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ARTICLE

Special Feature: Tropical Forest Responses to Repeated Large-scale Experimental Hurricane Effects

Long-term responses of gastropods to simulated hurricanes in a tropical montane rainforest

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Abstract

Climate-induced disturbances such as hurricanes affect the structure and functioning of ecosystems, especially those in the Caribbean Basin, where high-energy storms have long affected ecosystem dynamics. Because climate change will likely continue to alter the frequency and intensity of hurricanes in the Caribbean, it is increasingly important to understand the mechanistic bases for ecosystem responses. Although long-term surveys and nonmanipulative "natural experiments" provide considerable insight, manipulative experiments are required to decouple confounded factors associated with high-intensity storms. To address this, we exploited a replicated factorial design to experimentally isolate the long-term effects of canopy opening and debris deposition on population- and community-level characteristics of gastropods in the Luquillo Experimental Forest of Puerto Rico. The canopy trimming experiment included four treatments: (1) the reference treatment received no manipulations; (2) canopy trimmed, but debris from trimming not deposited on the forest floor (trim only); (3) canopy not trimmed, but debris deposited on the forest floor (debris only); and (4) canopy trimmed and debris deposited on the forest floor (trim and debris). After 10 years, the trim and debris treatment was repeated to simulate reoccurring hurricane events, whereas the trim-only and debris-only treatments were not subject to additional manipulation at this time. We evaluated responses to treatment and time for gastropod populations (abundance) and communities (biodiversity and composition). Population-level responses were species specific. Three species and total gastropod abundance exhibited consistent responses to treatments regardless of time, four species exhibited consistent temporal trends regardless of treatment, and five species exhibited an interaction in which the effects of time depended on treatment. In general, point-, α-, and γ-biodiversity decreased through time, whereas β-biodiversity increased through time. Gastropod populations and communities were resistant and resilient to the simulated disturbances, exhibiting quick recovery from any short-term changes in abundance or biodiversity. From an evolutionary perspective, long-term exposure to hurricane-induced disturbances likely leads to species-specific adaptations that enhance resistance and resilience.

KEYWORDS
climate change, disturbance, Luquillo Mountains, manipulative experiment, Puerto Rico, snails, Special Feature: Tropical Forest Responses to Repeated Large-scale Experimental Hurricane Effects, tabonuco forest

INTRODUCTION

The Anthropocene is a time of unprecedented, accelerating, anthropogenically induced environmental change (Monastersky, 2015), precipitating the onset of a biodiversity crisis that has been labeled the Earth's sixth mass extinction (Ceballos et al., 2015). Perturbations caused by human activities include both pulse (e.g., land-use change, habitat fragmentation, fires, and floods) and press (e.g., warming, ocean acidification, and sea level rise) disturbances (Dukes & Mooney, 1999; Sasaki et al., 2015). In addition, synergisms occur between press and pulse disturbances, such as the press disturbance of global warming increasing the frequency and intensity of pulse disturbances such as hurricanes (Bhatia et al., 2018; Holland & Bruyère, 2014). The combined effects of pulse and press disturbances have profound consequences to the spatiotemporal dynamics of populations, communities, and ecosystems (Schowalter et al., 2021; Willig et al., 2021), as well as to the delivery of critical ecosystem services (Mooney et al., 2009; Prather et al., 2013; Wagner, 2020).

The role of disturbance in molding the structure and function of ecosystems has emerged as a paradigm guiding much ecological research from theoretical (Holling, 1973; Holt, 2006; Pickett et al., 1989; Willig & Walker, 1999) and empirical (Schowalter et al., 2021; Walker et al., 1991, 1996; Willig et al., 2007, 2011, 2021) perspectives. Tropical forests in the Greater Caribbean Basin are disturbance-mediated systems that are structured as a consequence of a long-history of repeated, intense storms (Waide & Lugo, 1992; Walker et al., 1991, 1996; Zimmerman et al., 2020). Spatiotemporal variation in the structure, physiognomy, and composition of these ecosystems arises from repeated cycles of hurricane-induced disturbance and secondary succession. However, the current combination of increasing temperatures and increasing frequency of major hurricanes may create conditions beyond those historically experienced by these biotas, leading to novel species combinations and new types of communities and ecosystems (Lugo, 2013; Lugo et al., 2012; Willig et al., 2021).

Intense hurricanes have two primary, immediate impacts on forests: removal of the canopy and deposition of vegetative debris, including trunks, branches, and leaves on or near the forest floor (Brokaw & Greer, 1991; Uriarte et al., 2019; Whigham et al., 1991; Zimmerman et al., 1994). Loss of canopy cover results in multiple physical changes to forested environments, including increased levels of light at or near the soil surface (Bellingham et al., 1996; Fernández & Fetcher, 1991), and a corresponding increase in temperature (see supporting information from Schowalter et al., 2021). In terrestrial habitats, greater temperatures and increased air circulation at ground level lead to increased evaporation from litter and soil, thereby decreasing litter and soil moisture (Lodge, 1996). In addition, the deposition of debris by storms significantly alters the structure of the understory and represents a major influx of carbon and many nutrients into detrital food webs (Lodge et al., 2014; Miller & Lodge, 1997; Ostertag et al., 2003). Because these changes occur in concert, nonmanipulative natural experiments cannot isolate the effects associated with each aspect of hurricane-induced environmental change.

Isolating mechanistic bases of responses to hurricane-induced disturbance is difficult to study because of the unpredictable timing of these disturbances and because of the interrelated suite of environmental factors that are associated with hurricanes. In addition, many studies of pulse disturbances are restricted to before and after "snapshots" (Adams, 2001) that are not able to clearly distinguish mechanistic bases for change or to characterize post-disturbance trajectories during secondary succession. Recent comprehensive assessments of long-term responses of tropical arthropods and gastropods to repeated major hurricanes as well as to global warming found that effects of pulse disturbances created by hurricanes and subsequent secondary succession on populations and communities trumped those associated with global warming (Schowalter et al., 2021; Willig et al., 2021). Although these observational studies provide considerable insight, they cannot decouple the relative importance of mechanisms associated with changes in the abiotic environment (increased light, temperature, evapotranspiration, and aridity) caused by the loss of forest canopy from those associated with the massive pulse of debris deposition and modified physical structure (increased nutrient input, altered soil moisture, and deposition of course woody debris). Consequently, a large-scale and long-term manipulative experiment (canopy trimming experiment [CTE]) was designed to distinguish the effects of canopy opening and debris deposition on population, community, and ecosystem characteristics of Luquillo Experimental Forest of Puerto Rico. The CTE originated as a replicated 2×2 factorial design to disentangle the effects

of canopy opening from those of debris deposition, creating four treatments: (1) the reference treatment that received no manipulation; (2) the trim-only treatment in which the canopy was trimmed, but debris was not deposited on the forest floor; (3) the debris-only treatment in which the canopy was not trimmed, but debris was deposited on the forest floor; and (4) the trim and debris treatment in which the canopy was trimmed and the debris was deposited on the forest floor. After 10 years, the trim and debris treatment was repeated to simulate multiple hurricane events, whereas the trim-only and debris-only treatments were not manipulated again. Thus, the cross-factorial nature of the experiment was effectively abandoned so that consistent effects of canopy opening regardless of debris deposition, consistent effect of debris deposition regardless of canopy opening, and interactive effects between canopy opening and debris deposition could not be evaluated directly. Instead, we could only address (1) consistent differences among treatments, regardless of time; (2) consistent temporal differences, regardless of treatment; and (3) differences over time that depend on treatment (equivalent to differences among treatments that depend on time). Previous work (Shiels & González, 2014; Willig et al., 2014) evaluated immediate and short-term responses to CTE manipulations. In contrast, this research leveraged 15 years of data from the CTE to address two over-arching questions concerning gastropod responses to long-term successional dynamics: (1) Do canopy loss or debris deposition associated with pulse disturbances have consistent long-term effects, and (2) are the forms (increasing, decreasing, modal, saturating) of long-term trajectories consistent among the four experimental treatments? Our a priori expectations were that: (1) canopy loss generally has negative consequences for gastropod abundance, biodiversity, and composition; (2) debris deposition generally has positive effects on gastropod abundance, biodiversity, and composition; and (3) this combination creates a "environmental severity gradient" related to treatments. More specifically, we hypothesize that the severity of treatments, from most to least severe from the perspective of gastropods, is trim only > trim and debris ~ reference > debris only.

MATERIALS AND METHODS

Study area

Situated within the hurricane-prone Caribbean (Figure 1), the Luquillo Experimental Forest (LEF) comprises 11,300 ha of mountainous terrane in northeastern Puerto Rico (Figure 1a) and is a site in the National Science Foundation's Long-Term Ecological Research network. Sampling was conducted in tabonuco forest near El Verde Field Station (18.321°N, 65.820°W; 340–470 m above sea level) (Figure 1b). Tabonuco forest is the most extensive and best-studied portion of the LEF (Brokaw et al., 2012). It is a lower montane subtropical wet forest and is characterized by the dominant hardwood species, *Dacryodes excelsa* (Burseraceae). Mature forest canopy height is >20 m, with emergent trees up to 35 m. Rainfall in tabonuco forest averages 346 cm per year (McDowell & Estrada-Pinto, 1988). Humidity is consistently high, and seasonal or diurnal variation in temperature is small, with mean monthly temperatures ranging from 21 to 24°C (Harris et al., 2012).

During the past few decades, three major hurricanes (Hugo in 1989, Georges in 1998, and Maria in 2017) have passed over eastern Puerto Rico. Each produced considerable damage to tabonuco forest, but the three hurricanes differed in intensity, extent, and severity. Hurricane Hugo, a category 4 storm with maximum sustained winds of 227 km/h, produced large canopy openings and deposited much coarse woody debris on the forest floor (Scatena & Larsen, 1991). Hurricane Georges, a category 3 storm with sustained winds of 177 km/h (Ostertag et al., 2003), caused extensive defoliation of trees but did not produce large quantities of coarse woody debris. Hurricane Maria, a category 4 storm with sustained winds of 250 km/h, caused extensive tree mortality and canopy opening over much of the LEF, and deposited large amounts of coarse woody debris on the forest floor (Uriarte et al., 2019). These storms only represent part of the disturbance regime in the LEF, as many minor hurricanes have impacted the island, including Hurricanes Luis and Marilyn in 1995, Bertha and Hortense in 1996, Debby in 2000, Jeanne in 2004, Irene in 2011, and Irma in 2017. Moreover, the frequency and intensity of hurricanes will likely continue to increase in the future due to effects of climate change (Bhatia et al., 2018; Holland & Bruyère, 2014).

Study organisms

Terrestrial gastropods are diverse, abundant, and easily sampled in many ecosystems, making them useful models for population (Willig et al., 1998, 2014; Willig & Camilo, 1991), community (Stanisic et al., 2007; Wronski & Hausdorf, 2010), or metacommunity research (Presley et al., 2011; Willig et al., 2011, 2013, 2021). Moreover, gastropods are declining in abundance and biodiversity at a global scale and require attention from conservation managers (Lydeard et al., 2004). Terrestrial gastropods are ectotherms, have low vagility, and are constrained in distribution and behavior by desiccation stress (Cook, 2001). Consequently, direct (e.g., increasing temperature, more intense droughts) and indirect (e.g., changes in disturbance regimes) effects of global warming, combined with increased intensity of other anthropogenic activities, may subject these faunas to greater risk of local or regional extirpation.

