1 **TITLE**

2 Understory plant communities show resistance to drought, hurricanes, and experimental warming in a
3 wet tropical forest
4

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20 **ABSTRACT**

21 Global climate change has led to rising temperatures and to more frequent and intense climatic events,
22 such as storms and droughts. Changes in climate and disturbance regimes can have non-additive effects
23 on plant communities and result in complicated legacies we have yet to understand. This is especially
24 true for tropical forests, which play a significant role in regulating global climate. We used understory
25 vegetation data from the Tropical Responses to Altered Climate Experiment (TRACE) in Puerto Rico to
26 evaluate how plant communities responded to climate warming and disturbance. The TRACE understory
27 vegetation was exposed to a severe drought (2015), two years of experimental warming (4°C above
28 ambient in half of the plots, 2016-2017 and 2018-2019), and two major hurricanes (Irma and María,
29 September 2017). Woody seedlings and saplings were censused yearly from 2015 to 2019, with an
30 additional census in 2015 after the drought ended. We evaluated disturbance-driven changes in species
31 richness, diversity, and composition across ontogeny. We then used Bayesian predictive trait modeling
32 to assess how species responded to disturbance and how this might influence the functional structure of
33 the plant community. Our results show decreased seedling richness after hurricane disturbance, as well
34 as increased sapling richness and diversity after warming. We found a shift in species composition
35 through time for both seedlings and saplings, yet the individual effects of each disturbance were not
36 significant. At both ontogenic stages, we observed about twice as many species responding to
37 experimental warming as those responding to drought and hurricanes. Predicted changes in functional
38 structure point to disturbance-driven functional shifts towards a mixture of fast-growing and drought-
39 tolerant species. Our findings demonstrate that the tropical forest understory community is more
40 resistant to climatic stressors than expected, especially at the sapling stage. However, early signs of
41 changes in species composition suggest that, in a warming climate with frequent droughts and
42 hurricanes, plant communities might shift over time towards fast-growing or drought-tolerant species.
43

44 **KEYWORDS**

45 tropical forest
46 global warming
47 climate change
48 drought
49 hurricane
50 plant functional traits
51 ontogeny
52 TRACE
53
54 **INTRODUCTION**

55 The function and composition of tropical forests are shaped by legacy effects of prior disturbance and
56 recovery events (Zimmerman et al., 2020; Johnstone et al., 2016). The ecological consequences of these
57 events can vary substantially depending on the timing, severity, and duration of the disturbance, the
58 interactions among disturbances, and the biotic and abiotic conditions of the forest in question (Smith,
59 2011; Johnstone et al., 2016). Currently, tropical forests are projected to experience more frequent and
60 intense disturbance events atop significant changes in temperature and precipitation due to
61 anthropogenic climate change (Emanuel, 2013; Knutson et al., 2013; Holland and Bruyère, 2014; Stott,
62 2016; Ummenhofer and Meehl, 2017). These complex and interactive dynamics, paired with the large
63 uncertainties that persist in tropical climate models (Grainger, 2010; Cavaleri et al., 2015; Gallup et al.,
64 2021), complicate our understanding of how tropical forests respond to climate change. Reducing this
65 uncertainty is of high importance because tropical forests harbor a significant portion of Earth's
66 biodiversity and play a disproportionately large role in regulating future climate (Malhi, 2012; Mitchard,
67 2018). In this study, we contribute to reducing this knowledge gap by evaluating how a decadal drought,
68 hurricane disturbance, and experimental warming affect the species composition and functional
69 structure of understory plant communities in a tropical forest.

70 Alterations in disturbance regimes have already been observed in Puerto Rico and other tropical
71 Caribbean islands, which have recently experienced increased exposure to extreme climatic events such
72 as hurricanes and droughts (Henareh Khalyani et al., 2016; Mote et al., 2017; Feng et al., 2020). Yet, due
73 to a long disturbance history, plant communities in these forests often develop adaptation strategies
74 that increase their resistance (i.e., ability to withstand a stressor) and resilience (i.e., speed and amount
75 of recovery after a stressor) to a wide range of stressors (Ostertag et al., 2005; Zimmerman et al., 2020).
76 The question remains, however, whether these plant communities will continue to exhibit high
77 resistance and resilience to increased and repeated disturbances within the context of a changing
78 climate. Changes in disturbance regimes (i.e., frequency, severity, size, or timing) could result in rapid
79 reorganization of plants into new communities by generating large gaps that favor the establishment of
80 pioneer and early successional species (Canham et al., 2010). Moreover, directional changes in climate
81 (e.g., warming temperatures) can erode resistance and resilience of plant communities in ways that may
82 not be observed until a major disturbance occurs, which could further alter plant community
83 composition and result in novel ecosystem states (Johnstone et al., 2016).

84 There is a wealth of research on how tropical forest communities respond to physical disturbance and
85 climate variability (Brokaw and Walker, 1991; Zimmerman et al., 1994; Canham et al., 2010; Uriarte et
86 al., 2012; Uriarte et al., 2016; Zimmerman et al., 2021). Most studies, however, tend to focus on only
87 one disturbance event - such as plant community recovery following hurricane disturbance in Puerto
88 Rico (see summaries by Brokaw and Walker, 1991; Zimmerman et al., 2021). This body of research has
89 provided valuable insights regarding which tree species are at highest risk (Zimmerman et al., 1994;
90 Canham et al., 2010) and how the forest regenerates following a hurricane event (Uriarte et al., 2012).

91   Drought effects on plant communities have also been documented for many ecosystems, including
92   tropical moist forests (Phillips et al., 2010; Corlett, 2016). These studies have shown that drought is
93   generally associated with increased tree mortality (Efarnian et al., 2017), decreased species richness,
94   and subsequent changes in forest composition (Costa et al., 2020).

