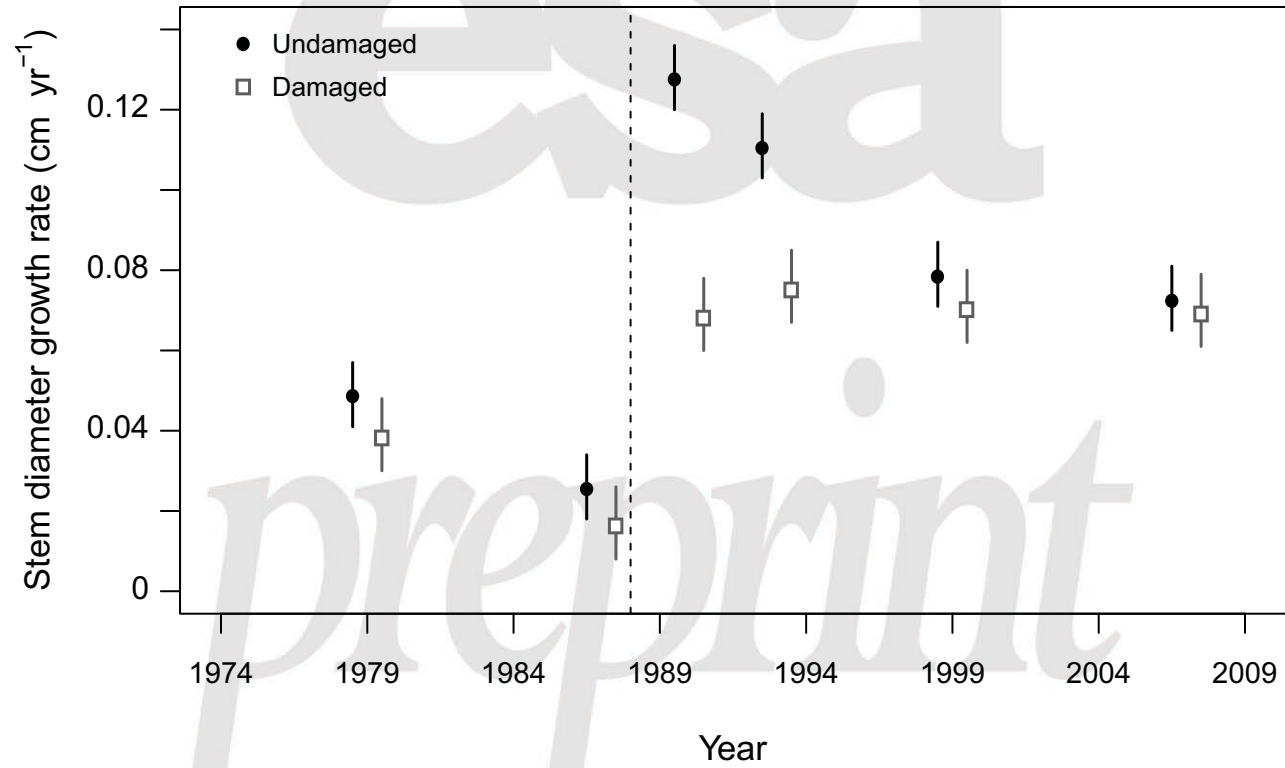
570

571 **Figure 3.** Effects of hurricane damage on stem mortality (mean \pm SE) across the whole study
 572 period. The dashed line marks the year of the hurricane (1988), data are plotted in the middle of
 573 the census period.

574

575





esa