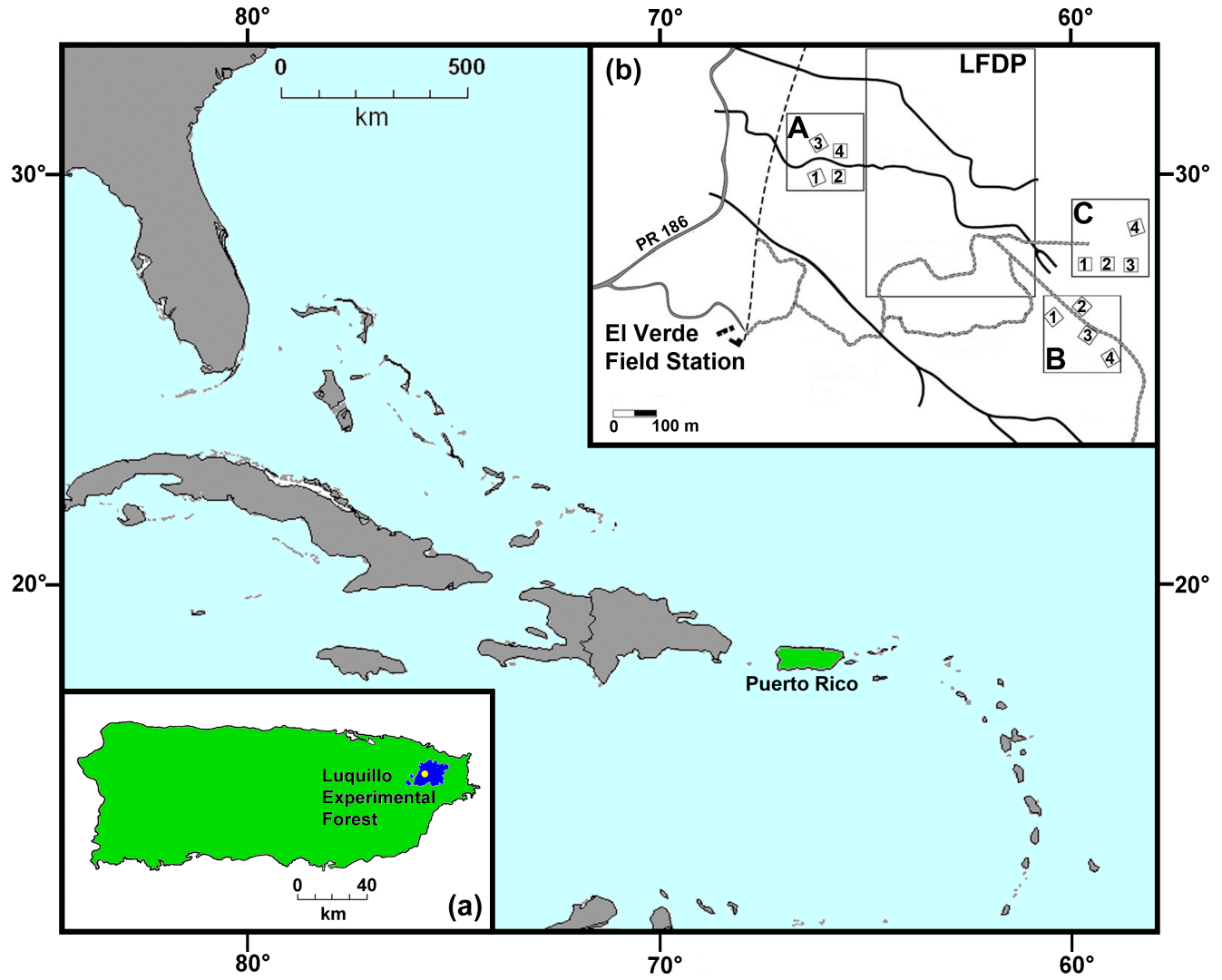

FIGURE 1 Map showing the locations of Puerto Rico (green) within the Caribbean and of the Luquillo Experimental Forest in Puerto Rico (blue shading in inset a), solid yellow circle within the Luquillo Experimental Forest indicates the location of the canopy trimming experiment. Plots (1, 2, 3, and 4) within each replicated block (A, B, and C) were located within the Sonadora River watershed (inset b) in tabonuco forest near the Luquillo Forest dynamics plot (LFDP). Road = gray, trail = gray with dashed edge, streams = solid lines

In the LEF, terrestrial gastropods are well understood taxonomically (Garrison & Willig, 1996). Although 44 species have been recorded from the four forest types and along the broad elevational range of the LEF, fewer than 20 of these species forage above the leaf litter in tabonuco forest, and many are rare or maintain low population densities. Terrestrial gastropods in the LEF respond to small-scale (Alvarez & Willig, 1993; Willig et al., 2014) and broadscale (Willig et al., 2007, 2021; Willig & Camilo, 1991) disturbances. Moreover, the habitat associations of some species are well documented, as are the long-term spatiotemporal dynamics of this fauna (Bloch & Willig, 2006; Presley et al., 2011; Willig et al., 1998, 2011, 2021). Due to their biodiversity and numerical abundance, gastropods in the LEF are functionally important to decomposition and nutrient cycling (Heatwole & Heatwole, 1978). Abundant (*Nenia tridens*) and large (*Caracolus caracolla*) gastropods forage on plant material (live and dead leaves, wood, bark), diatoms, and fungi (Garrison & Willig, 1996), promoting leaf litter loss, increasing microbial biomass, and producing large quantities of feces that promote decomposition and nutrient cycling (Theenhaus & Scheu, 1996; Vos et al., 2011).

Field methods

The canopy trimming experiment

This long-term experiment was designed to simulate hurricane effects on tabonuco forest while disentangling two confounded direct effects: the loss of forest canopy and

the deposition of debris. The original experiment (Shiels & González, 2014) was conducted as a 2 × 2 factorial design (canopy trimming × debris deposition; Figure 2) applied to each of three experimental blocks (A, B, and C of Figure 1b). Blocks were chosen to control for variation associated with land-use history (>80% forest cover since 1936), elevation (340–485 m), soil type (Zarzal clay), and slope (<35%, average 24%) and were located within the Sonadora watershed in closed canopy tabonuco forest (Shiels & González, 2014). Each block contained four 30 m × 30 m plots that were randomly assigned to one of the four treatments (Figure 2). Each plot was surrounded by a 5 m wide buffer zone to reduce edge effects associated with nonmanipulated forest, and contained an inner square (20 m × 20 m), divided into 16 subplots (5 m × 5 m). Four subplots from each plot were chosen at random and surveyed for gastropods. The same subplots were sampled during each year of the experiment.

Full execution of experimental manipulations for Phase 1, including the trimming, weighing, and redistribution of debris, extended from 26 October 2004 to 16 June 2005 and is described in detail elsewhere (Shiels & González, 2014). Treatment implementation was time-intensive and hampered by adverse weather and the large amount of plant material that had to be collected, weighed, and redistributed manually. Within plots designated for canopy trimming, limbs and stems smaller than 10 cm diameter were removed from all trees larger than 15 cm dbh. Trees between 10 and 15 cm dbh were trimmed at 3 m height. The leaves of palms that reached above 3 m were trimmed, being careful to preserve the apical meristem. All material removed from the canopy of each trimmed plot (i.e., debris) was collected. Debris from one trimmed plot was returned to that plot (trim and debris treatment) and distributed homogeneously on the forest floor. Debris from the other trimmed plot (trim-only treatment) was removed and redistributed homogeneously to an untrimmed plots (debris-only treatment). Approximately 10 tons (fresh weight) of vegetation (111 tons/ha) was removed from each plot (~39% leafy twigs, 55% wood, and 6% palm fronds). The amount of debris added to each of the six debris addition plots was ~5.4 tons dry weight (60 tons/ha).

Phase 2 of the CTE involved a repeated implementation of only the trim and debris treatment (i.e., the trim and debris treatment was trimmed again with associated debris deposited on the forest floor) to the same plots that received the trim and debris treatment during Phase 1. The remaining treatments were not manipulated during this phase. Phase 2 was conducted during November and December in 2014 (Figure 3). Consequently, reference treatments represent background conditions without

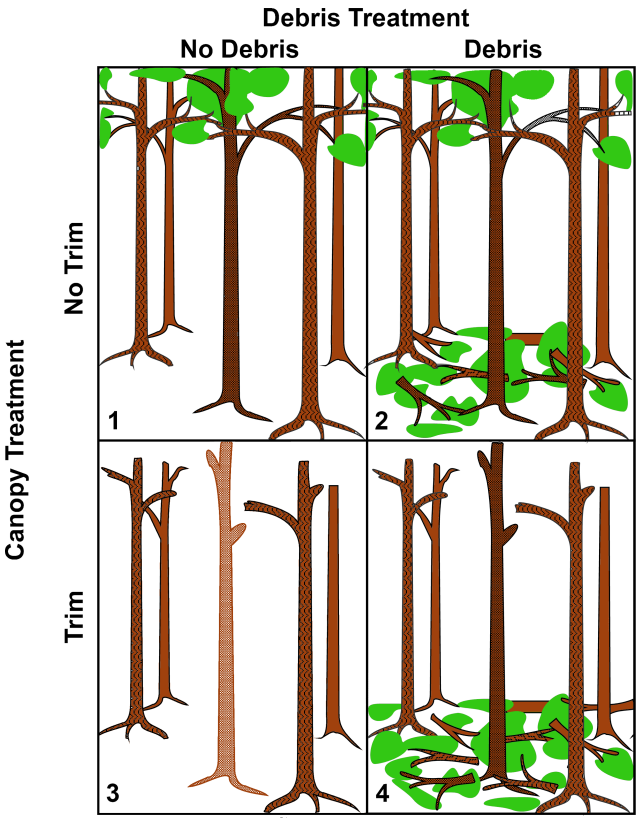

FIGURE 2 The first phase of the canopy trimming experiment (CTE) was completed in early 2005 and employed a cross-factorial design (canopy removal vs. debris deposition treatments) to disentangle the interacting effects of increased inputs of organic matter associated with hurricane-strength winds (i.e., debris addition) and the effects of solar insolation and warming associated with canopy removal (canopy trimming): 1, not trimmed and no debris addition (reference treatment); 2, debris addition without canopy trimming (debris-only treatment); 3, canopy trimming without debris addition (trim-only treatment); and 4, canopy trimming with debris addition (trim and debris treatment). In the second phase of the CTE, trimming and debris deposition was applied only to the trim and debris treatment in 2014, thereby destroying the original cross-factorial design, and resulting in a simple one-factor design with four levels corresponding to the original four treatment combinations (modified from Willig et al., 2012)

experimental manipulation for the duration of the experiment, including effects of naturally occurring disturbances (e.g., droughts, Hurricane Maria, climate change); trim and debris treatments represent effects of repeated hurricanes, with forest canopy removed and deposited on the forest floor in both 2004 and 2014; and trim-only and debris-only treatments represent effects of only canopy loss or only debris deposition, respectively, from a single hurricane for the duration of the experiment. In addition, Hurricane Maria struck the LEF in 2017, resulting in all experimental treatments being subjected to a major

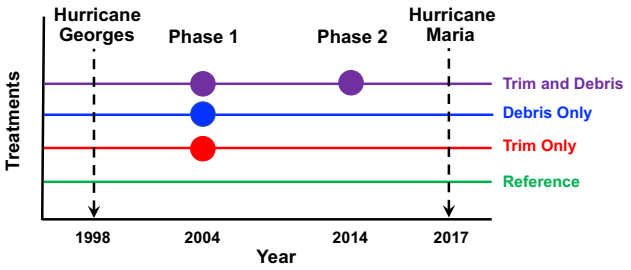

FIGURE 3 For each of four treatments in the canopy trimming experiment (CTE), timeline of natural and simulated hurricane-induced disturbances in tabonuco forest of the Luquillo Experimental Forest in Puerto Rico. Vertical dashed arrows indicate the occurrence of major hurricanes. Colored circles indicate the implementation of manipulations of Phase 1 and Phase 2 of the CTE. See text for details of experimental manipulation

natural hurricane with considerable canopy opening (Uriarte et al., 2019) and debris deposition (Figure 3). Importantly, comparisons of manipulative treatments to the reference treatment remain informative despite the impact of Hurricane Maria, as the latter continues to represent background conditions in this hurricane-mediated environment.