95   Conversely, much less research has been conducted on the effects of warming on tropical forest plant
96   communities, even though evidence suggests tropical trees are at certain times already operating above
97   their optimum temperature for photosynthesis and may be nearing a high temperature threshold (Clark
98   et al., 2003; Doughty and Goulden, 2008; Mau et al., 2018; Wood et al., 2019; Carter et al., 2021; Miller
99   et al., 2021). Increased temperatures have been associated with increased flower production in Puerto
100 Rico, but whether this results in increased seed production is yet to be determined (Pau et al., 2013;
101 Uriarte et al., 2016). The relative paucity of data on tropical forest warming effects is in part due to the
102 considerable difficulties involved in experimentally manipulating these forests (Zhou et al., 2013;
103 Cavaleri et al., 2015). Nevertheless, long-term data on understory plant communities have highlighted
104 important changes in seedling dynamics associated with both temperature and precipitation (see meta-
105 analyses by Way and Oren, 2010; Comita et al., 2014; Bachelot et al., 2015; Uriarte et al., 2018). Further,
106 the effects of multiple disturbances (e.g., hurricanes and warming) can be synergistic or antagonistic and
107 thus difficult to predict from the study of single disturbances (e.g., Norby and Luo, 2004). To better
108 understand how plant communities will respond to increased exposure to climate warming and
109 disturbance, there is great value in assessing the effects of climatic events within the context of
110 experimental manipulations that mimic changes in climate, such as the increasing temperatures
111 predicted with climate change.

112 The Tropical Responses to Altered Climate Experiment (TRACE), a field warming experiment located in
113 northeastern Puerto Rico, offers an ideal site to explore these questions. Since its inception in 2015,
114 TRACE has been exposed to naturally occurring stressors in addition to experimental warming, offering
115 an unprecedented opportunity to assess how varying disturbances affect seedling and sapling dynamics
116 (Fig. 1). In 2015, the Caribbean and Central American tropics were enduring the peak of the most severe
117 drought event experienced since 1950 (Herrera and Ault, 2017). Eastern Puerto Rico in particular
118 suffered rainfall deficits of up to 45 %, causing water shortages and rationing for more than two million
119 residents (Mote et al., 2017). Drought conditions were even harsher within the Luquillo Mountains, the
120 most biodiverse region in eastern Puerto Rico and where our study took place, with rainfall deficits
121 continuing until late October 2015 (Mote et al., 2017; Gutiérrez-Fonseca et al., 2020). TRACE began
122 warming understory plants and soil in a tropical forest by 4 °C higher than ambient in September 2016
123 (Kimball et al., 2018). During the very active 2017 hurricane season, eastern Puerto Rico was
124 subsequently struck by two major hurricanes, Irma (Sept 7th, Category 5) and María (Sept 20th, Category
125 4). As the strongest hurricane affecting Puerto Rico since 1928, María brought record-breaking rainfall
126 and sustained winds up to 250 km/hr (Keellings and Hernández Ayala, 2019) that had severe effects on
127 tropical forests across the island (Uriarte et al., 2019; Hall et al., 2020). After one year of monitoring
128 forest recovery after hurricane disturbance in the absence of experimental warming, TRACE resumed
129 warming once again in September 2018.

130 Taken together, the TRACE site experienced a severe drought, two major hurricanes, and for half of the
131 study area (i.e., the heated plots), significantly warmer understory temperatures. Previous research at
132 our study site revealed hurricane-driven changes in herbaceous community composition irrespective of
133 prior warming and drought (Kennard et al., 2020). However, drought and sustained warming induced
134 positive density-dependent controls on seedling mortality, which could accelerate the loss of species
135 diversity (Bachelot et al., 2020). Understanding how climate warming and disturbance affect seedling
136 and sapling communities is particularly important, both because they contribute significantly to carbon

137 cycling and biodiversity in tropical forests, and because they represent the potential forest community
138 of the future (Clark, 2006). As such, we take advantage of this unique combination of events to explore
139 the following questions: 1) How do drought, hurricanes, and warming affect seedling and sapling
140 richness, diversity, and species composition? 2) Which species demonstrate a stronger response to
141 drought, hurricanes, and warming across ontogeny? and 3) Do these observed changes alter the
142 functional composition of the forest?

143 We predicted that drought would lead to a decrease in richness and diversity as well as a significant shift
144 in plant community composition, with a functional shift towards drought-resistant strategies with high
145 water storage capacity and thus higher leaf succulence (von Willert et al., 1992; Uriarte et al., 2018). We
146 predicted that hurricanes would also lead to a decrease in richness and diversity as well as a significant
147 shift in plant community composition, with a functional shift towards fast-growing species (Zimmerman
148 et al., 1994). Finally, we predicted that experimental warming would be associated with a marked loss in
149 richness and diversity (Bachelot et al., 2020) as well as a significant shift in plant community
150 composition, with a functional shift towards fast-growing strategies (Way and Oren, 2010). Plant
151 sensitivity to biotic and abiotic factors shift throughout ontogeny, in part due to changes in functional
152 traits (Lasky et al., 2015). As such, we also predicted there would be differences in seedling and sapling
153 responses to stressors, with higher effects on seedling composition and abundance relative to saplings,
154 since the dynamics of seedlings are strongly altered by abiotic and biotic conditions. While changes in
155 plant community assembly are often observed over long timeframes (Lasky et al., 2014), given the
156 number and severity of stressors observed in a relatively short period (5 years), results from this study
157 provide key insights into the initial vulnerability of a tropical forest to disturbance under a changing
158 climate.
159
160 **MATERIALS AND METHODS**

161 *Study site*

162 This study was conducted in the Luquillo Experimental Forest (LEF; 18°18'N, 65°50'W) in northeastern
163 Puerto Rico. Categorized as a subtropical wet forest according to the Holdridge Life Zone System
164 (Holdridge, 1967), this site holds the TRACE experimental plots, which were established in 2015 in a
165 secondary forest that has regenerated naturally after agricultural development during the first half of
166 the 20th century (Kimball et al., 2018). Located at 100 m elevation, the site contains clay-rich and acidic
167 soils classified as Ultisols (Scatena, 1989), with >60 % of root biomass concentrated in the top 10 cm soil
168 layer (Silver and Vogt, 1993; Yaffar and Norby, 2020). In the study area, the dominant canopy trees are
169 *Syzgium jambos*, *Ocotea leucoxylon* and *Caseria arborea*, and the site is also dominated by the palm
170 *Prestoea montana*.