Gastropod surveys

During the wet season (June–August), annual surveys of gastropods were conducted from 2005 to 2019. Surveys were conducted at night, when terrestrial gastropods are most active to reduce desiccation stress (Heatwole & Heatwole, 1978). During each survey, each subplot was sampled three times, with one field worker searching all substrates (e.g., vegetation, logs, debris, rocks, upper surface of the leaf litter) for gastropods. Samples of the same subplot were conducted on different nights and at least 2 days apart. Sampling continued until all available surfaces were completely searched, or for 15 min, whichever time was longer. To minimize alteration of long-term study plots, substrates were not manipulated while searching for gastropods (i.e., rocks or woody debris were not moved, and leaf litter was not sifted). Although the gastropod fauna of the LEF comprises many large and arboreal taxa, such sampling limits the potential to detect small, litter-dwelling species. Importantly, differences among species in detectability would only affect species-level analyses if such differences were treatment-specific. Consequently, our inference space was constrained to include only macro-individuals that emerged above the soil or leaf litter. Gastropods were identified to species in the field and never removed from the subplots in which they were found.

Quantitative analysis

Abundance and biodiversity

We estimated population- and community-level metrics for each subplot to evaluate responses to treatments. In addition, we partitioned plot-level taxonomic biodiversity into α-, β-, and γ-components. The abundance of each species for each subplot was estimated as the total number of individuals of that species observed in the three samples for each year. These species-specific abundances were summed to estimate total gastropod abundance for each subplot as well as to inform estimation of each of the four metrics of taxonomic biodiversity (i.e., point biodiversity): species richness, Shannon diversity, Camargo evenness, and Berger–Parker dominance (Magurran & McGill, 2011). For ease of exposition, we refer to these metrics simply as richness, diversity, evenness, or dominance throughout the manuscript and use "biodiversity" to refer to the broad biological concept rather than to a particular metric. To ensure that metrics of biodiversity reflected desirable mathematical and biological properties, diversity, evenness, and dominance were converted to Hill numbers (Jost, 2006) prior to statistical analysis (this adjusts the index for dominance so that larger values represent higher biodiversity and lower dominance). Species richness is already a Hill number and does not require transformation. Hill numbers are scaled from 1 to empirical species richness and represent the number of equally abundant taxa required to obtain the empirical value of the metric (Jost, 2006).

To evaluate effects of experimental treatments on spatial configuration of taxonomic biodiversity, we partitioned each metric into α-, β-, and γ-components based on a multiplicative model (Jost, 2007):

$$\gamma = \alpha \times \beta.$$

Within this partitioning framework, α is mean point biodiversity for the four subplots within each plot, γ is biodiversity for the plot (all four subplots combined), and β is a measure of heterogeneity among subplots within a plot (estimated as γ/α). The partitioning was done at the block level, resulting in three replicates for each treatment in each year.

To characterize gastropod species composition, we conducted nonmetric multidimensional scaling (NMDS) based on species abundance distributions at subplot (sample within a block within a treatment) and plot (block within a treatment) levels. Abundances were double square root transformed (n^{-4}) prior to analysis to enhance the ability of less abundant species to contribute to differences among communities. We used the scores

from the first four axes from NMDS as response variables to evaluate effects of treatment, time, and their interaction on gastropod species composition. Four dimensions were necessary to reduce stress to acceptable levels for subplot- and plot-level data (0.126 and 0.099, respectively).

To evaluate differences in long-term responses of gastropods to experimental treatments, we conducted general linear mixed-effects models (GLMMs) with abundance or point biodiversity (i.e., richness, diversity, evenness, dominance) as the response variable, experimental block and subplot as random effects, and treatment, time (year), and a treatment by time interaction as explanatory variables based on type II sums of squares. To evaluate differences in long-term responses of α-, β-, or γ-components of biodiversity to experimental treatments, we conducted GLMMs with α, β, or γ as the response variable, experimental block as a random effect, and treatment, time, and a treatment by time interaction as explanatory variables based on type II sums of squares.

Because species composition is multidimensional, we conducted multivariate general linear models (GLMs) with the first four axes from NMDS based on subplot- or plot-level species abundance distributions as the response variables, and treatment, time, and their interaction as explanatory variables. In cases for which gastropod communities differed significantly between treatments, we performed pseudo-post hoc analyses by conducting multivariate GLMs that compared each possible pair of treatments to determine which contrasts contributed to the overall difference in the omnibus analysis.

Post hoc analyses were conducted to isolate the effect associated with each explanatory variable (treatment, time, or their interaction) evincing a significant effect on abundance or on a metric of biodiversity. In cases of a significant treatment effect, a Tukey test with a Holm-Šidák adjustment was used to identify differences between all possible pairs of treatments. In cases of a consistent effect of time, a GLMM with time as the explanatory variable, and block and subplot as random effects, was used to determine whether a response variable (abundance or metric of biodiversity) increased or decreased with time. In the case of a significant interaction, separate GLMMs were conducted for data associated with each treatment, with time as the explanatory variable, and block and subplot as random effects; thereafter, the temporal trajectories were compared among treatments to determine the nature of the interaction.

To explore temporal patterns in abundance and biodiversity, we used second-order polynomials to capture linear and nonlinear responses of each metric through time. These analyses were conducted separately for each treatment to evaluate temporal trajectories. Orthogonal polynomial regression (Dutka & Ewens, 1971) facilitates evaluation of independent estimates of a constant rate of change (b^*_1) and a varying rate of change (b^*_2) and decomposes the general relationship from ordinary polynomial regression into a suite of additive polynomials (0th-, 1st-, and 2nd-order relationships) whose coefficients (b^*_0, b^*_1, and b^*_2) are weightings that represent independent contributions of time (year) to variation in abundance or biodiversity. Companion ordinary polynomial regressions were conducted to derive the necessary parameters (intercept, linear, and quadratic coefficients) to illustrate the best-fit quadratic relationship. Importantly, overall variation explained by the model and significance is identical for orthogonal and ordinary polynomial regressions, only the ability to independently test each component of the relationship differs between methods.

To evaluate immediate responses (i.e., resistance) of gastropod abundance and biodiversity to simulated and natural hurricanes, we conducted GLMMs with abundance or point biodiversity as the response variable, experimental block and subplot as random effects, and treatment, time (before or after the disturbance), and a treatment by time interaction as explanatory variables based on type II sums of squares. To evaluate immediate responses of gastropod composition to simulated and natural hurricanes, we conducted multivariate GLMs with the first four axes from NMDS at the subplot level as the response variables, and treatment, time (before or after the disturbance), and a treatment by time interaction as explanatory variables. These analyses were conducted using data immediately before (2004) and after (2006) initiation of Phase 1 of the CTE, immediately before (2014) and after (2015) initiation of Phase 2 of the CTE, and immediately before (2017) and after (2018) Hurricane Maria. Because Phase 1 manipulations were conducted over several months, with manipulations in some plots completed as early as November of 2004 and others as late as June of 2005, data from 2006 rather than 2005 were used to characterize responses to Phase 1 treatments. Because this set of analyses was restricted to 2 years of data, species-level analyses were restricted to the three most abundant species (*C. caracolla*, *N. tridens*, and *Gaeotis nigrolineata*), which collectively comprised >90% of individuals recorded during the study.

All analyses were conducted in R version 3.6.1 (R Core Team, 2020). GLMMs were conducted using the lme function from the nlme package (Pinheiro et al., 2020). Multivariate GLMs were conducted using the manova function 2020). Type II sums of squares were implemented via the Anova function 2019). Tukey tests were conducted

TABLE 1 Results of general linear mixed-effects models (GLMMs) evaluating the consequences of treatment (reference, debris only, trim only, and trim and debris), time (years), and their interaction on population- and community-level characteristics of gastropods in the canopy trimming experiment

Abundance, composition, or component	Treatment	Time	Treatment × time
Abundance			
Alcadia alta	0.217	0.196	0.976
Allopeas gracile	0.277	0.437	0.949
Austroselenites alticola	0.557	**0.028**	0.376
Caracolus caracolla	**<0.001**	**0.004**	**<0.001**
Caracolus marginella	0.142	0.183	0.306
Cepolis squamosa	**0.039**	**0.041**	0.101
Diplosolenodes occidentalis	0.574	0.870	0.994
Gaeotis nigrolineata	**0.025**	**0.003**	0.721
Helicina striata	0.416	**<0.001**	**0.030**
Nenia tridens	**<0.001**	**<0.001**	0.527
Neopupina crocea	0.656	0.838	0.919
Oleacina glabra	0.088	**<0.001**	**0.035**
Oleacina playa	0.867	0.333	0.631
Platysuccinea portoricensis	**0.011**	**<0.001**	**0.026**
Polydontes acutangula	**<0.001**	**0.043**	**<0.001**
Stenogyra terebraster	0.075	0.225	0.606
Subulina octona	0.153	0.118	0.193
Total abundance	**<0.001**	0.066	0.289
Species composition			
Subplot level	**<0.001**	**<0.001**	0.610
Plot level	0.992	**0.015**	0.569
Biodiversity component			
Point biodiversity			
Species richness	0.264	**<0.001**	0.771
Shannon diversity	0.143	**<0.001**	0.285
Camargo evenness	0.054	**<0.001**	0.280
Berger–Parker dominance	0.116	**<0.001**	0.433
α-Component			
Species richness	0.253	**<0.001**	0.916
Shannon diversity	0.165	**<0.001**	0.597
Camargo evenness	0.148	**<0.001**	0.556
Berger–Parker dominance	0.275	**<0.001**	0.616
β-Component			
Species richness	0.916	**<0.001**	0.751
Shannon diversity	0.889	**0.003**	0.895
Camargo evenness	0.953	**0.002**	0.887
Berger–Parker dominance	0.875	**0.003**	0.815
γ-Component			
Species richness	0.280	**0.012**	0.938
Shannon diversity	**0.023**	**<0.001**	0.752

(Continues)

TABLE 1 (Continued)

Abundance, composition, or component	Treatment	Time	Treatment × time
Camargo evenness	**0.023**	**<0.001**	0.781
Berger–Parker dominance	**0.003**	**<0.001**	0.875

Note: At the subplot level, block and subplot were random effects (type II factors) and analyses were conducted separately for the abundance of each of 17 species of gastropod, for total gastropod abundance, and for each of four metrics of biodiversity (point biodiversity). At the plot level, block was a random effect and analyses were conducted separately for α-, β-, and γ-components of each of four metrics of biodiversity. Species composition was evaluated based on four axes from nonmetric multidimensional scaling at the subplot and plot levels using the GLMM designs described for abundance and biodiversity. Significant results ($p \leq 0.05$) are bold.

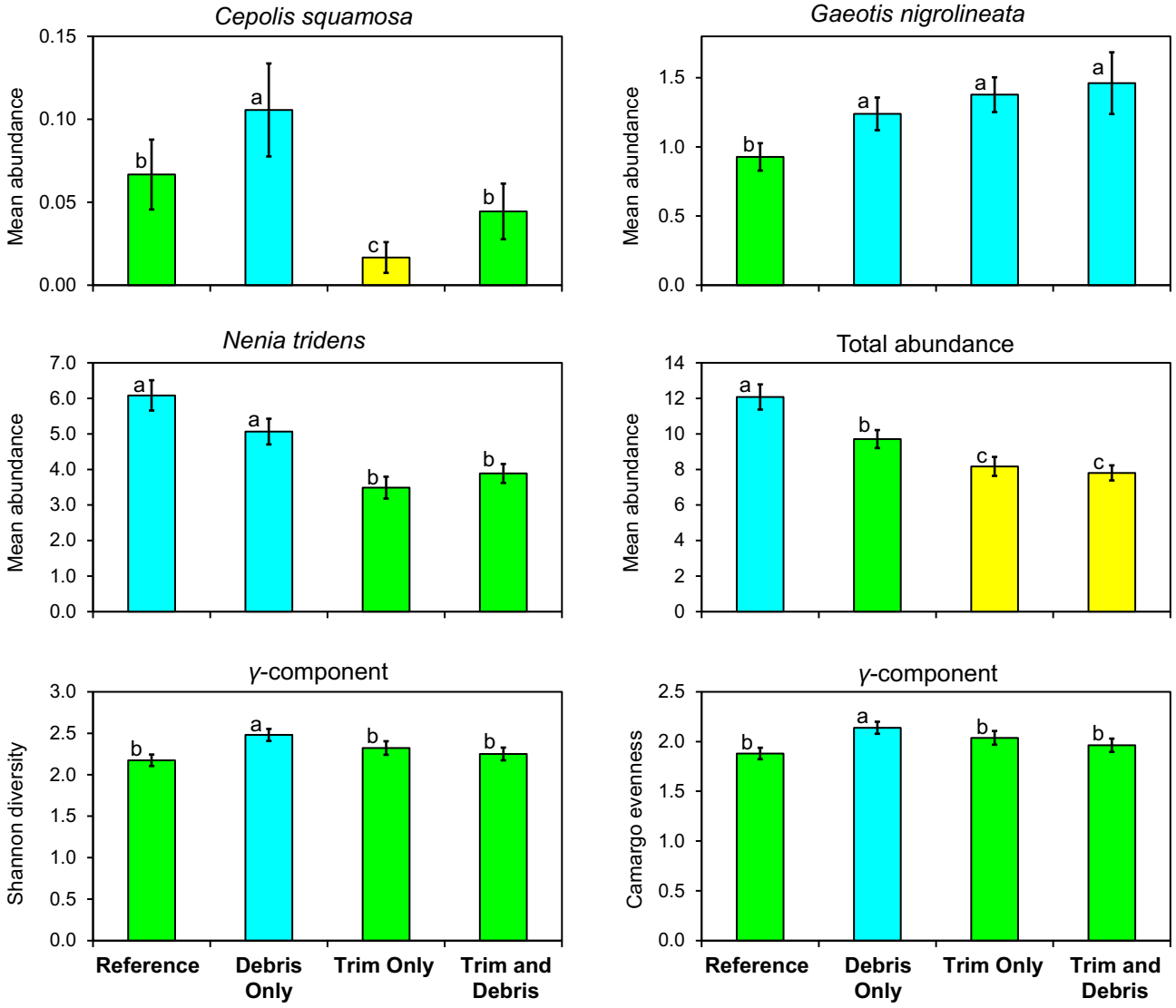

FIGURE 4 Consistent responses of gastropod abundance or aspects of biodiversity to treatments in the canopy trimming experiment. Statistically indistinguishable treatments share a common letter designation and color. Reference treatment = no manipulation; debris-only treatment = canopy not trimmed and debris added to forest floor; trim-only treatment = canopy trimmed and debris not added to forest floor; and trim and debris treatment = canopy trimmed and debris added to forest floor. Mean abundances per subplot for 2005–2019, with error bars representing ±1 SE

using the glht function from the multcomp package (Hothorn et al., 2008). Orthogonal and ordinary polynomial regressions were conducted using the lm function from the stats package (R Core Team, 2020). NMDS was conducted using the nmds function from the ecodist package (Goslee & Urban, 2007).

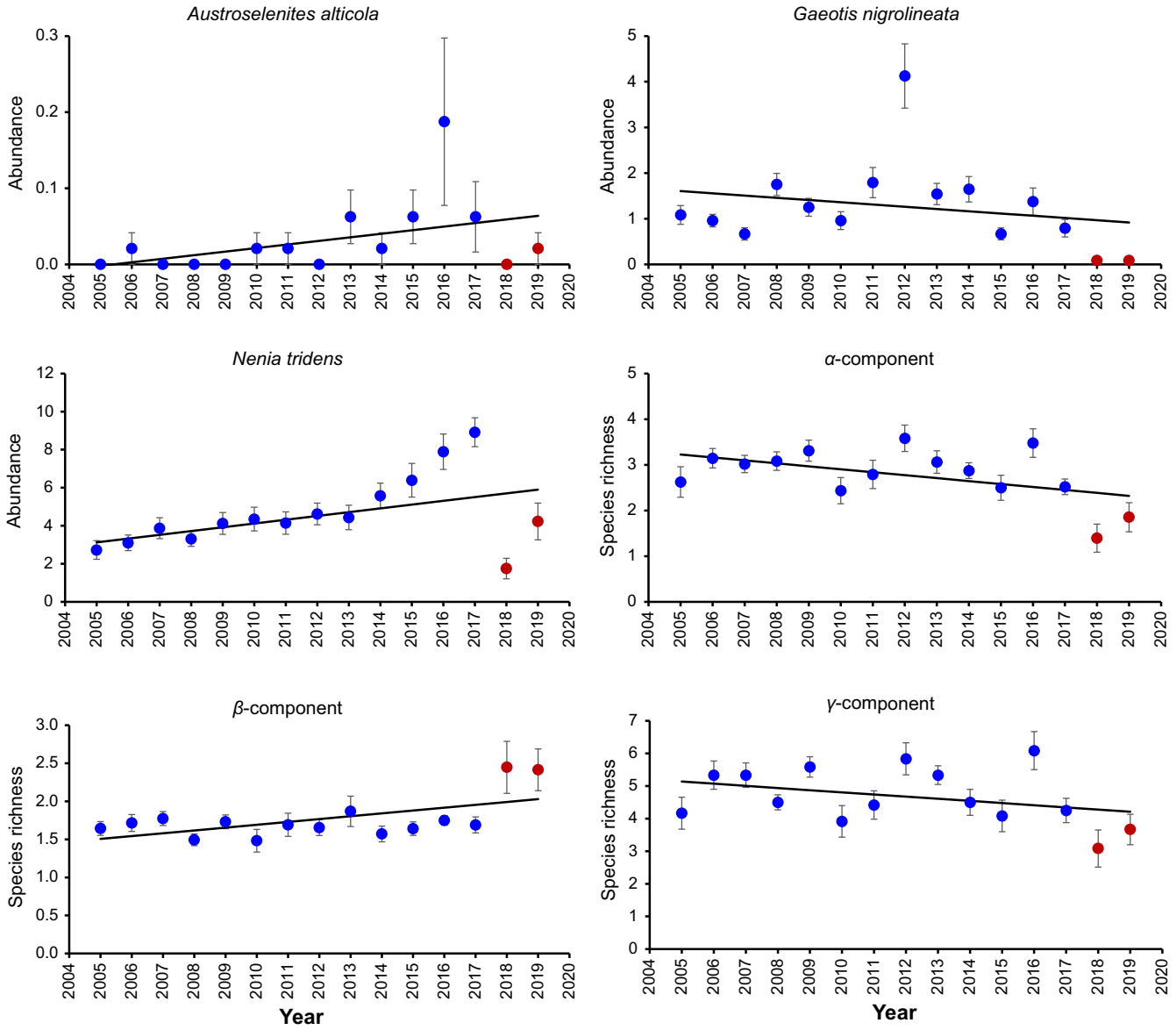

FIGURE 5 Consistent temporal responses of gastropod abundance or species richness during the canopy trimming experiment. Species or communities exhibited consistent temporal patterns regardless of treatment, likely as a consequence of background changes in the forest associated with hurricane-induced disturbance, succession, and climate change. Blue and red dots indicate pre- and post-Hurricane Maria data, respectively. Solid lines indicate the best-fit regression line. Mean abundances per subplot or mean components of species richness per plot, with error bars ±1 SE

RESULTS

A total of 6798 gastropods representing 17 species were recorded from the CTE between 2005 and 2019. All 17 of the commonly captured species of terrestrial gastropod in tabonuco forest (Willig et al., 2021) were recorded from the reference treatment. The fewest number of species (13) was recorded from the trim-only plots, likely because this treatment increases desiccation stress (higher understory temperatures and evapotranspiration rates) in combination with low nutrient input. *C. caracolla*, *N. tridens*, and *G. nigrolineata* were the first, second, and third most abundant species, respectively, in each treatment. *Allopeas gracile*, *Stenogyra terebraster*, and *Subulina octona* were recorded from every treatment except for trim only. These three species are all small, litter-dwelling gastropods (Garrison & Willig, 1996) that likely suffered from warm, dry, and low litter density conditions in this treatment. *Neopupina crocea* occurred only in the treatments that were not trimmed; this species is a litter-dwelling gastropod and likely suffered from desiccation stress in the warmer and drier understory. Gastropod abundance was greatest in the reference

TABLE 2 Regression coefficients derived from ordinary and orthogonal polynomial regressions describing the relationship between time (year) and the abundance of each of 17 species, total gastropod abundance, and each combination of aspects of biodiversity and hierarchical component (point biodiversity, α, β, and γ)

Response metric	Ordinary polynomial regression			Orthogonal polynomial regression					Model fit	
Treatment	b_0	b_1	b_2	b^*_0	b^*_1	$p_{b^*_1}$	b^*_2	$p_{b^*_2}$	R^2	p
Abundance										
Alcadia alta										
Reference	−6983	6.9	−0.002	0.044	0.138	0.552	−0.384	0.099	0.017	0.215
Trim and debris	−3273	3.3	−0.001	0.017	0.069	0.591	−0.180	0.163	0.013	0.326
Debris only	−1666	1.7	0.000	0.011	0.086	0.414	−0.091	0.387	0.008	0.492
Trim only	−5294	5.3	−0.001	0.039	0.173	0.435	−0.291	0.189	0.013	0.312
Allopeas gracile										
Reference	−2210	2.2	−0.001	0.017	0.052	0.688	−0.121	0.347	0.006	0.592
Trim and debris	−1938	1.9	0.000	0.039	0.086	0.748	−0.106	0.692	0.001	0.878
Debris only	−1450	1.4	0.000	0.022	0.155	0.512	−0.079	0.737	0.003	0.762
Trim only	0	0.0	0.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000
Austroselenites alticola										
Reference	−4189	4.2	−0.001	0.050	0.535	0.182	−0.229	0.567	0.012	0.348
Trim and debris	671	−0.7	0.000	0.022	0.293	**0.048**	0.037	0.799	0.022	0.135
Debris only	−1470	1.5	0.000	0.017	−0.069	0.593	−0.081	0.531	0.004	0.712
Trim only	−2110	2.1	−0.001	0.039	0.328	0.139	−0.115	0.602	0.014	0.291
Caracolus caracolla										
Reference	−156,532	155.8	−0.039	4.100	−11.16	**0.019**	−8.625	0.070	0.048	**0.013**
Trim and debris	−25,963	25.8	−0.006	1.700	−1.139	0.493	−1.429	0.390	0.007	0.546
Debris only	−94,768	94.3	−0.023	2.422	−4.071	0.077	−5.217	**0.024**	0.045	**0.017**
Trim only	−192,041	190.8	−0.047	2.500	3.468	0.277	−10.549	**0.001**	0.064	**0.003**
Caracolus marginella										
Reference	−3510	3.5	−0.001	0.067	−0.190	0.543	−0.193	0.535	0.004	0.685
Trim and debris	483	−0.5	0.000	0.017	0.207	0.108	0.027	0.834	0.015	0.268
Debris only	5091	−5.1	0.001	0.039	0.190	0.328	0.280	0.149	0.017	0.219
Trim only	4867	−4.8	0.001	0.028	0.362	0.063	0.268	0.169	0.030	0.070
Cepolis squamosa										
Reference	−4995	5.0	−0.001	0.067	0.190	0.517	−0.274	0.349	0.007	0.522
Trim and debris	8668	−8.6	0.002	0.044	−0.776	**<0.001**	0.475	**0.035**	0.086	**<0.001**
Debris only	31,437	−31.2	0.008	0.106	−0.259	0.483	1.727	**<0.001**	0.113	**<0.001**
Trim only	2790	−2.8	0.001	0.017	−0.276	**0.031**	0.153	0.230	0.034	**0.048**
Diplosolenodes occidentalis										
Reference	−1444	1.4	0.000	0.006	−0.017	0.818	−0.079	0.289	0.007	0.555
Trim and debris	0	0.0	0.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000
Debris only	0	0.0	0.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000
Trim only	−1526	1.5	0.000	0.006	0.000	1.000	−0.084	0.263	0.007	0.533
Gaeotis nigrolineata										
Reference	−80,984	80.5	−0.020	0.928	−2.312	0.083	−4.456	**0.001**	0.075	**0.001**
Trim and debris	−180,259	179.2	−0.045	1.461	−2.243	0.459	−9.912	**0.001**	0.060	**0.004**
Debris only	−139,897	139.1	−0.035	1.239	−2.053	0.181	−7.693	**<0.001**	0.133	**<0.001**