171 Mean annual temperature of the site is 24 °C with relatively low seasonal variation, and mean annual
172 rainfall is 3,500 mm (García-Martinó et al., 1996). During the 2015 drought, total precipitation measured
173 at a neighboring site (El Verde Research Station, ~15 km away) was 48 % less than the mean in the
174 previous decade (O'Connell et al., 2018). On September 6, 2017, Hurricane Irma brought >300 mm of
175 rain to the northeast of the island, and just two weeks later on September 20, 2017 Hurricane María
176 brought ~1,500 mm of rain in only 48 hours (Hall et al., 2020).

177 *Experimental plots*

178   The understory plant community was evaluated inside each of the six 12 m^2 hexagonal TRACE plots (i.e.,
179   three heated and three control), which range in slope from 15-26 ° and are separated by at least 10 m.
180   All plots contain naturally occurring understory vegetation but were installed in areas with no adult
181   trees to allow space for experimental equipment. To evaluate the effects of warming on understory
182   plants and soil, three of the plots were warmed with infrared (IR) heaters +4 °C above ambient
183   temperatures of the three control plots. Temperatures at the heated plots were constantly controlled to
184   maintain a 4±0.1 °C increase in hourly average temperatures compared to control plots, as sensed by IR
185   thermometers (Kimball et al., 2018). The design of the warming system was adapted from Kimball et al.
186   (2008), with six IR heaters (Model Raymax 1010, Watlow Electric Manufacturing Co., St. Louis, MO) per
187   warmed plot installed on crossbars at approximately 3.6 m from the ground and aimed downwards to
188   maintain uniform and constant temperatures for long periods of time. Control plots contained the same
189   infrastructure (i.e., concrete footings, posts, crossbars) but with sheet metal plates the same size as the
190   heaters to control for potential effects of shading and equipment installation. More details on the layout
191   of the experimental site, infrastructure of the plots, and success of the warming method can be found in
192   Kimball et al. (2018). Experimental warming began in September 2016, was paused in September 2017
193   due to the passage of Hurricanes Irma and María, and was resumed in September 2018 after one year of
194   monitoring hurricane disturbance effects.

195   *Seedling surveys*

196   All woody seedlings (≥10 cm and <20 cm height) and saplings (≥20 cm height) inside the TRACE
197   experimental plots were initially tagged and identified to species in June 2015 (Census 0; C0), during the
198   peak of the drought. Previously tagged seedlings were reassessed for drought damage in November
199   2015 (C1), after the rains resumed. The following censuses were conducted in June 2016 (C2; control
200   year, 10 mo. after the drought ended), June 2017 (C3; 8 mo. after the warming started), May 2018 (C4; 7
201   mo. after the hurricanes, in the absence of warming) and April 2019 (C5; 7 mo. after warming resumed
202   and 14 mo. after the hurricanes). Seedlings that surpassed 20 cm height in a census year were
203   reclassified as saplings. Additional details about the seedling surveys can be found in Fig. 1A and
204   Bachelot et al. (2020). Raw data from these seedling and sapling surveys is available on the ESS-DIVE
205   data archive at https://doi.org/10.15485/1873618.

206   *Functional traits*

207   Functional trait data for the woody tree and shrub species found in our plots were obtained from the
208   Luquillo Forest Dynamics Plot (LFDP) database, which were measured with standard procedures
209   (Cornelissen et al., 2003; Swenson et al., 2012) within the Luquillo Experimental Forest (~15 km away
210   from our study site; Swenson et al., 2019). We selected functional traits that capture life history
211   differentiation among tree species (Kraft et al., 2010; Wright et al., 2010), which included: wood density
212   (WD; g/cm^3), specific leaf area (SLA; cm^{-2}/g^1), and leaf succulence (LS; g H20/cm^2 leaf area), as well as
213   leaf phosphorous (P; percentage P of oven-dry mass), leaf nitrogen (N; percentage N of oven-dry mass),
214   and leaf carbon (C; percentage C of oven-dry mass) concentrations. Wood density was measured on 10
215   samples per species using an increment borer in trees of 10-20 cm diameter at 1 m height, or using
216   branch material for smaller trees (Swenson et al., 2012). Leaf traits were measured on 25 samples per
217   species using sun-exposed leaves or on leaves from the crown of large trees (Swenson et al., 2012).

218   For each treatment (i.e., disturbance type), we calculated the community-weighted means (CWM) of
219   each functional trait by averaging the trait value across all species present in each plot weighted by the
220   number of stems in that same plot. Measuring the CWM trait value is one of the most common
221   approaches for quantifying functional composition at the community level and analyzing trait-

222   environment relationships (Funk et al., 2016). These values were calculated separately for seedlings and
223   saplings, to evaluate changes in CWMs observed along ontogeny.