(Continues)

TABLE 2 (Continued)

Response metric / Treatment	Ordinary polynomial regression			Orthogonal polynomial regression					Model fit	
	b_0	b_1	b_2	b^*_0	b^*_1	$p_{b^*_1}$	b^*_2	$p_{b^*_2}$	R^2	p
Trim only	−141,165	140.4	−0.035	1.378	−4.779	**0.003**	−7.768	**<0.001**	0.155	**<0.001**
Helicina striata										
Reference	44,172	−44.0	0.011	0.361	3.537	**0.002**	2.435	**0.028**	0.080	**<0.001**
Trim and debris	13,836	−13.8	0.003	0.294	1.121	0.113	0.763	0.280	0.021	0.159
Debris only	56,011	−55.7	0.014	0.289	0.897	0.262	3.080	**<0.001**	0.084	**<0.001**
Trim only	−95	0.1	0.000	0.217	0.397	0.419	−0.004	0.993	0.004	0.720
Nenia tridens										
Reference	−94,995	94.3	−0.023	6.083	6.504	0.272	−5.209	0.378	0.011	0.371
Trim and debris	−91,427	90.7	−0.023	3.889	10.437	**0.004**	−5.005	0.169	0.055	**0.007**
Debris only	−191,358	190.0	−0.047	5.067	14.491	**0.003**	−10.490	**0.032**	0.071	**0.001**
Trim only	−169,744	168.5	−0.042	3.489	14.509	**<0.001**	−9.302	0.024	0.091	**<0.001**
Neopupina crocea										
Reference	1201	−1.2	0.000	0.011	−0.035	0.744	0.066	0.533	0.003	0.780
Trim and debris	0	0.0	0.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000
Debris only	1823	−1.8	0.000	0.022	0.086	0.716	0.100	0.672	0.002	0.855
Trim only	0	0.0	0.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000
Oleacina glabra										
Reference	2832	−2.8	0.001	0.056	−0.707	**0.002**	0.154	0.493	0.055	**0.006**
Trim and debris	−5822	5.8	−0.001	0.061	−0.311	0.237	−0.321	0.222	0.016	0.237
Debris only	6546	−6.5	0.002	0.078	−0.914	**<0.001**	0.358	0.170	0.075	**0.001**
Trim only	−3513	3.5	−0.001	0.017	−0.086	0.502	−0.193	0.133	0.015	0.258
Oleacina playa										
Reference	−6515	6.5	−0.002	0.039	0.017	0.929	−0.358	0.065	0.019	0.182
Trim and debris	−5678	5.6	−0.001	0.044	0.242	0.242	−0.312	0.132	0.020	0.162
Debris only	−2505	2.5	−0.001	0.039	−0.069	0.723	−0.138	0.480	0.004	0.731
Trim only	−4694	4.7	−0.001	0.028	0.173	0.295	−0.258	0.118	0.020	0.171
Platysuccinea portoricensis										
Reference	7354	−7.3	0.002	0.139	−1.415	**<0.001**	0.402	0.326	0.069	**0.002**
Trim and debris	−4249	4.2	−0.001	0.033	−0.104	0.566	−0.234	0.196	0.011	0.367
Debris only	−6516	6.5	−0.002	0.178	−1.535	**0.005**	−0.361	0.505	0.046	**0.016**
Trim only	−13,718	13.6	−0.003	0.083	−0.587	0.104	−0.755	**0.037**	0.038	**0.031**
Polydontes acutangula										
Reference	12,917	−12.8	0.003	0.050	0.104	0.759	0.710	**0.036**	0.025	0.106
Trim and debris	−3956	3.9	−0.001	0.139	−0.690	0.133	−0.219	0.633	0.014	0.288
Debris only	16,252	−16.2	0.004	0.133	0.604	0.180	0.894	**0.048**	0.032	0.058
Trim only	−13,506	13.5	−0.003	0.333	−1.967	**0.003**	−0.746	0.249	0.057	**0.006**
Stenogyra terebraster										
Reference	−9089	9.0	−0.002	0.050	0.362	0.365	−0.499	0.213	0.013	0.305
Trim and debris	−220	0.2	0.000	0.006	0.069	0.357	−0.012	0.873	0.005	0.646
Debris only	−220	0.2	0.000	0.006	0.069	0.357	−0.012	0.873	0.005	0.646

(Continues)

TABLE 2 (Continued)

Response metric / Treatment	Ordinary polynomial regression b_0	b_1	b_2	Orthogonal polynomial regression b^*_0	b^*_1	$p_{b^*_1}$	b^*_2	$p_{b^*_2}$	Model fit R^2	p
Trim only	0	0.0	0.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000
Subulina octona										
Reference	−1421	1.4	0.000	0.011	0.104	0.327	−0.078	0.460	0.008	0.470
Trim and debris	1090	−1.1	0.000	0.039	0.000	1.000	0.060	0.788	0.000	0.964
Debris only	−1764	1.7	0.000	0.044	0.552	0.114	−0.096	0.783	0.015	0.274
Trim only	0	0.0	0.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000
Total abundance										
Reference	−304,391	302.7	−0.075	12.078	−4.296	0.660	−16.739	0.088	0.017	0.211
Trim and debris	−298,037	296.1	−0.074	7.806	7.263	0.210	−16.367	**0.005**	0.052	**0.009**
Debris only	−324,452	322.4	−0.080	9.711	8.160	0.241	−17.818	**0.011**	0.043	**0.020**
Trim only	−539,750	536.3	−0.133	8.172	11.714	0.096	−29.644	**<0.001**	0.105	**<0.001**
Point biodiversity										
Species richness										
Reference	−22,959	22.9	−0.006	2.767	−2.829	**0.039**	−1.267	0.354	0.028	0.078
Trim and debris	−78,407	78.0	−0.019	2.644	−3.468	**0.006**	−4.316	**<0.001**	0.100	**<0.001**
Debris only	−32,308	32.2	−0.008	3.000	−4.399	**<0.001**	−1.784	0.159	0.074	**0.001**
Trim only	−149,303	148.5	−0.037	2.706	−4.296	**<0.001**	−8.214	**<0.001**	0.238	**<0.001**
Shannon diversity										
Reference	−1042	1.1	0.000	2.174	−2.259	**0.019**	−0.062	0.948	0.031	0.062
Trim and debris	−55,414	55.2	−0.014	2.250	−3.792	**<0.001**	−3.053	**0.003**	0.116	**<0.001**
Debris only	−23,391	23.3	−0.006	2.480	−4.670	**<0.001**	−1.295	0.174	0.129	**<0.001**
Trim only	−116,795	116.2	−0.029	2.321	−4.321	**<0.001**	−6.428	**<0.001**	0.262	**<0.001**
Camargo evenness										
Reference	1320	−1.3	0.000	1.880	−1.898	**0.018**	0.069	0.931	0.031	0.061
Trim and debris	−44,037	43.8	−0.011	1.963	−3.538	**<0.001**	−2.427	**0.005**	0.123	**<0.001**
Debris only	−16,843	16.8	−0.004	2.139	−3.855	**<0.001**	−0.933	0.242	0.123	**<0.001**
Trim only	−92,870	92.4	−0.023	2.037	−3.766	**<0.001**	−5.112	**<0.001**	0.250	**<0.001**
Berger–Parker dominance										
Reference	2076	−2.0	0.000	1.610	−1.675	**0.015**	0.111	0.871	0.033	**0.022**
Trim and debris	−31,044	30.9	−0.008	1.655	−3.134	**<0.001**	−1.712	**0.018**	0.1229	**<0.001**
Debris only	−15,077	15.0	−0.004	1.766	−2.855	**<0.001**	−0.834	0.180	0.115	**<0.001**
Trim only	−63,570	63.2	−0.016	1.733	−2.872	**<0.001**	−3.500	**<0.001**	0.189	**<0.001**
α-Component										
Species richness										
Reference	−22,959	22.9	−0.006	2.767	−1.415	0.194	−0.634	0.558	0.047	0.361
Trim and debris	−78,407	78.0	−0.019	2.644	−1.734	0.085	−2.158	**0.034**	0.159	**0.026**
Debris only	−32,308	32.2	−0.008	3.000	−2.200	**0.026**	−0.892	0.356	0.128	0.056
Trim only	−149,303	148.5	−0.037	2.706	−2.148	**0.011**	−4.107	**<0.001**	0.440	**<0.001**
Shannon diversity										
Reference	−1042	1.1	0.000	2.174	−1.129	0.110	−0.031	0.965	0.060	0.275
Trim and debris	−55,414	55.2	−0.014	2.250	−1.896	**0.017**	−1.527	0.051	0.196	**0.010**

(Continues)

TABLE 2 (Continued)

Response metric / Treatment	Ordinary polynomial regression b_0	b_1	b_2	Orthogonal polynomial regression b^*_0	b^*_1	$p_{b^*_1}$	b^*_2	$p_{b^*_2}$	Model fit R^2	p
Debris only	−23,391	23.3	−0.006	2.480	−2.335	**0.002**	−0.647	0.358	0.224	**0.005**
Trim only	−116,795	116.2	−0.029	2.321	−2.161	**0.001**	−3.214	**<0.001**	0.485	**<0.001**
Camargo evenness										
Reference	1320	−1.3	0.000	1.880	−0.949	0.091	0.034	0.950	0.06649	0.236
Trim and debris	−44,037	43.8	−0.011	1.963	−1.769	**0.007**	−1.214	0.059	0.219	**0.006**
Debris only	−16,843	16.8	−0.004	2.139	−1.928	**0.001**	−0.467	0.409	0.230	**0.004**
Trim only	−92,870	92.4	−0.023	2.037	−1.883	**<0.001**	−2.556	**<0.001**	0.500	**<0.001**
Berger–Parker dominance										
Reference	2076	−2.0	0.000	1.610	−0.838	0.065	0.055	0.901	0.079	0.177
Trim and debris	−31,044	30.9	−0.008	1.655	−1.567	**0.001**	−0.856	0.069	0.266	**0.002**
Debris only	−15,077	15.0	−0.004	1.766	−1.428	**<0.001**	−0.417	0.290	0.258	**0.002**
Trim only	−63,570	63.2	−0.016	1.733	−1.436	**<0.001**	−1.750	**<0.001**	0.447	**<0.001**
β-Component										
Species richness										
Reference	−7531	7.5	−0.002	1.785	0.715	0.295	−0.206	0.762	0.028	0.548
Trim and debris	44,454	−44.2	0.011	1.756	1.507	**0.005**	1.224	**0.021**	0.256	**0.002**
Debris only	55,948	−55.7	0.014	1.730	1.248	**0.007**	1.540	**0.001**	0.325	**<0.001**
Trim only	53,405	−53.1	0.013	1.810	0.865	0.117	1.469	**0.010**	0.191	**0.012**
Shannon diversity										
Reference	−2958	2.9	−0.001	1.381	0.692	0.321	−0.080	0.908	0.024	0.604
Trim and debris	57,569	−57.3	0.014	1.396	1.068	0.065	1.584	**0.007**	0.215	**0.006**
Debris only	51,901	−51.6	0.013	1.394	1.088	**0.028**	1.428	**0.005**	0.251	**0.002**
Trim only	50,300	−50.0	0.012	1.469	0.570	0.316	1.383	**0.018**	0.145	**0.038**
Camargo evenness										
Reference	−1734	1.7	0.000	1.296	0.701	0.275	−0.046	0.942	0.028	0.547
Trim and debris	57,452	−57.1	0.014	1.305	1.138	0.051	1.581	**0.008**	0.220	**0.005**
Debris only	45,786	−45.5	0.011	1.303	1.009	**0.033**	1.260	**0.009**	0.229	**0.004**
Trim only	42,027	−41.8	0.010	1.357	0.583	0.281	1.156	**0.036**	0.123	0.064
Berger–Parker dominance										
Reference	8386	−8.4	0.002	1.145	0.655	0.235	0.232	0.672	0.037	0.448
Trim and debris	57,320	−57.0	0.014	1.186	1.184	**0.050**	1.577	**0.010**	0.213	**0.007**
Debris only	35,788	−35.6	0.009	1.200	0.951	**0.048**	0.985	**0.041**	0.170	**0.020**
Trim only	28,119	−28.0	0.007	1.240	0.490	0.378	0.774	0.167	0.062	0.261
γ-Component										
Species richness										
Reference	−75,432	75.0	−0.019	4.733	−1.760	0.343	−2.077	0.264	0.050	0.342
Trim and debris	−121,264	120.6	−0.030	4.333	−1.208	0.450	−3.335	0.041	0.107	0.094
Debris only	39,540	−39.2	0.010	4.956	−2.519	0.151	1.082	0.533	0.057	0.292
Trim only	−164,373	163.5	−0.041	4.667	−2.174	0.106	−4.522	**0.001**	0.257	**0.002**
Shannon diversity										
Reference	−24,749	24.6	−0.006	2.805	−1.280	0.132	−0.683	0.417	0.067	0.231

(Continues)

TABLE 2 (Continued)

Response metric / Treatment	Ordinary polynomial regression			Orthogonal polynomial regression					Model fit	
	b_0	b_1	b_2	b^*_0	b^*_1	$p_{b^*_1}$	b^*_2	$p_{b^*_2}$	R^2	p
Trim and debris	−41,643	41.5	−0.010	2.854	−2.276	**0.015**	−1.149	0.208	0.161	**0.025**
Debris only	39,317	−39.0	0.010	3.231	−2.394	**0.012**	1.076	0.242	0.167	**0.022**
Trim only	−85,471	85.0	−0.021	3.230	−2.463	**0.005**	−2.354	**0.008**	0.281	**<0.001**
Camargo evenness										
Reference	−24,001	23.9	−0.006	2.310	−0.943	0.181	−0.661	0.346	0.062	0.263
Trim and debris	−26,944	26.8	−0.007	2.318	−1.800	**0.013**	−0.744	0.289	0.158	**0.027**
Debris only	35,075	−34.8	0.009	2.621	−1.673	**0.018**	0.961	0.165	0.161	**0.025**
Trim only	−66,014	65.7	−0.016	2.649	−1.836	**0.012**	−1.818	**0.013**	0.246	**0.003**
Berger–Parker dominance										
Reference	−9704	9.7	−0.002	1.760	−0.816	0.090	−0.268	0.571	0.074	0.201
Trim and debris	−10,858	10.8	−0.003	1.759	−1.296	**0.011**	−0.301	0.537	0.152	**0.031**
Debris only	15,370	−15.2	0.004	2.000	−0.876	0.072	0.421	0.380	0.091	0.135
Trim only	−50,388	50.1	−0.012	2.085	−1.256	0.053	−1.387	**0.033**	0.173	**0.018**

Note: Analyses of abundance and point biodiversity used subplot-level data; analyses of α-, β-, and γ-components used plot-level data. Analyses were conducted separately for each of the four treatments for each abundance and biodiversity metric. Ordinary polynomial regression was used to estimate the intercept (b_0), slope (b_1), and quadratic (b_2) terms that describe the relationship. Orthogonal polynomial regression decomposes the relationship from ordinary polynomial regression into a suite of additive independent polynomials whose coefficients represent the independent contributions of the magnitude, linear and nonlinear components (b^*_0, b^*_1, and b^*_2). $p_{b^*_1}$ and $p_{b^*_2}$ are p-values for b^*_1, and b^*_2, respectively. Accordingly, the fit of the quadratic model is the same for both regression approaches. Significant orthogonal coefficients are bold ($p \leq 0.05$).

treatment, followed by the debris-only treatment, with trimmed treatments having about 65% the abundance of the reference treatment.

Effects on abundance

Three species (*Cepolis squamosa*, *G. nigrolineata*, and *N. tridens*) and total gastropod abundance exhibited consistent responses to treatments regardless of time, four species (*Austroselenites alticola*, *C. squamosa*, *G. nigrolineata*, and *N. tridens*) exhibited consistent responses to time regardless of treatment, and five species (*Helicina striata*, *C. caracolla*, *Oleacina glabra*, *Polydontes acutangula*, and *Platysuccinea portoricensis*) exhibited an interaction in which the effects of treatment depended on time (Table 1). Nearly half (8 of 17) of gastropod species failed to exhibit any response to treatment or time, all of which exhibit consistently low incidence and abundance.

Although the abundances of three species consistently responded to treatments, each evinced a different pattern (Figure 4). For *C. squamosa*, three groups were evident, with highest abundance in the debris-only treatment, lowest abundance in the trim-only treatment, and intermediate abundances in the other two treatments. For *G. nigrolineata*, two groups were evident, with lower abundance in the reference treatment and higher in the manipulated treatments. For *N. tridens*, two groups were evident, with greater abundances in the treatments without trimming and lower abundances in the treatments with trimmed canopy. Total gastropod abundance was greatest in the reference treatment, intermediate in the debris-only treatment, and least the two trimmed treatments.

The directions of response for populations that exhibited consistent temporal effects regardless of treatment were split, with *A. alticola* and *N. tridens* increasing in abundance through time and *C. squamosa* and *G. nigrolineata* decreasing in abundance through time (Figure 5). Although significant decreasing abundance of *C. squamosa* and *G. nigrolineata* may have been caused by Hurricane Maria, clear patterns in pre-Maria data for these species are not evident (Figure 5). None of the five species with significant treatment by time interactions exhibited opposing (increasing vs. decreasing) responses to different treatments. Rather, in one or two treatments, species exhibited temporal increases (i.e., *H. striata* in the reference treatment) or decreases (i.e., *C. caracolla*, *O. glabra*, and *P. portoricensis* in reference and debris-only treatments; *P. acutangula* in the trim-only treatment) in abundance, while evincing no consistent response in remaining treatments.

Orthogonal polynomial regressions more fully characterized temporal trajectories within each treatment. With the exception of *A. alticola*, for which no significant

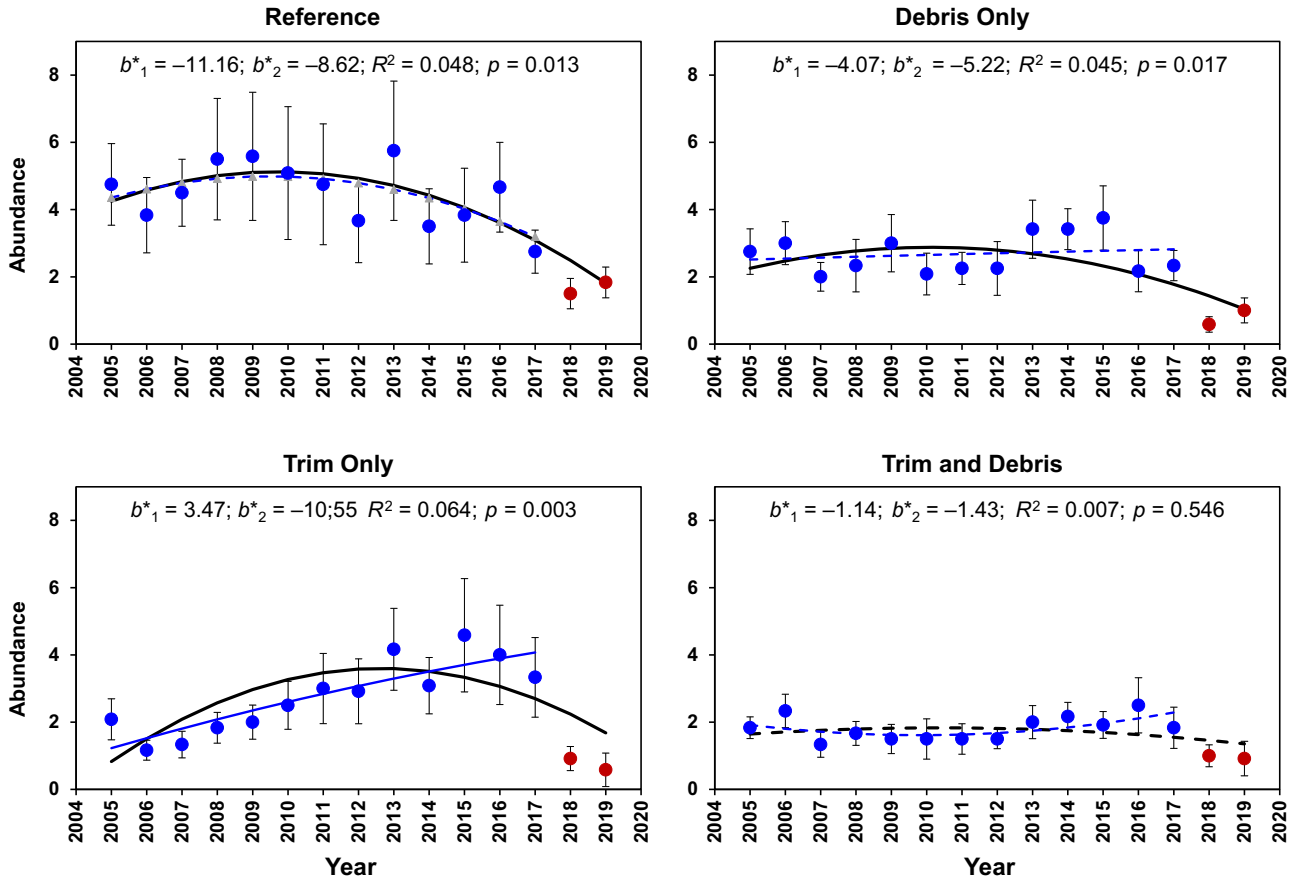

FIGURE 6 Separately for each treatment in the canopy trimming experiment, temporal trajectories of mean abundance per subplot for *Caracolus caracolla*. Black lines show the best-fit relationships from second-order polynomial regressions. Blue lines show the best-fit relationships from second-order polynomial regressions that exclude data after the impact of Hurricane Maria. Solid and dashed lines indicate significant and nonsignificant relationships, respectively. Results from orthogonal polynomial regression include linear (b^*_1) and quadratic coefficients (b^*_2), variation explained (R^2), and overall model significance (p). Treatments are as follows: Reference = no manipulation; debris only = canopy not trimmed and debris added to forest floor; trim only = canopy trimmed and debris not added to forest floor; and trim and debris = canopy trimmed and debris added to forest floor. Blue and red dots indicate pre- and post-Hurricane Maria data, respectively. Mean abundances per subplot, with error bars representing ±1 SE

temporal trends were detected within treatments, total abundance and abundance of each species that exhibited a significant response to treatment, time, or their interaction (Table 1) evinced a significant quadratic relationships with time for at least two treatment categories (Table 2). Species that failed to exhibit responses to treatment, time, or their interaction evinced no significant quadratic relationships with time. In general, treatments did not exhibit different forms (increasing vs. decreasing) for a particular gastropod species (Figure 6). Rather, some treatments exhibited similar and significant responses, while remaining treatments exhibited no significant response. Importantly, the primary result of Hurricane Maria occurring near the end of the experiment on temporal patterns was to create or accentuate significant nonlinear trends (compare black and blue regression lines in Figure 6).