224   ***Statistical analyses***

225   To assess how plant community responses to climate warming and disturbance differed across
226   ontogeny, we conducted all the analyses described below separately for seedlings and saplings. First, we
227   investigated how climatic events influenced broad biodiversity patterns by running linear mixed models
228   of species richness (i.e., number of species) and diversity (i.e., Shannon's Diversity Index) as a function of
229   treatment (i.e., control, drought, hurricanes, warming). Since each of the six plots was censused six
230   times from 2015-2019, we used plot identity as a random effect to account for repeated measurements.
231   All linear mixed models were run in R (R Core Team, 2020) with the *lmerTest* package (Kuznetsova et al.,
232   2017), using the Satterthwaite method for calculating degrees of freedom and corresponding *p* values
233   from *t* tests.

234   We then investigated how each event was associated with changes in species composition. As
235   heterogeneity in dispersions across groups can alter the results of composition analyses (Anderson and
236   Walsh, 2013), we tested for homogeneity of dispersions in species composition and found no significant
237   differences in dispersions across censuses (seedling: $F_{5,30} = 0.54$ and $P = 0.77$, sapling: $F_{5,30} = 0.11$ and $P = $
238   0.97) or across treatments (seedling: $F_{3,32} = 0.62$ and $P = 0.57$, sapling: $F_{3,32} = 0.08$ and $P = 0.94$). To
239   detect significant changes in species composition at the beginning and the end of the study period, we
240   used permutational multivariate analysis of variance (PERMANOVA) using data from the first (C0) and
241   last (C5) censuses. Then, to evaluate how variation in plant community composition was explained by
242   time (six census dates) and treatment (i.e., control, drought, hurricanes, warming), we used distance-
243   based redundancy analysis (RDA; Rao, 1964). We also used PERMANOVAs to investigate changes in
244   species composition following each individual treatment. This enabled us to assess specifically how
245   species composition changed following drought (by comparing composition in all plots in C0 and C2),
246   warming (by comparing composition in all plots in C2 and C3), hurricanes (by comparing composition in
247   all plots in C2 and C4), and warming before and after hurricanes (by comparing composition in the
248   heated plots in C3 and C5). All analyses were run in R (R Core Team, 2020) with the vegan package
249   (Oksanen et al., 2020), using 999 permutations and based on standardized Euclidean dissimilarity
250   matrices of the raw abundances (count of plant individuals) aggregated per plot in a given census (Clarke
251   and Warwick, 2001). We visualized all the results using nonmetric multidimensional scaling (NMDS;
252   Kruskal, 1964).

253   To evaluate how individual species responded to treatments and to predict the consequences for the
254   functional composition of the forest, we used generalized joint attribute modeling (GJAM; Clark et al.,
255   2017) in order to implement a Bayesian predictive trait model (Clark, 2016). This approach models
256   species weights as composition data, using multivariate normal distribution, before using them to
257   predict traits. Specifically, we modelled species weights (w_i, a vector of relative species abundances in
258   plot *i*) of all species found inside the plots as a function of treatment and plot as random effect
259   (contained in the predictor vector x_i) using a multivariate normal distribution:
260
261    $$w_i \sim MVN(\beta' x_i, \Sigma)$$
262
263   where β is the matrix of coefficients and Σ the species covariance matrix. Once this first step is
264   achieved, a variable change allows the fitted model to be transformed to traits from which trait
265   predictions can be made. Specific details about the model implementation can be found in Clark et al.
266   (2017). This method allows evaluating changes in species abundances not only in response to the

267   variables of interest (with treatment and plot as random effect to account for repeated measurements)
268   but also to the other species. Since species influence each other, using a multivariate normal distribution
269   is more appropriate than using a linear regression on individual species. Furthermore, this method has
270   been shown to perform better than directly modeling traits (Clark, 2016). To fit the model, we used
271   three chains with 2000 iterations and 500 burn-ins. Model fit was assessed with predictive checks of
272   both species counts and CWMs of functional traits. All analyses were conducted in R (R Core Team,
273   2020), using the *GJAM* package for predictive trait modeling (Clark et al., 2017).
274
275   **RESULTS**

276   Across the five years of data collection, we tagged 5197 individuals from 50 different tree species.
277   Specifically, we tagged 3498 individuals from 44 species at the seedling stage, and 1699 individuals from
278   47 species at the sapling stage. Seven species were common at the seedling stage with more than 100
279   tagged individuals and making up more than 80 % of the entire seedling cohort: *Rourea surinamensis* (31
280   % of the seedlings), *Guarea guidonia* (18 %), *Psychotria brachiata* (11 %), *Inga vera* (7 %), *Ocotea*
281   *leucoxylon* (6 %), *Nectandra turbacensis* (6 %), and *Piper glabrescens* (5 %). Three species were common
282   at the sapling stage with more than 100 tagged individuals and making up 47 % of the entire sapling
283   cohort: *Psychotria brachiata* (26 % of the saplings), *Piper glabrescens* (13 %), and *Rourea surinamensis* (8
284   %). We further describe observed changes in biodiversity, species composition, and functional
285   composition below.

286   ***Changes in biodiversity and species composition***

287   To assess changes in broad biodiversity patterns, we evaluated variations in species richness and
288   diversity throughout the study period using linear mixed models. As expected, responses to drought,
289   hurricanes, and experimental warming depended on plant ontogenic stage (Fig. 2). Hurricane
290   disturbance was marginally associated with a decrease in seedling richness (t_{27} = -2.01, P = 0.055), while
291   seedling diversity showed no significant response to any disturbance type. In contrast, sapling richness
292   (t_{28} = 3.40, P = 0.002) and diversity (t_{28} = 3.40, P < 0.001) were positively associated with experimental
293   warming, and sapling diversity was marginally associated with drought (t_{27} = 1.87, P = 0.072). Full results
294   of linear mixed models can be found in Supplementary Table 1.

295   As expected, seedling and sapling species composition significantly changed between the first and last
296   census (Table 1, History model). However, the effects of disturbance type and time on species
297   composition were not as pronounced (Fig. 3). Redundancy analyses showed that 27 % of the variation in
298   seedling composition was explained by disturbance and time (RDA, *pseudo-F$_{6,29}$* = 1.82, P = 0.027, Table
299   1). Specifically, disturbance type, although marginally significant, explained 11 % of the variation in
300   seedling composition (*pseudo-F$_{3,29}$* = 1.51, P = 0.103) and time captured 16 % of the variation in seedling
301   composition (*pseudo-F$_{3,29}$* = 2.13, *P*= 0.023). Meanwhile, sapling composition did not show a strong
302   response to disturbance and time (RDA, *pseudo-F$_{6,29}$* = 1.82, P = 0.188, Table 1). When evaluating the
303   individual effects of each disturbance type on species composition, we detected no significant effects of
304   drought, hurricanes, or warming on either seedling or sapling composition (Table 1).
305
306   ***Changes in functional composition***

307   Several species showed significant changes in abundance associated with disturbance at both the
308   seedling and the sapling ontogenic stages (Fig. 4, Supplementary Table 2). In general, drought and
309   warming were more often associated with higher abundance in both seedlings and saplings, while the
310   effects of hurricanes were more varied (Fig. 4). Across the three disturbance types, warming was
311   significantly associated with about twice as many species as drought and hurricanes. Warming resulted

312   in high abundance of 6 species in the seedling stage and 7 species in the sapling stage, and with low
313   abundance of 2 species in the seedling stage and 3 species in the sapling stage. In contrast, drought was
314   significantly associated with high abundance of 4 species and low abundance of 1 species in the seedling
315   stage and with high abundance of 2 species and low abundance of 1 species at the sapling stage. Finally,
316   hurricanes were associated with high abundance of 2 species in the seedling stage and 3 species in the
317   sapling stage, and with low abundance of 3 species in the seedling stage and 1 species in the sapling
318   stage. These species covered a wide range of life forms and successional status (Table 2).

319   Some of these species demonstrated a significant response to more than one disturbance type. For
320   example, seedlings of one of the most common species in the study area, the early successional shrub
321   *Psychotria brachiata* (PSYBRA), showed significantly lower abundance during drought but higher
322   abundance under warming conditions. Meanwhile, seedlings of the early successional tree *Tabebuia*
323   *heterophylla* (TABHET) showed increased abundance during drought but lower abundance after
324   hurricane disturbance. Observed responses of plant species to the different disturbances also showed
325   variation across ontogenic stages. In particular, the previously mentioned *P. brachiata* shrub had higher
326   abundance at the seedling stage but lower abundance at the sapling stage under warming conditions.
327   Lastly, a few other species showed a consistent response to the disturbances across ontogenic stages,
328   such as the early successional shrub *Piper glabrescens* (PIPGLA), which showed higher abundance during
329   drought and lower abundance during warming at both the seedling and sapling stages (Fig. 4).

330   We found no disturbance effect on any of the six sapling CWM functional traits for predicted changes in
331   the functional structure of the forest (Fig. 5, Supplementary Table 3). Specifically, drought had no effect
332   on the functional structure of either seedling or sapling communities in our study site. In contrast,
333   hurricane and experimental warming were significantly associated with changes in CWM functional
334   traits of seedling communities (Fig. 5). Both the hurricanes and the experimental warming led to an
335   increase in CWM leaf P concentrations and leaf succulence, and a decrease in CWM leaf C
336   concentrations in seedlings. The seedling CWMs for wood density, specific leaf area and leaf N
337   concentrations showed no association to any of the disturbance types included in our study.
338
339   **DISCUSSION**

340   In this study, we document the effects of multiple climatic stressors in a tropical forest understory plant
341   community. Within the time frame of this study (2015-2019), seedlings and saplings in the TRACE plots
342   experienced stronger than average natural hazards and significantly warmer temperatures. As such, we
343   anticipated severe losses in biodiversity as well as a shift in species and functional composition of the
344   understory plant community. In stark contrast to our expectations, we observed only a slight reduction
345   in seedling richness after hurricane disturbance, while drought and experimental warming increased
346   sapling diversity. There was also no evidence of pronounced shifts in species composition in response to
347   the various disturbance types, as our analyses detected only minor effects of disturbance and time on
348   seedling composition. Several species showed significant changes in abundance in response to the
349   various stressors, leading to predicted changes in functional composition of these forest sites for the
350   seedling community. Yet the overall lack of strong changes in the understory plant community, despite
351   increased exposure to climatic extremes, highlights the high capacity of these forests to resist
352   environmental stressors and their potential to continue supporting critical ecosystem functions and
353   services in the face of a changing climate.

354   ***Minimal effects of disturbance on seedling and sapling communities***

355   Despite the observed shift in species composition between 2015 and 2019, we found few significant
356   changes in seedling and sapling communities specifically associated with drought, hurricanes, and

8

357 experimental warming. This result suggests that the woody understory might be more resistant to
358 climate warming and disturbance than expected. As mentioned in previous studies, plant communities
359 in this forest may have already developed pre-existing tolerance to a wide range of stressors over a long
360 history of repeated disturbance events, increasing their resistance and resilience through time (Ostertag
361 et al., 2005; Zimmerman et al., 2020; Zimmerman et al., 2021). Alternatively, the lack of marked shifts in
362 seedling and sapling communities associated with these disturbances might suggest lagged responses
363 that take longer to emerge (Xie et al., 2020).