Effects on biodiversity

All combinations of biodiversity metric (i.e., richness, evenness, dominance, and diversity) and hierarchical component (i.e., point biodiversity, as well as α-, β-, and γ-components) exhibited consistent temporal effects regardless of treatment. In contrast, only γ-diversity, γ-evenness, and γ-dominance exhibited consistent responses to treatments (Table 1), with each being greater in the debris-only treatment, and being smaller and indistinguishable from each other in the remaining treatments (Figure 4). For each metric of biodiversity, point-, α-, and γ-components decreased through time, whereas corresponding β-components increased through time (Figure 5). As with patterns of abundance, these apparent trends in biodiversity appear to have been influenced by the 2 years of data following Hurricane Maria (Figure 5).

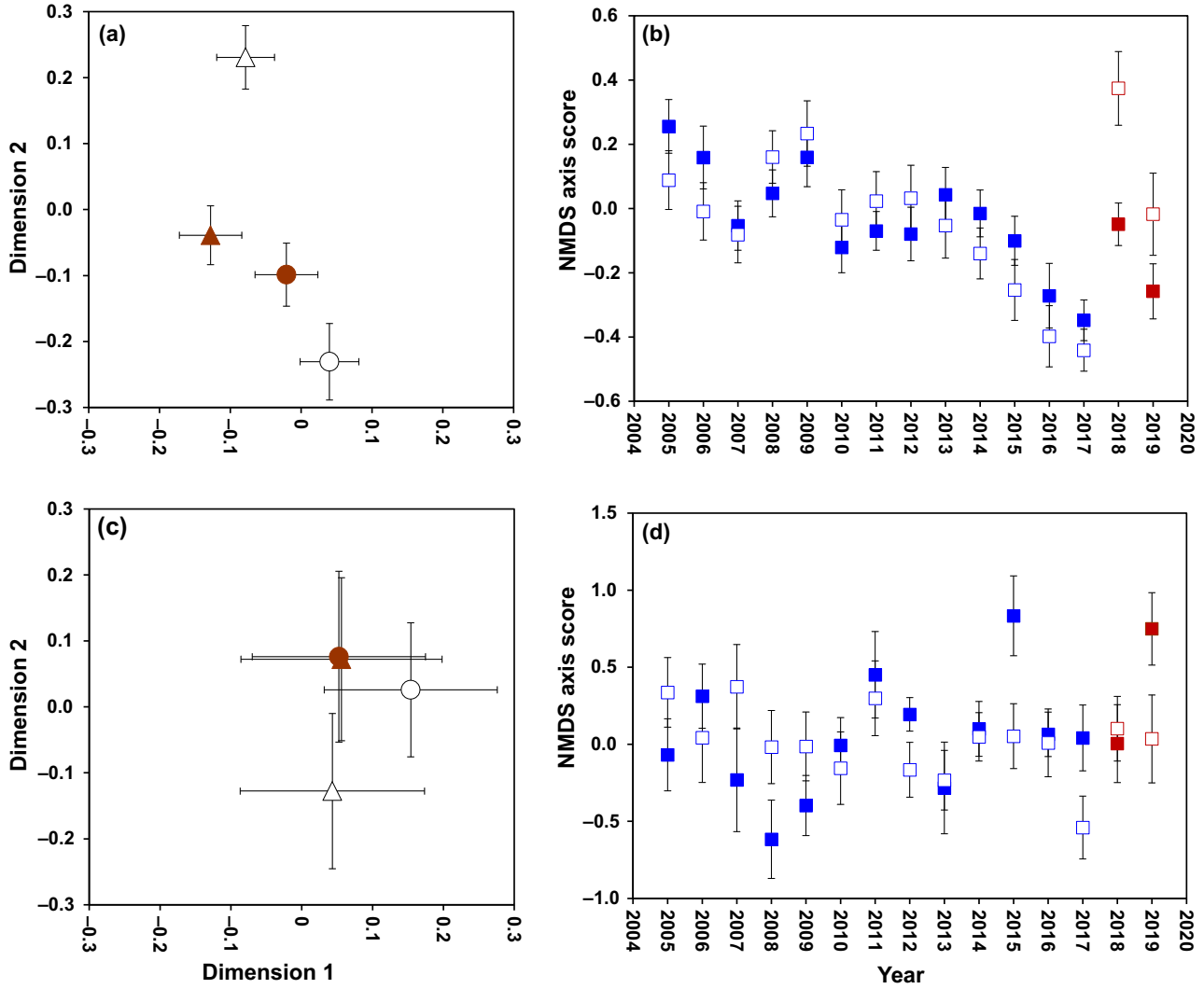

FIGURE 7 Visualizations of the effects of the canopy trimming experiment on community composition of gastropods based on the first two axes of nonmetric multidimensional scaling at the subplot and plot scales (NMDS; Table 1). (a) Treatments at the subplot scale: Reference (open circle), debris only (red circle), trim only (open triangle), and trim and debris (red triangle). (b) Changes in community composition of gastropods through time at the subplot scale as reflected in NMDS dimensions 1 (solid squares) and 2 (open squares). (c) Treatments at the plot scale: Reference (open circle), debris only (red circle), trim only (open triangle), and trim and debris (red triangle). (d) Community composition of gastropods through time at the plot scale as reflected in NMDS dimensions 1 (solid squares) and 2 (open squares). Blue and red squares indicate pre- and post-Hurricane Maria data, respectively. Error bars are ±1 SE

At least one of the four treatments exhibited a significant quadratic relationship through time for each combination of metric (richness, diversity, evenness, dominance) and component (point biodiversity, as well as α-, β-, and γ-components), with the largest number of quadratic relationships for point biodiversity (Table 2). In general, point-, α-, and γ-components exhibited increasing and saturating (positive b_1 and negative b_2) trends through time, whereas β-components exhibited decreasing and saturating (negative b_1 and positive b_2) trends through time (Table 2).

Effects on community composition

Community composition responded to treatment and to time in a consistent manner at the subplot level and responded to time in a consistent manner at the plot level (Table 1). At the subplot level, gastropod composition differed between all possible pairs of treatments (Figure 7a). Species that contributed to differences in composition among treatments include *C. squamosa*, *G. nigrolineata*, and *N. tridens*, whereas species that contributed to consistent differences in composition through time include *A. alticola*, *C. squamosa*, *G. nigrolineata*, and *N. tridens*

TABLE 3 Results of general linear mixed-effects models (GLMMs) evaluating the consequences of treatment (reference, debris only, trim only, and trim and debris), time (before and after disturbance), and their interaction on abundance and biodiversity of gastropods in the canopy trimming experiment

Disturbance type / Response metric	Mean		GLMM results		
	Before	After	Treatment	Time	Treatment × time
Phase 1					
Abundance					
Caracolus caracolla	2.60	2.58	**<0.001**	0.953	0.220
Gaeotis nigrolineata	1.15	0.96	0.504	0.382	0.321
Nenia tridens	2.19	3.10	0.105	0.116	0.830
Total abundance	6.71	7.65	0.002	0.245	0.390
Biodiversity					
Species richness	3.02	3.15	0.322	0.606	0.326
Shannon diversity	2.66	2.68	0.455	0.898	0.256
Camargo evenness	2.34	2.32	0.576	0.947	0.383
Berger–Parker dominance	1.94	1.93	0.430	0.932	0.641
Species composition	–	–	0.346	0.201	0.417
Phase 2					
Abundance					
Caracolus caracolla	3.04	3.52	0.099	0.237	0.482
Gaeotis nigrolineata	1.65	0.67	0.975	**<0.001**	0.143
Nenia tridens	5.58	6.40	0.015	0.388	0.245
Total abundance	10.81	11.00	0.054	0.880	0.266
Biodiversity					
Species richness	2.88	2.50	0.362	**0.031**	0.384
Shannon diversity	2.42	2.05	0.377	**0.005**	0.689
Camargo evenness	2.11	1.78	0.475	**0.003**	0.622
Berger–Parker dominance	1.83	1.52	0.577	**0.002**	0.767
Species composition	–	–	0.529	0.125	0.864
Hurricane Maria					
Abundance					
Caracolus caracolla	2.56	1.00	0.317	**<0.001**	0.458
Gaeotis nigrolineata	0.79	0.08	0.940	**<0.001**	0.940
Nenia tridens	8.92	1.75	0.381	**<0.001**	0.591
Total abundance	12.69	3.33	0.239	**<0.001**	0.445
Biodiversity					
Species richness	2.52	1.40	0.775	**<0.001**	0.206
Shannon diversity	1.96	1.27	0.823	**<0.001**	0.520
Camargo evenness	1.66	1.17	0.868	**<0.001**	0.738
Berger–Parker dominance	1.40	1.07	0.888	**0.006**	0.848
Species composition	–	–	0.424	**<0.001**	0.852

Note: Analyses were conducted at the subplot level with block and subplot as random effects (type II factors), and analyses were conducted separately for abundance of each of the three most abundant species of gastropod, for total gastropod abundance (based on all 17 species), and for each of four metrics of biodiversity (point biodiversity). Significant results ($p \leq 0.05$) are bold. Before and After are abundance or biodiversity values immediately before or immediately after the respective disturbance.

(Table 1). Gastropod composition changed in a gradual and consistent fashion through time until the impact of Hurricane Maria, after which community composition changed considerably (Figure 7b).

Immediate responses

The absence of a significant interaction between treatment and time (Table 3) for any response variable, including those at the population or community level, suggests that resistance is indistinguishable among treatments regardless of disturbance type (i.e., Phase 1 manipulations, Phase 2 manipulations, or Hurricane Maria). Nonetheless, resistance to Phase 1 manipulations was high, as no consistent time effect existed and differences among treatments only characterized abundance of *C. caracolla* and total gastropod abundance. Abundances of *C. caracolla* and *N. tridens*, as well as total abundance and species composition, were resistant to Phase 2 manipulations (i.e., no significant time effect or interaction), whereas abundance of *G. nigrolineata* differed before and after experimental manipulations (a mean decrease in abundance of 59%). Metrics of biodiversity were not resistant to Phase 2 manipulations (Table 3), with each significantly decreasing immediately after manipulation. Finally, the abundance of each species of gastropod was not resistant to disturbance from Hurricane Maria, with abundances of common species decreasing between 61% (*C. caracolla*) and 89% (*G. nigrolineata*). Total gastropod abundance decreased significantly (74%). Similarly, species composition and metrics of biodiversity were not resistant to Hurricane Maria, with biodiversity decreasing between 24% (dominance) and 45% (richness).

DISCUSSION

Gastropod populations and communities in tabonuco forest are resilient to hurricanes (Willig et al., 2021). Although short-term effects (low resistance) do manifest after particularly intense hurricanes that cause extensive tree mortality and canopy loss (e.g., Hurricane Maria; Figures 5 and 6), populations quickly rebound to pre-hurricane levels within a few years. Moreover, the magnitude of short-term responses by gastropods is associated with the extent of forest damage caused by hurricanes (Willig et al., 2021) or the CTE, with small declines (i.e., high resistance) in abundance after disturbances that cause relatively modest forest damage (e.g., Hurricane Georges, CTE) compared with responses after hurricanes that cause extensive tree mortality and canopy loss (e.g., Hurricanes Hugo and Maria). Importantly, gastropod populations and communities in the CTE remained resilient to disturbances despite experiencing a disturbance regime that included major Hurricanes (Hugo in 1989, Georges in 1998, Maria in 2017), CTE manipulations in 2004 and 2014, and the ongoing press disturbance of climate change. Some level of climate change and hurricane frequency will likely have lasting negative effects on this gastropod fauna, but those levels of disturbance have not yet manifested.