364 Tropical seedlings have been shown to be sensitive to water availability (Bunker and Carson, 2005; Slot
365 and Poorter, 2007; Álvarez-Yépiz et al., 2018; Uriarte et al., 2018). However, the effects of drought on
366 seedlings have mostly been assessed with experimental manipulations, which may simulate more
367 extreme conditions than those observed in nature and thus exacerbate seedling responses to water
368 stress. In addition, controlled experiments might obscure the balancing effects of other natural
369 occurring mechanisms, such as indirect effects on soil pathogens and mycorrhizal associations that
370 influence seedling survival (Liang et al., 2015; Bachelot et al., 2020). Observational studies provide more
371 realistic data for understanding these cross-trophic dynamics, but extreme climatic events are
372 unpredictable and often with long return intervals (Scatena and Larsen, 1991; Boose et al., 2004).
373 Further, the results may be confounded by other biotic or abiotic components of the ecosystem (Soong
374 et al., 2020).

375 Our results show a slight increase in sapling diversity in response to drought. In the TRACE site, Bachelot
376 et al. (2020) found higher seedling growth and survival during the 2015 drought when compared to
377 other censuses, which could in turn influence sapling diversity. However, given that we have no data
378 prior to the drought, we were unable to assess the drought response with respect to the baseline. Thus,
379 the survey in the drought year recorded late-stage effects of the drought and might represent an
380 assessment of seedlings and saplings that already possessed high fitness and drought tolerance
381 (Zimmerman et al., 2021).

382 Tropical forests in Puerto Rico have shown a high degree of resistance and resilience to hurricanes
383 (Beard et al., 2005, Zimmerman et al., 2021). Yet Hurricane María's combined extreme precipitation and
384 strong winds caused significantly higher stem breakage and tree mortality than Hurricanes Hugo (1989)
385 and Georges (1998) in the Luquillo Experimental Forest (Uriarte et al., 2019). Despite the unprecedented
386 strength of this storm, we only found a mild reduction in seedling richness following the hurricanes, and
387 no effects on diversity or species composition. Reductions in seedling richness might have been caused
388 by the significant increase in herbaceous cover observed after the hurricanes within the TRACE plots
389 (Kennard et al., 2020), potentially leading to an increase in intra and interspecific competition for
390 resources. In the initial years following a hurricane, tropical forest understory herbs, shrubs, and newly
391 recruited tree saplings tend to increase in abundance due to higher light availability (Zimmerman et al.,
392 2021). However, as canopy cover increases through successional time, we can expect a reduction in
393 herbaceous cover, leaving space for shade-tolerant woody species to grow and recover (Scatena et al.,
394 1996; Chinea, 1999; Walker and Sharpe, 2010).

395 Species richness and diversity of saplings, but not seedlings, increased in response to warmer
396 temperatures. This finding contrasts with our expectation that temperature would negatively affect
397 tropical plant diversity (Stork et al., 2009; Wright et al., 2009). Warmer temperatures might be selecting
398 for pioneer species that thrive in hotter conditions, leaving the forest in a transition phase comprised of
399 a mix of species where species that are not doing well have yet to die out (Connell, 1978; Corlett, 2011).
400 The TRACE site is also a secondary forest with a long history of climatic and anthropogenic disturbance
401 (Kimball et al., 2018). Secondary forests have been shown to retain high levels of late successional

402 species, possibly in response to environmental filtering that has selected for species that do well under a
403 range of conditions (e.g., Chazdon et al., 2009). Species composition in our study did not change in
404 response to warming, which supports the idea that, while there is a shift in diversity of the saplings, the
405 community is relatively resistant to change. Yet recent evidence of a decrease in root production and
406 slower root recovery after hurricane disturbance in the TRACE heated plots points to complex
407 interactive effects of warming and disturbance that could affect biodiversity patterns in the long-term
408 (Yaffar et al., 2021). As such, whether this resistance continues under persistent and longer-term
409 warming is yet to be determined.

Responses to disturbance were variable across ontogeny

411 Seedling and sapling communities differed in their responses to the various climatic stressors assessed in
412 our study. This was expected, as ontogeny alters many ecological processes that influence plant
413 demographics (Lasky et al., 2015) and responses to environmental change (Comita et al., 2009; Fortunel
414 et al., 2020). In the case of drought, we only found a marginal increase in sapling richness and a
415 significant response from a few species at the seedling and sapling stage. The abundance of *Piper
416 glabrescens*, an early successional shrub, was significantly higher during the drought at both the seedling
417 and sapling stages. This result is in line with the theory that shrubs in Puerto Rico might have adapted to
418 a wide range of soil moisture conditions (Zimmerman et al., 2021). However, the abundance of another
419 early successional shrub species, *Psychotria brachiata*, was reduced at the seedling stage during the
420 drought. This range of results emphasizes the need to understand the functional characteristics of each
421 plant species.

422 Hurricane disturbance had varied effects on seedling and sapling communities. Only seedling richness
423 was negatively affected by hurricane disturbance, which could suggest that seedlings are more sensitive
424 than saplings due to their lower belowground biomass or higher desiccation potential (Uriarte et al.,
425 2005). Previous studies have highlighted life history differentiation amongst tropical woody species that
426 result in varied susceptibility to hurricanes (Zimmerman et al., 1994; Walker et al., 2003; Canham et al.,
427 2010). These studies support our results of both positive and negative effects of hurricane disturbance
428 on different species. For example, the early-mid successional shrubs *P. brachiata* and *Piper hispidum*
429 showed contrasting responses to hurricanes as well as drought, which supports niche differentiation
430 (Connell, 1978; Uriarte et al., 2004). Heterogeneity in the severity and timing of disturbance might
431 enable these two competing shrubs to coexist in the understory.