The forest damage from the CTE more closely approximated that associated with a large treefall gap or post-hurricane conditions after an event-like Hurricane Georges than the more extensive damage associated with Hurricanes Hugo or Maria (Uriarte et al., 2019). Canopy loss in the CTE was nearly complete in small 30 m × 30 m plots, while the surrounding forest remained intact. Surrounding closed canopy forest can ameliorate the effects of canopy loss on the abiotic environment in the CTE. Nearby closed canopy tabonuco forest (mature tree height varies from 20 to 35 m) reduces the amount of sunlight that reaches the ground under adjacent open canopy, and closed canopy forest maintains higher levels of humidity. These adjacency effects can moderate the effects of gaps on temperature and humidity in the understory, each of which cause physiological stress to gastropods. In addition to moderating the effects of relatively small areas of lost canopy in the CTE, nearby closed canopy forest provides source populations to quickly recolonize impacted areas once environmental conditions were favorable for gastropod survival and reproduction (Alvarez & Willig, 1993). These nearby populations may contribute to source–sink dynamics or mass effects (Leibold & Chase, 2018) between CTE treatments and surrounding forest, which could potentially homogenize spatial patterns in abundance, biodiversity, or species composition among sites regardless of the direct effect experimental treatments on resident gastropods.

A history of disturbance

The montane tropical rainforests of Puerto Rico have experienced hurricane-induced disturbances for millennia (Zimmerman et al., 2020). For understory species, exposure to repeated disturbances through evolutionary history likely has resulted in broad fundamental niches compared with the typical understory environment in closed canopy montane rainforest. The ability for portions of a population to persist through increased temperatures and low humidity would be required for long-term survival in these disturbance-mediated habitats. This high tolerance to abiotic environmental variation has likely resulted in animal populations and communities in tabonuco forest that are highly resistant to press disturbances associated with

climate change (Schowalter et al., 2021; Willig et al., 2019, 2021), and likely accounts for the relatively weak responses of gastropods to the CTE from both short- (Willig et al., 2014) and long-term (Table 1) perspectives. Only three species (*C. squamosa*, *G. nigrolineata*, and *N. tridens*) and the γ-component for diversity, evenness, and dominance exhibited consistent responses to treatment, and these responses typically represented increases in abundance (*C. squamosa*, *G. nigrolineata*) or biodiversity (all metrics) compared with the reference treatment, rather than negative effects. The long-term story of gastropod responses to hurricanes (whether naturally occurring or experimental) is one of resilience and successional dynamics, rather than any form of persistent negative effects from disturbance. Resilience to hurricane-induced disturbances is likely a necessary adaptation for species to persist in disturbance-prone systems such as the LEF and is likely to manifest in other regions that have an extensive history of frequent, intense, cyclonic storms (Southern Asia, Australia, Caribbean, Central America).

Temporal trajectories in gastropod abundance, biodiversity, and composition are evident during succession after both natural (Willig et al., 2021) and simulated (Tables 1 and 2) hurricanes. Indeed, six species (*H. striata*, *C. squamosa*, *N. tridens*, *O. glabra*, *P. portoricensis*, and *P. acutangula*), richness, diversity, evenness, and species composition exhibited consistent successional responses after Hurricanes Hugo, Georges, and Maria, as well as after manipulations during the CTE. Importantly, Hurricane Maria contributed to some of the temporal trends observed in the CTE (Figure 5), including to nonlinear temporal trends as shown by analyses restricted to data from before the impact of Hurricane Maria (Figure 6). Temporal patterns for total gastropod abundance were similar on the nearby Luquillo Forest dynamics plot and on the CTE plots, with abundances slowly increasing from 2005 through 2017, followed by a sharp decline in 2018 after the impact of Hurricane Maria (Willig et al., 2021). These consistent responses suggest that gastropods in the LEF are able to efficiently track spatiotemporal environmental variation during succession (Willig et al., 2021) and have the behavioral and physiological capacities to effectively navigate potentially inhospitable habitats to locate forest patches that represent favorable conditions and abundant resources (Willig et al., 2007).

Hurricanes and spatiotemporal heterogeneity

Biodiversity exhibited consistent trends after application of manipulative treatments associated with the CTE at scales of point biodiversity as well as for α-, β-, and γ-components of biodiversity (Tables 1 and 2; Figure 5). Point biodiversity, as well as α- and γ-components, exhibited negative trends during post-manipulation succession, whereas the β-component of biodiversity increased during post-manipulation succession (Table 2; Figure 5). This suggests that community composition of subplots was most homogenous just after application of manipulative treatments and that compositional heterogeneity among subplots steadily increased during subsequent succession. However, the CTE was initiated 15 years after extensive forest damage caused by Hurricane Hugo and 6 years after the modest forest damage caused by Hurricane Georges. Moreover, Hurricane Maria had a large effect on gastropods in the CTE (Figures 5 and 6). The disturbance and successional context of the forest surrounding the CTE, and potential source populations, likely influenced the trajectory of community composition in the CTE more so than did the manipulations of the CTE itself, as treatment had no effect on point biodiversity or on α- or β-components of biodiversity (Table 1).

In 2017, Hurricane Maria effectively converted all plots in the CTE into trim and debris treatments (Figure 3). The loss of canopy caused by Hurricane Maria decimated populations of gastropods in the CTE (Figures 5 and 6) as well as the potential source populations in adjacent forest (Willig et al., 2021). Despite wide-spread destruction of the forest, the β-component of biodiversity was greater after Hurricane Maria (Figure 5) than at any time during the first 13 years of the CTE. This likely arises because of the devastating effect of Hurricane Maria, which reduced the populations of typically common and wide-spread species (e.g., *N. tridens*, *G. nigrolineata*) to zero in many plots, resulting in more heterogeneity among gastropod communities than previously recorded during the experiment.

Confoundingly, species composition at the subplot level was distinct for each treatment, whereas species composition at the plot level evinced no significant differences among treatments (Table 1; Figure 7). The differences between these analyses were that: (1) data for all the four subplots were combined into a single species abundance distribution for analysis at the plot level, and (2) the loss of spatial resolution associated with removing subplot as a random factor effectively reduces statistical power. This combination of results shows that controlling for microspatial environmental variation and associated heterogeneity among communities can enhance the ability to detect treatment effects. The pattern of compositional differences among treatments (Figure 7a) represents a gradient of environmental harshness from the perspective of gastropods: from the reference treatment (lower temperature, higher humidity) to the trim-only treatment (higher temperature, lowest humidity).

Debris deposition ameliorates the effect of canopy opening on litter moisture (Lodge et al., 2014), making the trim and debris treatments a slightly more hospitable environment for gastropods during early succession compared with the trim-only treatment.

Gastropod species composition exhibited consistent change through time, particularly when evaluated at the subplot scale (Figure 7b). This temporal pattern was driven primarily by changes in the abundance of *N. tridens* (Figure 5), the most abundant gastropod in closed canopy tabonuco forest (Bloch & Willig, 2006). Indeed, the abrupt change in subplot species composition (Figure 7b) after Hurricane Maria was caused primarily by the steep decline in abundance of *N. tridens* after the hurricane (Figure 5). Its small size, thin shell, and arboreal habitat preferences likely result in low resistance to disturbances associated with high-intensity storms. In contrast, its ability to find refuge in suitable habitat or microhabitat remnants after hurricanes, combined with a high reproductive rate, results in high resilience and recolonization of forest as the lower canopy begins to fill.

Resistance and the extent of disturbance

We expected applications of CTE treatments during Phase 1 and Phase 2 to result in significant treatment by time (before vs. after) interactions because relatively homogeneous forest before Phase 1 applications received different manipulations and because the trim and debris treatment received a second manipulation while other treatments did not. However, no such interactions occurred (Table 3). The lack of immediate treatment-specific responses, particularly between the reference treatment and manipulated treatments, suggests high resistance by gastropods to the nature of these manipulations or to their environmental context in the CTE.

In contrast, we expected only a consistent effect of time (before vs. after) in analyses related to the impact of Hurricane Maria, as all CTE treatments suffered extensive damage from high cyclonic winds. All metrics of abundance, biodiversity, and composition exhibited consistent differences before and after Hurricane Maria, with gastropods showing much less resistance to the extensive damage caused by the hurricane, suffering large reductions in abundance and biodiversity. This difference in response between the small-scale (30 m × 30 m) disturbances created for the CTE and large-scale damage caused by Hurricane Maria (Uriarte et al., 2019) suggests that source populations from surrounding closed canopy forest likely moderate local effects of the CTE on gastropods. Few species (3 of 17) exhibited consistent differences between CTE treatments (Table 1), with only *C. squamosa* and *N. tridens* exhibiting a preference for reference treatments over treatments with a trimmed canopy (Figure 4). Studies of the effects of tree fall gaps in the LEF on gastropods found similar patterns. With the exception of *C. caracolla*, gastropod abundances were similar in tree fall gaps and surrounding closed canopy forest (Alvarez & Willig, 1993). In addition, habitat selection experiments showed that *C. caracolla* preferred closed canopy forests to tree fall gaps (Bloch & Stock, 2014). In combination, these results show that the majority of gastropod species are either unaffected by small-scale canopy openings (such as those created by the CTE) or that they are able to recolonize these habitats early in succession while canopy openings persist. These responses lend support to the idea that effects of small-scale canopy loss on gastropods may be ameliorated by contributions from source populations from the surrounding forest.

Conclusions and synthesis

A comprehensive evaluation of the short-term effects of the CTE showed terrestrial gastropods in the LEF to be relatively resistant to small-scale disturbance events such as those represented by the CTE (Willig et al., 2014). A longer-term perspective shows that gastropods are highly resilient to small-scale disturbances (Table 2). Such quick responses by gastropods to CTE treatments likely arise from cross-scale interactions among habitat patches (Willig et al., 2007), with source–sink dynamics augmenting populations in less hospitable habitats (particularly trim-only treatments) soon after canopy loss. Populations in nearby closed canopy forest (with positive replacement rates) supply colonists to open canopy sites (temporarily with negative replacement rates) until those local populations can persist on their own once conditions ameliorate because of plant growth and canopy closure. In general, the CTE provided evidence that canopy loss had a negative effect on gastropod abundance (Figure 4) and a large effect on gastropod composition (Figure 7a). In addition, adding debris to a site with an intact canopy enhanced gastropod abundance and biodiversity (Figure 4) compared to other effects from other treatment combinations, including the reference treatment. Moreover, debris deposition had a homogenizing effect on gastropod community composition at multiple spatial scales (Figure 7a,c). The extent of disturbance is an important factor when interpreting responses to natural and simulated hurricanes. The extent of disturbance associated with Hurricane Maria was much greater than that of any manipulation in the CTE, and gastropods exhibited less resistance to Hurricane Maria than to

either Phase 1 manipulations or Phase 2 manipulations of the CTE (Table 3; Figures 5–7). Nonetheless, gastropods generally exhibited great resilience even to this large-scale intense hurricane (Willig et al., 2021), likely a necessary trait for long-term persistence in disturbance-mediated environments such as those in the LEF. The resilience of gastropods in the LEF to disturbance is likely important to the speed of forest recovery, as they increase the rate of litter decomposition and nutrient cycling to enhance resources available to early successional plants.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Gastropod and experimental manipulation data (Willig 2020) are available in the Luquillo Long-Term Ecological Research Data Catalog, https://luq.lter.network/data/luqmetadata152, as well as an EDI Data Portal, https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-luq.152.762253.

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