432 To date, TRACE is the only field-scale *in situ* warming experiment of understory plants in a tropical forest
433 ecosystem (Kimball et al., 2018). As such, knowledge of how increased temperatures might affect
434 seedling and sapling dynamics in tropical forests is still in its infancy, which is critical to predict future
435 global carbon balance (Clark, 2004; Reed et al., 2012; Zuidema et al., 2013). Previous studies have shown
436 high thermal tolerance during juvenile growth (Cheesman and Winter, 2013; Slot and Winter, 2018).
437 Similarly, we found stronger effects of warming on sapling rather than seedling biodiversity, with species
438 showing both positive and negative responses to warming. In particular, *P. brachiata* responded
439 positively to warming at the seedling stage but negatively at the sapling stage, while *P. glabrescens*
440 responded negatively to warming at both the seedling and sapling stages. After one year of warming
441 prior to the hurricanes, *P. brachiata* demonstrated greater photosynthetic thermal acclimation capacity
442 than *P. glabrescens* (Carter et al., 2020). The differing capacity of these understory shrubs to
443 physiologically acclimate to warming could explain why the abundance of *P. brachiata* saplings increased
444 with warmer temperatures, while the abundance of *P. glabrescens* did not. Finally, this variability in
445 species responses to climate warming and disturbance can act as a mechanism to maintain species
446 biodiversity through non-linearity (Bachelot and Lee, 2020; Chesson, 2000).

447 *Evidence of functional shift in woody understory community following disturbance*

448 Overall, our finding of species-specific effects of disturbance suggests that the functional composition of
449 the forest might eventually change. In other words, disturbance-driven changes in species abundance
450 were predicted to significantly influence the functional composition of seedling and sapling
451 communities. We predicted that drought would lead to higher leaf succulence (i.e., higher water storage
452 capacity), while warming and hurricanes would lead to the prevalence of pioneer and early successional
453 species with fast-growing strategies. Contrary to our expectations, however, we found no change in leaf
454 succulence, or any other functional traits, associated with drought. This result could reflect the lack of
455 pre-drought data on the woody composition, such that the community already reflects traits that are
456 best adapted to drought.

457 Previous studies have shown that tropical forest seedlings and saplings experience drastically different
458 environments following a hurricane, including increased water input more similar in chemistry to rainfall
459 when compared with water that has passed through a closed canopy forest (Heartsill-Scalley et al.,
460 2007). However, despite the increased water input, forests recovering from hurricane disturbance tend
461 to have drier litter layers with slower decomposition rates due to increased temperature and solar
462 radiation (González et al., 2014), which could in turn increase water stress and select for seedling
463 communities with higher leaf succulence, as we observed. Similar to prior studies that have followed
464 recruitment after hurricane disturbance (Zimmerman et al., 1994), we also found a shift towards fast-
465 growing strategy traits such as low leaf carbon and high leaf phosphorus concentrations at the seedling
466 stage. Overall, our findings support our hypothesis that hurricanes would shift the understory plant
467 community towards fast-growing or drought-tolerant species, at least at the seedling ontogenic stage.
468 Specifically, our results show two distinct shifts through time (Reich, 2014) – water stress immediately
469 after the hurricanes selects for drought-resistant species, while subsequent changes in the environment
470 favor the recruitment of fast-growing species (Zimmerman et al., 1994).

471 Surprisingly, many more species were significantly influenced by warming when compared with drought
472 and hurricanes, and most responded with an increase in abundance. As expected, most of these favored
473 species were pioneer trees and shrubs such as *Cecropia schreberiana*, *Miconia racemosa*, and *Psychotria*
474 *berteriana*. As a result, we found a shift towards low leaf carbon and high leaf phosphorus, which is
475 consistent with a community shifting towards fast-growing strategies (Strauss-Deberiedetti et al., 1996;
476 Bonal et al., 2007). Similar to the functional shifts observed after the hurricane, warming also favored
477 drought-resistant species with high leaf succulence, which tend to be slow-growing species (Reich,
478 2014). The selection of contrasting strategies might be the result of the short length of our study –
479 warming favors fast-growing strategies in the short-term, but drought-tolerant species with
480 conservative strategies might be favored under prolonged warming stress. While we did observe these
481 shifts for the seedlings, there was no significant change in CWM of functional traits for the saplings in
482 response to warming. Together, this might suggest that significant environmental filtering is occurring at
483 the seedling stage (Lebrija-Trejos et al., 2010), while prevailing shrubs already possess traits that are
484 responsive to changing environmental conditions.

485 *Conclusions*

486 Overall, we found that both the seedling and sapling communities exhibited strong resistance to a wide
487 range of climatic stressors in this forest. However, it is possible that multiple disturbance legacies and
488 interactions are confounding our results, making it difficult to decouple the effects of each of these
489 events on the understory plant community. When we examine responses at the individual and
490 functional level, we see that both warming and drought generally had positive effects on species
491 richness and diversity, with drought having a stronger influence on the seedling and warming on the

sapling ontogenic stages. Despite repeated hurricane disturbance in this forest, the hurricanes had an overall negative effect on richness and diversity, with more species doing poorly under these conditions. Taken together, these findings suggest that past disturbances may have already selected for a range of species that are better adapted to shocks and stressors, with different species being "released" depending on the environmental change. Longer-term monitoring of seedling and sapling dynamics in this forest is needed to understand the long-term implications of repeated disturbances in a warmer world. However, disturbance-driven changes in species dominance and functional structure suggest that longer-term and repeated disturbance will ultimately shift the community composition of this forest, particularly if precipitation declines, temperature continues rising, and hurricane disturbance becomes more frequent and severe in the tropics.

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837
838 **FIGURE CAPTIONS**

839 Figure 1. (A) Timeline of disturbance events and seedling and sapling censuses (C0 = June 2015, C1 =
840 November 2015, C2 = June 2016, C3 = June 2017, C4 = May 2018, C5 = April 2019). (B) Changes in the
841 understory plant community observed in one of the TRACE warming plots (Plot 2) from December 2016
842 to July 2019.

843 Figure 2. Richness (number of species) and Diversity (Shannon's diversity index) of seedlings (left panels)
844 and saplings (right panels) during control (C), drought (D), hurricanes (H), and warming (W). Black
845 asterisks above bars denote significant differences from the control at $\alpha=0.05$, while black filled circles
846 denote significant differences at $\alpha=0.1$ resulting from Linear Mixed Models.

847 Figure 3. Non-metric multidimensional scaling of seedling (left panel) and sapling (right panel) species
848 composition. Each symbol represents the species composition in an experimental plot, during a specific
849 census date (symbols; C0 = June 2015, C1 = November 2015, C2 = June 2016, C3 = June 2017, C4 = May
850 2018, C5 = April 2019) and disturbance type (colors; C = control, D = drought, H = hurricanes, W =
851 warming).

852 Figure 4. Results of predictive trait modeling, showing species with abundances that were significantly
853 associated with each disturbance type at the seedling (circles) and sapling (squares) ontogenic stages.
854 Lines expand to the 95 % credible intervals. Full species name, life form, and successional status can be
855 found on Table 2.

856 Figure 5. Results of predictive trait modeling, showing the predicted effects of each disturbance type on
857 the community-weighted means of functional traits for both seedlings (circles) and saplings (squares).
858 Lines expand to the 95 % credible intervals. Open symbols show non-significant effects (credible
859 intervals overlap with 0), whereas filled symbols indicate significant effects. Data are shown for the
860 intercept (μ, green) and for drought (D, blue), hurricanes (H, purple), and warming (W, red). Traits
861 include wood density (WD; g/cm^3), specific leaf area (SLA; cm^{-2}/g^1), leaf succulence (LS; g H_2O/cm^2 leaf
862 area), leaf phosphorous (P; percentage P of oven-dry mass), leaf nitrogen (N; percentage N of oven-dry
863 mass), and leaf carbon (C; percentage C of oven-dry mass).
864
865 **TABLES**

866 Table 1. Results of permutational multivariate analysis of variance (PERMANOVA) between each
867 disturbance type and its respective control conditions for seedling and sapling species composition. Each
868 row shows the results of a different model where we focused on detecting the individual effects of time
869 (i.e., history model), drought, hurricanes, warming, or the interactions between warming and
870 hurricanes. In the Model Structure column, codes represent census dates (C0 = June 2015, C1 =
871 November 2015, C2 = June 2016, C3 = June 2017, C4 = May 2018, C5 = April 2019). The last row shows
872 the results of the distance-based redundancy analyses (RDA), where we evaluated the overall effects of
873 time (six census dates) and treatment (i.e., control, drought, hurricanes, warming) on species
874 composition. Significant models at α=0.05 are highlighted in bold.
875

Disturbance type	Model structure	Seedlings		Saplings	
		Pseudo F	*P*	*Pseudo F*	*P*
History	C0 vs. C5	5.68	**0.002**	2.62	**0.003**
Drought	C0 vs. C3	0.95	0.40	0.34	0.87
Hurricanes	C2 vs. C4	1.21	0.28	0.85	0.54
Warming	C2 vs. C3	1.02	0.40	1.36	0.24
Warming * Hurricanes	heated plots in C2 vs. C5	2.67	0.20	2.33	0.10
All disturbances (RDA)	treatment + time	1.82	**0.03**	1.82	0.19

876
877 Table 2. Species codes with the full scientific name, family, life form, and successional status of plant
878 species that were significantly associated with drought, hurricanes, or warming (i.e., as shown in Fig. 4).
879 Asterisk (*) indicates that the successional status is unclear.
880

Species Code	Scientific Name	Family	Life form	Successional Status
ANDINE	*Andira inermis* (W. Wright) Kunth ex DC.	Fabaceae	Tree	Late
CECSCH	*Cecropia schreberiana* Miq. subsp. schreberiana	Urticaceae (Cecropiaceae)	Tree	Pioneer
GONSPI	*Gonzalagunia spicata* (Lam.) M. Gómez	Rubiaceae	Shrub	Early*
GUAGUI	*Guarea guidonia* (L.) Sleumer	Meliaceae	Tree	Late
IXOFER	*Ixora ferrea* (J. F. Gmel.) Benth.	Rubiaceae	Tree	Late
MICMIR	*Miconia mirabilis* (Aubl.) L. O. Williams	Melastomataceae	Tree	Pioneer
MICRAC	*Miconia racemosa* (Aubl.) DC.	Melastomataceae	Tree	Pioneer
MICTET	*Miconia tetrandra* (Sw.) D. Don	Melastomataceae	Tree	Late*
MYRSPL	*Myrcia splendens* (Sw.) DC.	Myrtaceae	Tree	Mid
OCOSIN	*Nectandra turbacensis* (Kunth) Nees (= *Ocotea sintensis*)	Lauraceae	Tree	Late
PIPGLA	*Piper glabrescens* (Miq.) C. DC.	Piperaceae	Shrub	Early
PIPHIS	*Piper hispidum* Sw.	Piperaceae	Shrub	Mid*
PSYBER	*Psychotria berteriana DC.*	Rubiaceae	Shrub/Small tree	Pioneer
PSYBRA	*Psychotria brachiata* Sw.	Rubiaceae	Shrub	Early
ROYBOR	*Roystonea borinquena* O. F. Cook	Arecaceae	Tree (palm)	Palm
SCHMOR	*Schefflera morototoni* (Aubl.) Maguire	Araliaceae	Tree	Pioneer
TABHET	*Tabebuia heterophylla* (DC.) Britton	Bignoniaceae	Tree	Early
TETBAL	*Tetragastris balsamifera* (Sw.) Oken	Burseraceae	Tree	Mid
TRIPAL	*Trichilia pallida Sw.*	Meliaceae	Tree	Late

881